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A STUDY OF COMPETITIVE RELATIONSHIPS BETWEEN
SELECTED GRASSES DURING THE ESTABLISHMENT PHASE

A THESIS

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ABSTRACT

Competition has been identified as a major phenomenon affecting the growth of pasture species in mixtures. Thus a study comprising of field, glasshouse and climate laboratory experiments was conducted to identify the occurrence and the nature of competitive relationships during establishment and early growth of three common grass species used in the pastoral industry of New Zealand. Simple models of competitive situations were created by the use of the de Wit replacement series principle, in order to carry out these studies.

The results of all experiments demonstrated that the selected species, namely perennial ryegrass (*Lolium perenne* L.) "Grasslands Nui"; prairie grass (*Bromus catharticus* Vahl) "Grasslands Matua" and cocksfoot (*Dactylis glomerata* L.) "Grasslands Apanui" compete for the same environmental resources. The competitive abilities of the three species were in the order of prairie grass > ryegrass > cocksfoot. The superior performance of the more competitive species when compared with its monoculture was associated with a corresponding proportional decrease in the performance of the weaker species in a mixture. These relationships were observed within 3-4 weeks after planting and did not alter under the adopted experimental conditions. In addition, the field experiment illustrated that these relationships were persistent in the second year, under an infrequent cutting regime, although seasonal growth patterns of the three species were identified.

Initial and subsequent plant size had a deterministic effect on the respective competitive abilities of the selected grasses. This was assisted by their growth patterns and earlier germination of the more competitive species. Seed characters also showed a positive relationship with the plant size and competitive abilities of the selected grasses.

Yields of the mixtures lay between those of the respective monocultures in all experiments, irrespective of seasonal growth patterns of the species. Simulated spring and autumn temperatures

within the climate laboratories did not change the pattern of yield or the competitive abilities and relationships of these three species.

Evaluation of the effects of competition on the growth of individual plants of these species when grown in mixtures revealed that both tiller appearance rate and to a greater extent the rate of leaf appearance on the main stem in all species were affected by competition during early growth. These effects were associated with the dry matter accumulation patterns of the selected species in mixtures.

Root competition began earlier and had a greater impact on the overall competitive relationships between the selected species than shoot competition. This was attributed to the earlier and greater intermingling of the root systems than shoot systems. Evaluation of the root growth of species both as single plants and in mixtures supported this conclusion. However, the mechanisms of root competition were not elucidated.

In order to identify the pasture establishment practices of farmers and thereby relate the results of these studies to the practical situation, a survey was carried out among farmers in central New Zealand. The results highlighted that farmers use seed mixtures containing 2-4 grasses to establish their pastures. The grasses selected for this study were shown to be those most commonly used by farmers.

The results of the experiments of this study are discussed in relation to the pastoral industry of New Zealand.

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CHAPTER 1. INTRODUCTION AND OBJECTIVES

1.1 INTRODUCTION

The pastoral industry of New Zealand is based on approximately 9.3 million hectares of sown grasslands and 5 million hectares of tussock grasslands (Daly, 1973; N.Z. Dept of Stats, 1982), accounting for over a third of the total land area of the country. Surveys conducted on pasture development show that approximately 300,000 hectares are sown into new pastures annually (N.Z. Dept. Stats Year-books 1978-1982). When expressed in financial terms, this represents an annual multi-million dollar commitment by New Zealand farmers.

The process of pasture establishment consists of many stages, ranging from land development, seed bed preparation, selection of pasture species, method of establishment to early management of the establishing sward (Brougham, 1969). Although successful pasture establishment requires precise and specific conditions and more skill than most other farm crops (Greenwood, 1950; White, 1973); these conditions are seldom met in agricultural practice (Brougham, 1969). However, due to the importance of successful establishment to the life and productivity of the sward, care needs to be taken at the time of sowing pastures.

One of the most important factors in pasture establishment is the selection of pasture species. Its importance is further enhanced as seed costs account for approximately 20% of all establishment costs (Anon, 1980). Thus it becomes imperative to select the species or species combination best adapted to the climatic and edaphic conditions of the land and to the intended utilization of the established sward (White, 1973).

In the early stages of grassland farming, it was a common practice to include up to 20 species in seed mixtures (Davies, 1952; Levy, 1970), which included both improved and unimproved species available at the time. However, with the development of new and better cultivars, which were more suited to given climatic, soil and superior management conditions, seed mixtures have become more simple. A survey of seed mixtures sown in the North Island of New Zealand in 1968 showed that all seed mixtures surveyed consisted of an average

of 3.9 species, and the composition was predominantly two grasses and two legumes (Harris, 1968). This suggests that as knowledge of species and their productivity in relation to the environment and management became more available, seed mixtures were simplified with the introduction of these new improved cultivars. Furthermore, this shift from complex to simple mixtures has also been attributed to the availability of new genetic material in pasture species for either traditional or novel systems of pastoral agriculture, offering a further dimension to the agricultural scene (Lancashire, 1977).

Research conducted on mixtures of grasses has shown that when two species of grasses are grown in a mixture, the yield does not exceed that of the higher yielding monoculture (van den Bergh, 1968). This finding has also been reported by Donald (1963) and by England (1968) in a detailed study of combinations of *Lolium perenne* L. and *Dactylis glomerata* L. Trenbath (1974a) reviewing earlier literature also reported that yields of grass mixtures lie between those of the respective monocultures, although exceptions to the rule have also been reported (e.g. Whittington and O'Brien, 1968; Trenbath and Harper, 1973). Thus the general conclusion from observations under experimental conditions where all environmental factors and management conditions are kept at optimum levels, is that there is no advantage to the farmer in sowing a mixture of grass species, if his aim is to maximize dry matter production, under ideal and constant conditions, provided he is aware of the species that will yield the most under the given conditions (Harper, 1977; Remison and Snaydon, 1980).

Research on environmental conditions in pasture swards illustrates that climatic and soil conditions are particularly prone to changes (e.g. Gupta *et al.* 1975), which affect the productivity and composition of the sward. Under farming conditions, changes to the pasture environment can be effected by grazing animals (e.g. MacDiarmid and Watkin, 1971, 1972; Watkin and Clements, 1978) which can bring about changes in species productivity. Thus, due to the variations that occur within a sward environment in a farming situation, a species ideally suited to a given set of conditions may not perform up to expectations over time. As the effects of climatic changes and management on a given species cannot be accurately predicted in advance, especially under farming conditions, farmers still tend to use a mixture consisting of

a number of species or cultivars which have different environmental conditions for optimum growth. This is probably done as an insurance against the ill defined, unknown and ever-changing environmental conditions of pastures. Seed mixtures are also used to overcome failure of establishment of one species (Blaser *et al.* 1956), to combine the different peaks of seasonal production of the constituent species or cultivars and thereby extend the grazing season (Donald, 1963). Farmers also grow seed mixtures containing fast growing species in order to obtain early feed for livestock and suppress weeds (White, 1973). Thus, although pasture seed mixtures used in New Zealand are relatively simple and dominated by ryegrass and white clover (*Trifolium repens* L.) due to their complementary growth (Daly 1973; Langer, 1973), farmers still incorporate 2-3 species or cultivars of grasses with 1 or 2 pasture legumes in the seed mixtures, as seen in the survey conducted by Harris (1968).

In addition to climate, edaphic and management practices, competition between plants has long been identified (Stapledon and Davies 1927, 1928; Chippendale, 1932) as a major contributing factor to changes in populations and yields of mixed pasture swards. Due to its importance, research has continued in abundance up to the present time (e.g. de Wit, 1960; Donald, 1963; Rhodes, 1970; Trenbath, 1974a; Braakhekke, 1980). More recently, with the development of computer technology, the trend towards a more comprehensive, mathematical approach to the understanding of these complex interactive forces of competition (e.g. Thomas 1970; Machin and Sanderson, 1977; Trenbath, 1978) has provided added stimulus to scientists in this field.

Clements, Weaver and Hanson (1929) stated "It would seem correct to assume that if competition does take place, it is most likely to occur, or at least have its greatest severity, before the plants are mature, since it is during these stages of development that the greatest demands are being made upon the essential factors of the environment." In pasture species frequent reference has been made to the occurrence and significance of interplant competition in the establishment phase (e.g. Charles, 1961; Rhodes, 1968a, 1970; Cocks, 1969). Studies on this phase have become important as the pasture plant is subjected to varying degrees and forces of competitive stress in both

naturally and artificially created grassland communities from the time of germination. Thus a greater understanding of the competitive parameters in the establishment phase with reference to the growth and development of the herbage plant becomes important to ascertain the response of an individual within a plant association. The value of studies on the early growth phase is further enhanced as competitive hierarchies established in this phase tend to persist at later stages, even when conditions have become favourable to initially suppressed species (Harkess, 1970; Harris, 1973; Engel and Trout, 1977).

1.2 OBJECTIVES

In view of the importance of pasture establishment in the New Zealand grassland economy and the significance of plant competition between and within simple mixtures of pasture species and cultivars, it was considered of value and relevance to examine the nature of the competitive relationships that develop in the early growth phase in mixtures of pasture grasses. Emphasis was placed on some recently released cultivars of species commonly used in New Zealand. It was also considered useful to ascertain the agronomy of this concept more closely since such competitive relationships established in the early growth phase have a deterministic effect on subsequent performance of the sward.

The specific objectives of this study were therefore - to investigate

- (i) The performance of species components in binary mixtures of grasses when compared with their monocultures in the early growth phase, and to determine the competitive relationships that develop during this phase.
- (ii) The effect of competitive relationships that develop in the early growth phase on subsequent productivity of grass mixtures.
- (iii) The development pattern of competitive relationships between the selected species when sown as seeds and the response of individual species to competitive stress in terms of agronomically significant aspects of their growth and development during the establishment phase, in a defined situation.
- (iv) Morphological and growth characters associated with the competitive abilities of grass species during early growth.

(v) Seed establishment practices of New Zealand farmers and evaluate the research findings in relation to agricultural practices adopted in the pastoral farming scene of New Zealand.

Many grass species are used in grassland farming in New Zealand (Lambrechtsen, 1975) but one or more ryegrass cultivars play a dominant role in the pastoral scene (Levy, 1970; Mitchell, 1970; Langer 1973). "Grasslands Ruanui" perennial ryegrass has been identified as the standard cultivar of ryegrass grown in New Zealand (Scott 1975), and Harris (1968) identified it as the major component of pasture seed mixtures. However, "Grasslands Nui" ryegrass, a cultivar accepted in 1972 has been reported to outyield "Grasslands Ruanui", and is considered to be broadly adapted to a wide range of apparently diverse environments, with a great potential as a late spring and autumn producer (Rumball 1969; Baars *et al.* 1976; Sheath *et al.*, 1976, 1982; Armstrong, 1977; Harris *et al.*, 1977; Lancashire *et al.*, 1978).

Cocksfoot (*Dactylis glomerata* L.) was seen in 54% of the seed mixtures surveyed by Harris (1968) and has been considered a valuable pasture species in the drier regions of New Zealand for a long time (Corkill, 1954; Douglas, 1966, 1974; Langer, 1973; Musgrave, 1981).

Prairie grass (*Bromus catharticus* Vahl) is recognized as a valuable species for dairy pastures in warm and fertile areas of the country (Burgess, 1951; Jordan 1957; Pantall, 1961; Moss, 1962; Langer, 1973). While its main value lies in its cool season activity, rapid germination and establishment and apparent resistance to insect pests (Langer, 1973; Rumball, 1974; Lancashire, 1982; Lancashire and Brock, 1983), research also highlights prairie grass as a summer producer (Lancashire, 1978; Sithamparanathan, 1979).

Due to the importance of these three pasture species to New Zealand's grassland agriculture, a programme of research was developed using the most recently accepted cultivars of the 3 species, at that time, namely "Grasslands Nui" perennial ryegrass, "Grasslands Matua" prairie grass and "Grasslands Apanui" cocksfoot. These were grown in binary mixtures and as pure swards according to the replacement series principle of de Wit (1960), in order to identify competitive relation-

ships that occur between grass species with different growth habits and climatic requirements, particularly in their early growth phase. The programme of research developed included 7 experiments and a survey to investigate the stated objectives.

CHAPTER 2. LITERATURE REVIEW

2.1 INTRODUCTION

Competition between plants, stress by environmental factors and the effects of disturbance on plant growth have been suggested as three major determinants of vegetation (Grime, 1973, 1974). A review by Grubb (1977) also highlighted factors causing species richness in plant communities, where special emphasis was placed on the theory of niche regeneration as a causal factor.

Plant ecologists consider competition to be the major factor determining species richness in plant communities (Zimdhal 1980). Thus, much scientific work has been conducted on this phenomenon in terms of plant productivity and performance in mixtures. Comprehensive reviews since that presented by Clements *et al.* (1929) include Aiyer (1949); Simmonds (1962); Baldy (1963); Donald (1963); Trenbath (1974a, 1976); Foti (1975); Harper (1977); Snaydon and Harris (1979) and Braakhekke (1980).

Competitive relationships between plants occur due to "neighbour effects" caused by other plants in the same environment (Jacquard, 1965; Harper, 1977). These effects can develop due to the presence of the same species (intraspecific competition) or another species (Interspecific competition). A major part of intraspecific competitive effects encompasses yield-density relationships within a species population, which have been highlighted by the work of Japanese scientists (Kira *et al.*, 1953; Koyama and Kira, 1956; Yoda *et al.*, 1957, 1963) and by Harper and associates in Wales (Harper, 1977).

Interspecific competition between plants can be classified into two major categories:-

(A) Competition between species of different families - This is well illustrated in intercropping research based on cereal/legume associations, grass/legume associations and in weed/crop interactions. Research on intercropping has been reviewed by many

scientists including Aiyer (1949); Dalrymple (1971 - cit. Mead and Riley, 1981); Crooksten (1976); Trenbath (1976) and Willey (1979 a,b). Associations between grasses and legumes have also been studied and reviewed by many scientists, especially in temperate regions (Nichol, 1935; Wilson, 1940; de Wit *et al.*, 1966; Bakhuis and Kleter, 1965; Vallis, 1978; Haynes, 1980; Snaydon and Baines, 1981), while reviews of weed-crop competition and its mechanisms have been presented by Zimdhal (1980); Glauningner and Holzner (1982), and Spitters and van den Bergh (1982).

(B) Competition between species of the same family - This is most commonly associated with relationships between pasture grasses or legumes, cereal/grass associations and, less frequently, with weeds and crops of the same family. Much attention has been focused on grass associations, as evidenced by work such as that of de Wit and van den Bergh (1965); England (1965, 1968); van den Bergh (1968); Rhodes (1967, 1970); Cocks (1969); Risser (1969) and Braakhekke (1980). Research on interspecific competition in cereals; with special emphasis on breeding is presented by Spitters (1979). Studies on competition between cereals, and between cereals and grasses have been published by many including van Dobben (1955); de Wit (1960); Santhirasegaram (1962); Black (1966); Blijenburg and Snee (1975); Appleby *et al.* (1976), Rerkasem *et al.* (1980 a,b,c) and Watkinson (1981).

A considerable volume of literature is available on all aspects of competition between plants in various agricultural situations. However, this review will be largely restricted to competitive relationships between herbage grasses.

2.2 DEFINITION OF PLANT COMPETITION

Clements *et al.* (1929) first postulated a definition of plant competition in their monograph entitled "Plant Competition". Since then many definitions of competition between plants have been proposed (Williamson, 1957).

A literal translation of the latin term "Competere" means "to coincide" (Williamson, 1957), while the Oxford English Dictionary defines competition as "the action of endeavouring to gain what another endeavours to gain at the same time, the striving of two or more for the same object

- rivalry". However precise this definition is, the exact meaning in terms of plant associations is confused in the literature. Milne (1961), an animal ecologist, has proposed reasons for the development of this confusion in the definitions and has reviewed proposals developed by Birch (1955); Aspinall and Milthorpe (1959); Bleasdale (1960) and Mather (1961).

The most accepted definition for the term competition among biological organisms was developed by Donald (1963). He defined competition as "a phenomenon which occurs when two or more organisms seek the measure they require of any particular factor or thing, and when the immediate supply of the particular factor or thing is below the combined demand of the organisms". This is now widely accepted (Hill and Shimamoto, 1973) and was developed on the basis of Clements *et al's* (1929) definition of plant competition and Milne's (1961) definition of animal competition. However, many researchers including Troughton (1957); Aspinall and Milthorpe (1959); Odum (1959); Black (1960a); Bunting (1960); Milthorpe (1961); Greig-Smith (1964) and Stern (1965) have used the term competition to describe various relationships between plants, and not unexpectedly this has led to much discussion and debate in the literature. (Birch, 1957; Harper, 1961, 1977; Miller, 1967; Tinnin, 1972; Rennie, 1974; Grime, 1977, 1978; Hall, 1978).

Due to the many definitions adopted for the term competition, Harper (1961) introduced the term "Interference" as a blanket word to describe "those hardships caused by proximity of neighbouring plants". However, due to the broad field of plant associations that fall under the scope of the term "interference", Hall (1974a) derived methods of differentiating competitive and non competitive interactions between plants. More recently, Braakhekke (1980) described different categories of plant associations that can be grouped under the broad concept of "interference", based on definitions of each aspect by Tinnin (1972) (Fig 2.1).

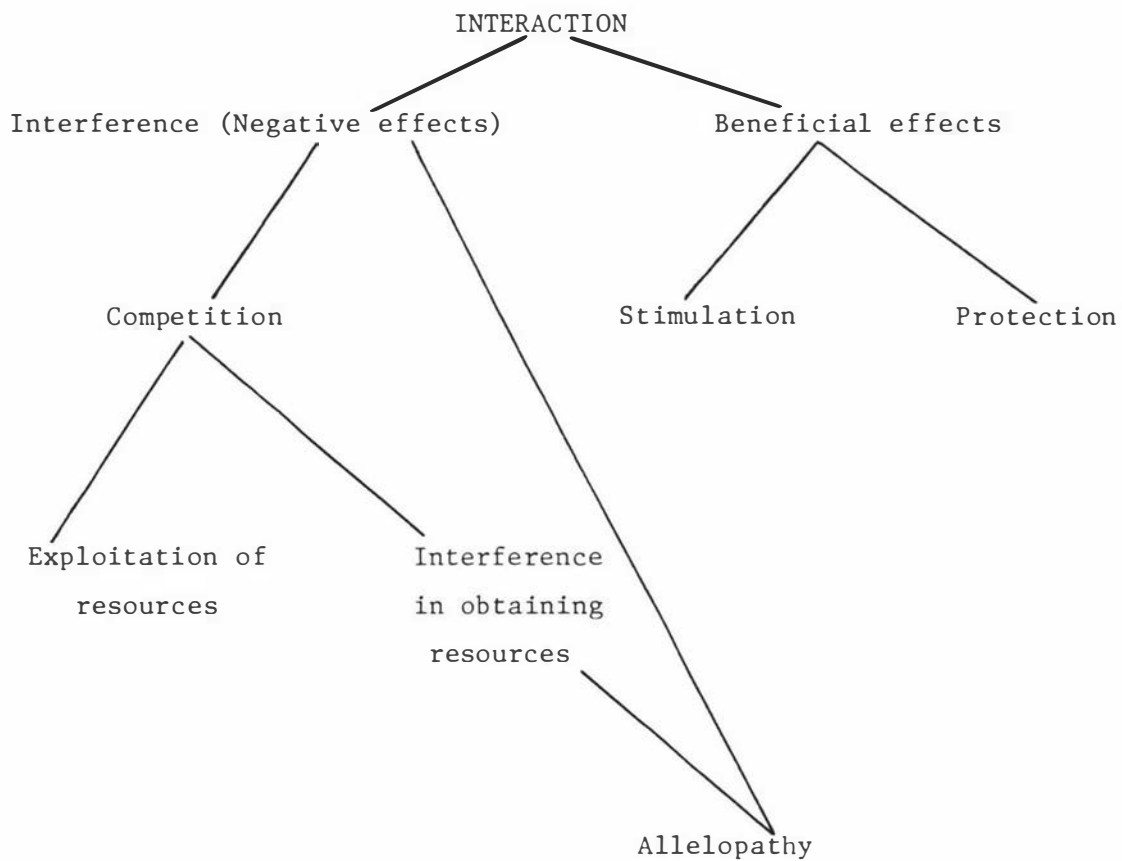


Figure 2.1 Relationships between various concepts of plant interrelationships based on Tinnin (1972); Braakhekke (1980).

2.3 INTERACTIVE RELATIONSHIPS IN GRASSLANDS

Interactions between plants in grassland associations play an important role in understanding species richness, stability, botanical composition and yields of swards, along with the performance of individual species (Braakhekke, 1980). Thus it is of interest to identify briefly the types of interaction that can occur in grasslands.

Figure 2.1 indicated two major aspects of plant interactions - namely interference and beneficial effects.

Beneficial effects encompass relationships such as mutualism, compensation and protection, which can occur reciprocally or to one species. The well known and commercially exploited example of beneficial effects is the grass-legume association in pastures. Even in natural vegetation, beneficial effects can be identified, where plants tend to protect each other from the harshness of the environment. Interesting possibilities of such interactions have been suggested by Trenbath (1976). However, mathematical evaluations of plant interaction models suggest that in nature, mutualism is less common than interference between plants (Goh, 1979). As stated by Braakhekke (1980), "This holds true in nature as beneficial effects will promote co-existence only if they compensate for the negative effects of the 'benefactor species' on the 'beneficiary species', and the beneficiary is not able to exclude the benefactor".

The word "interference" is generally preferred to indicate negative interactions between plants. Harper (1961) defined it as "those hardships which are caused by the proximity of neighbours". These interactions which impart detrimental effects to its neighbouring plants in either a direct or indirect manner can occur in two major ways - i.e.

- Competition
- Allelopathy.

2.3.1 PLANT COMPETITION

Plant competition is an active process within plant associations which affects the utilization of growth requirements by plants from the environment. Competitive relationships can occur both below and above ground, and the outcome is dependent on the relative abilities of component species to capture and utilize the available resources

(Black, 1958; Donald, 1958; Grime, 1974). These resources needed for plant growth have been identified as light, nutrients, water, and to a lesser extent carbon dioxide and oxygen (Donald, 1963). Competition for space for growth has also been cited in root crops (Donald, 1963) and in terms of suitable germination sites for grasses (Harper, 1961; Ross and Harper, 1972). All these environmental factors used by plants have been termed "Biological space" by de Wit (1960), which is defined as a composite of all growth factors and resources.

In a practical way, man has long been familiar with interspecific competition, in the form of adverse effects of weeds on crop plants. Man's awareness of intraspecific competition, although only in empirical terms, by observing the performance of plants under different seed rates was indicated by Donald (1963). In more recent times, competition has been studied by plant ecologists due to its considerable significance in determining the pattern of ecological success in natural populations. This has been derived from the observations that plant species in a given area modify each other's environment in such a way that they either impart harmful effects to neighbouring species or replace one another until an equilibrium or climax is reached (Harper, 1964).

For many years, pasture seed mixtures containing two or more species or cultivars have been sown in grassland farming (Donald, 1963). This use of mixtures develops artificial communities of plants, within which plant relationships observed in natural communities develop. However, emphasis on studying these relationships in artificially established plant communities was delayed as early plant ecologists regarded such communities as of little interest (Donald, 1963).

Many forms of competitive relationship develop within grassland communities and have been reported extensively in literature. These competitive relationships are listed along with important references.

(A) Competitive relationships within a species - i.e. yield-density-relationships (e.g. Donald, 1951; Kira *et al.*, 1953; Koyama and Kira, 1956; Yoda *et al.*, 1957; Stern, 1965; Ross and Harper, 1972; Kays and Harper, 1974; Harper, 1977).

(B) Competition between herbage species and weeds (e.g. Aspinall and Milthorpe, 1959; Risser, 1969; Drawe *et al.*, 1977; Zimdhal, 1980).

(C) Competition between grasses and legumes (e.g.¹ - Stapledon and Davies, 1928; Roberts *et al.*, 1942; Alberg *et al.*, 1943; Williams, 1947; Brougham, 1954a; Cullen, 1964; Bakhuis and Kleter, 1965; Charles, 1965; de Wit *et al.*, 1966; Ennik, 1970; Harris, 1972; Harris and Thomas, 1973; Harris and Hoglund, 1977; Pineiro and Harris, 1978a; Rhodes and Harris, 1979 and Haynes, 1980).

(D) Competition between two legumes (e.g. Black, 1958, 1960a,b; 1961a,b, 1963; Black *et al.*, 1963; Snaydon, 1962, 1971; Snaydon and Bradshaw, 1962a, 1969; Rossiter, 1974; Rossiter and Palmer, 1981; Brock and Charlton, 1977; Scott and Lowther, 1980).

(E) Competition between grass species (e.g. Stapledon and Davies, 1927; Donald, 1963; England, 1965, 1968; Rhodes, 1967, 1970; Remison and Snaydon, 1978, 1980; Harris *et al.*, 1981a).

All these reports highlight different aspects and also the importance of competitive relationships in determining overall productivity of pastures and also per plant performance when species mixtures are sown.

This thesis evaluates competitive relationships between selected grass species during establishment. Thus, the subsequent sections of this review of literature will be restricted to competitive relationships between herbage grasses and methods of evaluating these relationships.

2.3.1.1 Competition between herbage grasses

Seed mixtures used for establishment of pastures generally contain several grass species or cultivars (Harris, 1968; Levy, 1970). This practice is common to most pastures in the world. Thus research has been and is being conducted to identify the occurrence of competition between grasses, its causal factors and its importance in maintaining pasture productivity.

Competition between grasses in pastures can be identified in two categories - namely

- Competitive associations between grasses in the seedling phase
- Competitive associations between grasses in the established phase.

2.3.1.1.1 Competitive association between grasses in the seedling phase.

When a mixture of pasture species is sown onto a bare soil, a "struggle for survival" develops immediately after the seeds germinate. At this stage, the mixture of plants becomes a dynamic community because of differential reactions and responses among species to various environmental growth factors (Blaser *et al.*, 1952 a,b).

Frequent reference has been made to the occurrence and significance of interplant competition during this phase of pasture growth (e.g. Clements *et al.*, 1929; Lee, 1960; Rhodes, 1968a, 1970; Cocks, 1969). This competitive relationship can arise between different species of grasses or cultivars of a given grass species.

Extensive research has been conducted on the competitive ability of ryegrasses, during this early growth phase. Early research work reported by Findlay (1913); Cockayne (1919); Levy (1922); Stapledon and Davies (1927); Davies (1928, 1952); Davies and Thomas (1928); Thomas (1945) and Jones (1957) were some of the more important investigations on competitive relationships between seedlings of ryegrass and other grasses, especially meadow fescue (*Festuca pratensis*). These studies were concerned with problems in obtaining satisfactory establishment from sown seed mixtures, and they showed the ability of perennial ryegrass to suppress the growth of associated species even at the early establishment stages. Stapledon and Davies (1928) also reported the aggressive nature of ryegrass when compared with cocksfoot. Studies by Stapledon and Davies (1928) and Chippendale (1932) have shown the depression of seedling growth of *Phleum pratense* and *Poa trivialis* when combined with ryegrasses. More recently, Crocker and Martin (1964) studied more critically the competitive relationship between perennial ryegrass and meadow fescue under field conditions and conclusively demonstrated the depressive effect of ryegrass on the other species under normal farming conditions. Recent studies on competitive relationships between ryegrasses and other grass species in the establishment phase, include those reported by Greenaway and Budden (1960); Arens (1962); Cullen (1964); Rhodes (1968a); Cocks (1969, 1974); Harkess (1970); Engel and Trout (1971). These researchers compared the growth and development of other pasture grasses with that of ryegrass under competitive situations and established the occurrence and nature of

these interactions. Similar studies have also been reported by van den Bergh (1968) which involved ryegrass and other species. Harris and Thomas (1972) reported the competitive ability of cultivars of ryegrass in suppressing *Agrostis tenuis* during early growth, especially under infrequent defoliation. Haggar (1979) studied the effect of *Poa trivialis* seedlings on the establishment and growth of perennial ryegrass and showed the competitive effect of the former species on ryegrass during very early stages of growth. However, this trend was reversed after four weeks, when ryegrass showed competitive dominance.

Studies on competitive effects during the establishment phase of grass mixtures is not limited to ryegrasses. Frame and Hunt (1964) have shown the suppression of *Festuca arundinacea* by *Phleum pratense*, *Dactylis glomerata* and *Lolium perenne*. Cashmore (1934) and Cameron (1963) have reported the extreme susceptibility of *Phalaris tuberosa* to competition from other grass species during establishment. Superiority in terms of competitive ability of *Bromus* species when compared with *Agropyron* and other grass species has been reported by Tisdale (1947); Stewart and Hull (1949); Hulbert (1955); Evans (1961); Harris (1967); and Harris and Wilson (1970). A review by Risser (1969) illustrates the superior competitive ability of *Bromus* species when grown with other pasture species. Studies on other grass species include that of Erdmann and Harrison (1947) who reported the aggressiveness of red top (*Agrostis alba*) seedlings in relation to Kentucky blue grass (*Poa pratensis*) and chewings fescue (*Festuca rubra*). Smoliak and Johnston (1975) evaluated competitive relationships between *Agropyron* species and other native grasses of Canada.

Competitive relationships also occur between cultivars of the same species (Gardner and Hunt 1963). The occurrence of such intervarietal or intercultivar competitive relationships has been described by Jones (1958) and Charles (1961, 1964). Charles (1961) made a comprehensive study of differential survival of cultivars of *Lolium*, *Dactylis* and *Phleum* species, when mixtures were made up of cultivars of the same species. He evaluated the competitive relationships in order to identify characters associated with superior competitive ability in the early growth phase. Similar studies on different cultivars of *Dactylis glomerata* under different environmental conditions, and the physiological basis of such responses have been reported by Eagles (1967), and Eagles and Williams (1969, 1971). Competitive relationships in the

establishment phase of mixtures of *Dactylis* cultivars have also been reported by Ross and Harper (1972) and indicated the importance of different characteristics of seeds and seedlings in determining the dominance hierarchy of *Dactylis* populations. Intervarietal competitive effects and ability of ryegrass cultivars have been reported by Thomson (1970); Hill (1972, 1973, 1974) and Hill and Shimamoto (1973). Studies by Hill (1972, 1973, 1974) were conducted on five genotypes of perennial ryegrass (*Lolium perenne*) in ten binary combinations, and results indicate that nine out of the ten combinations exhibited competitive effects. Subsequent work by Harris (1973) and Harris and Thomas (1970) using two ryegrass cultivars shows the existence of competitive relationships in the early growth phase and its effect (and that of management) in determining the performance of mixed swards.

2.3.1.1.2 Competition between established swards and establishing seedlings

Milthorpe (1961) emphasized that success in the establishment of introduced species will depend on the seed reaching a favourable site, its germination and subsequent growth rates, and the proximity and growth rates of surrounding plants. It is reasonably certain that the successful establishment of plants from seed in vegetation occurs only in bare areas arising from the death of previous occupants or from incomplete coverage (Milthorpe, 1961).

Knapp (1959) in an investigation of microfacies found that grasses in such associations had an inhibitory influence on the development of seedlings of other species. Robertson and Pearce (1945) also reported the inability to establish seedlings of grass species when sown into a closed community of grasses which exhibited full coverage of the habitat. Rhodes (1968a) showed the competitive relationships between established swards and establishing seedlings of grass species and indicated severe competitive stress on the young plants. King (1971) also indicated similar effects in *Lolium perenne* and *Festuca rubra*. Similar studies conducted by Snaydon and Bradshaw (1962b), Harper (1967), Cavers and Harper (1967), Davies and Snaydon (1976) show that only a few plants survive when introduced into an established sward either as seeds or small plants. However, Pineiro and Harris (1978b) have suggested the importance of natural reseeding of prairie grass (*Bromus catharticus*) in regenerating established swards of this species.

2.3.1.1.3 Competition between grasses in established swards

Competition between grasses in established swards and the effects of environmental conditions and management on these relationships is well documented in the literature (e.g. England, 1968; McKell *et al.*, 1969; van den Bergh and Elberse, 1970; Rhodes, 1970; Evans and Young, 1972; Peterson, 1976). These studies highlight the superior competitive ability of a given species under specific climatic and/or management conditions, in established swards.

The competitive ability of plants changes with age, stage of development and environment (Charles, 1961, 1964, 1966; Rhodes, 1968a; Harris *et al.*, 1981b; Eagles *et al.*, 1982), and all these variations have a bearing upon the performance of component species of established swards. The plant responses to changes in environment also result in changes in productivity patterns of the swards (Anslow and Green, 1967).

Management of a sward has a direct bearing on competitive relationships and botanical composition of swards. This is well illustrated by early work of Jones (1933) and also in reports such as Arens (1962); Harris and Brougham (1968); Harris and Thomas (1970, 1972) and Harris (1978).

Recently competition in swards of euploid and aneuploid ryegrasses has been identified (Norrington Davies *et al.*, 1981) and this has been attributed to differences in chromosome numbers.

2.3.2 ALLELOPATHY

In contrast to competitive associations, allelopathy is not caused by the consumption of environmental resources needed for plant growth, but due to the exudation of harmful chemicals to the environment, which have inhibitory effects on the growth of the same species (auto-toxicity) or neighbouring plants of other species. Tukey (1969) and Rice (1974, 1979) have reviewed the role of allelopathy in agriculture, and its role in grasslands has been highlighted by Risser (1969); Newman and Rovira (1975) and Rice (1980).

Studies on allelopathy in grassland species have shown both self inhibitory processes and effects on other species. Autotoxic effects

have been identified during the growth of many pasture species, including *Bromus* species (Benedict, 1941), *Lolium perenne* (Newman and Rovira, 1975) wheat grass (*Agropyron smithii*) and blue grama (*Bouteloua gracilis*) (Bokhari, 1978). Allelopathic effects on neighbouring plants of other species is also reported. Resident tussock grasslands and residual roots of grasses have been shown to cause harmful effects on the growth of oversown grasses (Scott, 1974, 1975; Newberry (1979). Germination of diploid varieties of *Lolium perenne* has been inhibited or delayed in the presence of tetraploid varieties (Harries and Norrington-Davies, 1977; Norrington-Davies and Harries, 1977). Remison and Snaydon (1978) have suggested the possibility of the existence of allelopathic interactions in evaluating competitive relationships between grasses. Newman and Miller (1977) have reported the detrimental effects of root exudates on phosphorous uptake by pasture plants.

Grant and Sallens (1964) reported greater harmful effects of root extractions than shoot extractions on the growth of forage species. Research on *Lolium multiflorum* has shown that it suppresses the germination and growth of many pasture species in its vicinity (Naqvi, 1972) and subsequently Naqvi and Muller (1975) found that leachates of plant tops, decomposing residues and soil previously occupied by Italian ryegrass was toxic to many pasture species. Thus it is evident that allelopathic effects exist within and between pasture species.

2.3.3 GENERAL COMMENTS

As stated earlier, Grime (1974) suggests that competition, environmental stress and defoliation are the three main determinants of species richness and composition in herbaceous vegetation. While defoliation and stress are caused by external factors, competitive relationships that occur between pasture species can be considered an internal force within plant associations, which is modified by stress and defoliation (Gulmon, 1979). Thus competition between herbage species and cultivars has a significant role in the establishment, growth and yield of sown pasture mixtures.

Competition and allelopathy have been identified as the causal factors of harmful interactions between herbage plants. Current understanding of population balance in grasslands and performance of herbage mixtures suggests that competition is the major factor among plant interactions, especially among grass species. The existence of allel-

opathic effects, which are more difficult to study and prove than competitive relationships is reported in specific circumstances, and these play an important role in explaining specific relationships between herbage grasses.

The performance of a sown grass seed mixture is generally defined in terms of its yielding ability. Mixtures of grasses generally yield in between the yields of the monocultures of the component species (England, 1968; van den Bergh, 1968; Trenbath, 1974a) although exceptions have been reported (Alcock and Morgan, 1962; Whittington and O'Brien, 1968; Norrington-Davies and Crowley, 1969; Remison and Snaydon, 1980; Bebawi and Naylor, 1981). Greater yields can be obtained by sowing the highest yielding species under given situations rather than by sowing mixtures (Harper, 1977). However due to uncertainties of the environment, farmers generally use seed mixtures to obtain a better and more consistent yield. Thus competitive relationships between the species need to be given due consideration in establishing seed rates, times of sowing and subsequent management, especially during the early growth stages in order to obtain optimum yields from a sown grass mixture.

2.4 CHARACTERS ASSOCIATED WITH COMPETITIVE ABILITY IN HERBAGE SPECIES

The competitive ability of a plant in relation to its neighbours has been attributed to both genetic characters and causal effects of the environment. Traditionally, plant biologists have considered many characteristics such as life form, food reserves, rate and amount of seed germination, earliness of starting growth, efficient uptake of nutrients and water, density and depth of root systems to have a deterministic effect on the competitive ability of a plant (Clements *et al.*, 1929; Donald, 1961, 1963; Daubenmire, 1968). Yamada and Horiuchi (1960) reported that competitive ability is determined by quantitative differences in respect to characters governing the physiological processes involved in the intake of water, nutrients and light. These theories are generally accepted and are emphasized in published research and reviews. However, Sakai (1961) stated that competitive ability of plants was not necessarily associated with physiological and morphological characters which are advantageous in competition for light, nutrients and water. Sakai (1961) believed that competitive ability should be accepted as a genetic character and illustrated this with research on cereals. It was shown that competitive ability has a

genetic base as shown by highly significant specific and general combining abilities. Research also indicated low heritability values for competitive ability. Competitive ability was also subjected to the influence of environmental factors (Sakai, 1961). Other theories that have been developed to explain competitive ability have included a biochemical basis (Black *et al.*, 1969) who believed that the rate of carbon dioxide fixation and thus the growth rate is the major determinant of plant competition. The C_3 and C_4 carbon fixation pathways have also been related to competitive ability of plants (Baskin and Baskin, 1978).

The superior competitive ability of a species within a grass association can be related to many factors, which are genetically controlled characters of the species. The superior development of these characters in a species aids in the capture of limited resources from the environment to ensure successful growth. However, these characteristics can be modified with variations in the environment. In addition, superior performance of a species in terms of high yield in a monoculture cannot always be related to its success and competitive superiority in mixtures, and this apparent advantage of high yields can often be a drawback in making up mixtures, due to the inability of the species to overcome competitive stress imposed by other species (Sakai, 1955; van den Bergh, 1968). Such disadvantages have been recently reported by Norrington-Davies *et al.*, (1981) on mixtures with hyperploid ryegrass genotypes. The ability of a lower yielding species to become the dominant species in a mixture by suppressing a higher yielding species in a monoculture has been termed "the Montgomery effect" (Gustafsson, 1951; van den Bergh, 1968). This superior competitive ability of the lower yielding species when grown in a monoculture can be attributed to a genetic character, which inevitably becomes important in herbage mixtures, although environmental conditions will play a major role in the exhibition of these superior competitive characters.

Agriculturally, the first few months in the life of a herbage plant is important, as during germination and establishment, it exhibits characters which give it an advantage over other species in mixtures. In addition, the young seedlings are very sensitive to external factors of the environment, and thus competitive ability and growth rate exert their greatest influence on the botanical composition, productivity and density of plant populations in the sward (Troughton, 1956). Thus

the development of competitive relationships between grass species and cultivars in this establishment phase has a direct bearing upon competitive relationships and species performance within swards at later stages (e.g. Charles, 1961; Rhodes, 1968a; Harkess, 1970; Harris, 1973; Engel and Trout, 1977). Genetic changes resulting from differential plant mortality during pasture establishment and during seed multiplication in established swards have also been highlighted by Snaydon (1978). It is seen that genotypes which establish rapidly and/or seed prolifically have an advantage over other species, in terms of obtaining growth requirements from the environment. Thus plant characters which confer a competitive advantage on pasture species, more specifically grasses, during early establishment need to be identified because of their influence on competitive relationships that develop among the components of a pasture sward.

2.4.1 SEED CHARACTERISTICS

2.4.1.1 Seed size and weight

Seed size and weight are extremely important characteristics associated with seedling vigour. Davies (1927) summarized results of experiments carried out with common British grasses and stated that under normal field conditions, the size of the endosperm is an important factor in determining the potential ability of a species to establish itself.

One of the earliest papers published on the effect of seed size on subsequent seedling growth of cereals is by Zavitz (1908). Subsequently many published reports have emphasized the importance of a greater volume of endosperm food reserve in relation to seedling size and rate of growth (McKell, 1972). Kaufmann and Guitard (1967) report the importance of seed size on the initial leaf production of barley (*Hordeum vulgare*) and Austenson and Walton (1970) state that the size of spring wheat (*Triticum* sp.) seeds planted accounted for 2.5 - 4.5% of the observed variability in yield and other mature plant characters.

The effect of seed size on subsequent growth of pasture plants is frequently reported. Black (1956, 1957a,b,1958) clearly showed the importance of seed size and weight of clovers in determining subsequent performance in swards, and later comprehensively reviewed the importance of seed size in herbage legumes (Black, 1959). Beveridge and Wilsie (1959) reported similar results for alfalfa. The effect of seed size

in grasses has also received the attention of many scientists. Early research included reports by Kidd and West (1919), Davies (1927); Stapledon and Davies (1928); Chippendale (1932) and Plummer (1943). Stapledon and Davies (1928) presented the effect of seed size on subsequent growth as -

- (i) seeds with low "energies of germination" had low powers of establishment.
- (ii) smaller seeds had lower powers of establishment than larger seeds
- (iii) seeds with low "energies of germination" were prone to remain dormant in the soil and to establish plants more slowly
- (iv) the quick growing ryegrass species had higher powers of establishment than other species.

Subsequent research by Blaser *et al.* (1952 a,b); Rogler (1954); Kneebone and Cremer (1955); Herriot (1958) and Kalton *et al.* (1959) confirm the effect of seed size on growth and vigour in the early phase of a plant's life.

Most published research on the effect of seed size on subsequent growth is centered around seeds of the same species. Research reports by Kittock and Patterson (1962) on *Agropyron* seeds, Hove and Klinen-dorst (1957); Harkess (1965); Thomas (1966); Arnott (1969); Evans (1970); Shibuya *et al.* (1979) and Naylor (1980) on different types of ryegrasses illustrate the effect of seed size on subsequent growth of plants within a given species.

A review by Wright (1971) states that while there is a positive correlation between seed weight classes and seedling vigour within a species, there is very little effect of seed size when comparing different species. However, many reports do emphasize the importance of seed size in determining early growth and competitive advantage of species. Asher and Ozanne (1966) studied root growth in seedlings of annual pasture species and indicated that root penetration rate was closely correlated with seed weight until the roots reached a depth of about 20 centimetres. Aspinall and Milthorpe (1959) found that barley, with its larger seed and embryo size was a better competitor than white

persicaria (*Polygonum lapathifolium*) although the two species has similar growth rates. Aspinall (1960) attributed the superior performance of barley during early growth to its larger seed size, which gave the species an initial advantage. Cocks (1969) and Cocks and Donald (1973a) also reported the likely gaining of an early competitive advantage by *Hordeum leporinum* due to its larger seeds when compared with *Lolium rigidum*, especially in terms of shading by larger leaves developed by the larger seedling in natural reseeding of annual pastures. Studies of Evans (1973) on the effect of seed size on shoot and root growth of several grasses and legumes also demonstrate the importance of larger seeds in plant growth. Gulmon (1979) concludes that *Avena fatua* can maintain dominance in grassland vegetation by virtue of its larger grains and consequently larger seedlings. Brock (1973) also reported the better growth and seedling vigour of larger seeded tall fescue when compared with ryegrass, but did not attribute this to the seed size factor.

2.4.1.2 Endosperm-embryo relationships of seeds

Bremner *et al.* (1963) studied the effects of embryo and endosperm sizes on subsequent seedling growth in wheat. While there was little or no effect from variations in embryo size, variation in endosperm sizes had a considerable effect on seedling growth. This increased vigour of seedlings was attributed to a larger endosperm:embryo ratio, which indicates a greater reservoir of energy within seeds of faster and better growing species. In contrast Donald (1958) reported the greater competitive ability of *Lolium perenne*, which is a species possessing a larger embryo over *Phalaris tuberosa*, and Aspinall and Milthorpe (1959) attributed greater competitive ability of barley to its larger embryo, which gave larger plants than white *persicaria*. Cocks and Donald (1973a) reported larger embryos and endosperms in *Hordeum leporinum* when compared with *Lolium rigidum* and attributed the occurrence of larger seedlings of the former species to this relationship, which gave it a competitive advantage under high plant densities. Thus a species with a greater endosperm:embryo ratio can be expected to show a greater competitive ability than a species with smaller ratios due to its ability to produce a larger and more vigorous seedling soon after emergence. Such a seedling has a greater potential for capturing environmental resources and establishing itself within the plant community.

2.4.1.3 Seed Age

Seed age can be a negative factor in seedling vigour unless stored under conditions that prevent or retard embryo and endosperm deterioration. Older seeds have been shown to germinate more slowly (Crocker, 1948; Kittock and Law 1968), and may produce malformed, slower growing seedlings, giving them a disadvantage in competitive situations.

2.4.2 GERMINATION

Rapid seed germination is another plant characteristic that contributes to a vigorous and successful seedling, which has the ability to gain a competitive advantage within a herbage association. The importance of early germination as a factor determining survival in competition between different species of grasses has been clearly identified by Stapledon and Davies (1928) and Clements *et al.* (1929).

The rate of germination can have an important bearing on seedling competition, as the earlier established plant would have a definite advantage over later emerging plants (Blaser *et al.* 1952b). Similar studies by Pavlychenko and Harrington (1934), Rummel (1946), and Chippendale (1949) also indicate the importance of early and uniform germination in determining the success of a species in a competitive situation. In addition, it was stated that early germination gave the plants an opportunity to occupy the environment more rapidly and completely before other species with lower and slower rates of germination appeared on the ground surface. Similarly, Milthorpe (1961) emphasized that the degree of success of any species depended largely on its time scale of emergence relative to that of other species. Blaser *et al.* (1956) also attributed aggressiveness during establishment to early seedling emergence and survival.

More recently, many studies on the effect of rapid germination on seedling vigour and growth of grasses have been reported. Whalley *et al.* (1966) examined several grass species for their seedling vigour and its relation to growth of the young emerging seedling, before the onset of autotropic growth. It was seen that extreme rapidity of germination largely accounted for high seedling vigour of *Schismus arabicus*. Harris (1968) indicated that the earliness of germination also contributed to the competitive advantage of 'Manawa' ryegrass when grown with

'Ruanui' ryegrass. The ability of ryegrass to germinate rapidly even under conditions of moisture stress has been considered as one of the factors determining its success in field establishment (McWilliam and Dowling, 1970; McWilliam *et al.*, 1970). Harris (1967); McCown and Williams (1968); King (1971); Ross and Harper (1972) and Cocks and Donald (1973b) also highlighted the importance of early germination and emergence in determining competitive abilities of grasses. Similar studies on grasses have also been reported by Wright *et al.* (1978) and Elberse and de Kruyf (1979) and Hagggar (1979) noted the importance of early germination on the competitive effects between barley and *Chenopodium* species. The occurrence of a small delay at the time of establishment due to slower rates of germination of a species is shown to strongly reduce its competitive ability (Spitters, 1979). Harris *et al.* (1981b) also related the initial dominance of ryegrass over paspalum to the more rapid germination and establishment of the former species.

2.4.3 SEEDLING GROWTH

The establishment of a grass seedling begins with the emergence of the coleorhiza and coleoptile. Rate of growth of the seedling after emergence is partly dependent upon stored food reserves in the seed and partly on genetic factors (Blaser *et al.*, 1952b). Competitive success at establishment is achieved only when the plant has developed an adequate root system to obtain water and nutrients at a rate equal to or greater than other competing seedlings. In a similar manner, top growth must be in proportion to root growth and greater than competing seedlings (McKell, 1972).

Rate of seedling growth is often regarded as evidence of seedling vigour. Pasture species have been classified by Stapledon and Davies (1927) and Blaser *et al.* (1956) according to their aggressiveness. These workers have rated perennial ryegrass as being more aggressive than cocksfoot, using the criterion of relative weights of seedlings at some time after sowing, under high fertility levels.

Rapid shoot and root growth is considered a distinct advantage in seedling establishment of pasture grasses. Early studies of Stapledon and Davies (1927) and Davies and Thomas (1928) report the importance of early and rapid shoot growth of ryegrass in gaining competitive advantage over other grasses. Arens (1962) also shows similar effects

of perennial ryegrass as an aggressive species especially in the early growth phase. Dalrymple and Dwyer (1967) evaluated five grass species in America and indicated that seedling emergence, early growth and vigour were important characteristics of grasses to be used in reseeding pastures. Research by Cocks and Donald (1973b) also reports the importance of faster seedling growth rates of *Lolium* in suppressing larger *Hordeum* seedlings with time.

While rapid seedling growth is identified as a character favouring competitive advantage and aggressiveness of a species, it seems logical to evaluate the components of seedling growth - namely root and shoot development in the early growth phase. The growth of both shoots and roots determines the competitive advantage of a plant when compared to another, as these plant components are responsible for obtaining growth requirements from the environment.

2.4.3.1 Growth and development of the root system.

The rapid development of a root system sufficient to obtain water and nutrients for the young seedling is perhaps a higher priority than early top growth, especially if endosperm reserves in large seeds are still available (McKell, 1972). Roots can also be considered important as nutrient uptake has been identified in pasture grasses even before the complete exhaustion of endogenous food reserves (McWilliam *et al.*, 1970). Thus only plants with healthy and strong root systems are seen to produce luxuriant growth. In addition, the importance of root competition during seedling growth and its occurrence before shoot competition has been reported by many workers e.g. Rhodes (1970).

Many research workers indicate that patterns of root development play an important role in plant competition. Clements *et al.* (1929) stated that all plant parts were important in determining competitive ability, but emphasized the importance of root systems. Studies by Pavlychenko and Harrington (1934) and Pavlychenko (1937) on entire root systems showed the importance of the rate of root development in determining competitive ability of certain annual plants. Cashmore (1934) investigated some aggressive characteristics of *Lolium perenne* in comparison with *Phalaris tuberosa* under high fertility conditions. Using both single plants and mixtures, it was concluded that the superior growth and aggressiveness of *Lolium* in the seedling year was due

to its denser roots in the upper soil layers together with greater top growth. Milthorpe (1961) also associated the higher competitive ability of ryegrass over tall fescue with faster root growth of the former, along with more rapid tillering. The close association between rate and extent of nodal root production with seedling competitive ability in ryegrass was reported by Rhodes (1968b). Recent studies on plant characters affecting six perennial ryegrass clones have shown that the most competitive clone had the largest root system, and the least competitive clone, the smallest root system (Hoffmann and Ennik, 1980).

Studies on the relationship between competitive ability and early root growth of other grass species include that of Carter *et al.* (1957) who reported that the downward growth of roots in cheat grass (*Bromus secalinus*) was inhibited when grown in mixtures with red wheat. The importance of early penetration of roots in determining competitive relationships was also shown by Harris (1967) and McCown and Williams (1968). Harris (1976) studied the root phenology of three grasses as a factor of competition among seedlings. These studies showed that initial root growth and rapid extension of root-soil contact were very important characteristics of the more aggressive species, along with germination rates, and death rate of roots.

Donald (1958) and Aspinall (1960) suggested that slower growth of the less successful of two associated species was due to restricted nutrient uptake which was always associated with smaller root systems. Aspinall (1960) also stated "that as the roots expand, the only space available is that already occupied by the roots of the more aggressive species or that space from which nutrients had already been used up by the dominant species". This theory is likely to hold true in all agricultural situations as roots can find nutrients only by greater and extensive root growth and the more rapidly growing roots of the aggressive species gain access before those of the slower growing species. Research by other scientists also indicates the importance of root volume in utilizing soil nutrients. Lee (1960) reported the competitive superiority of a barley cultivar and ascribed this character to a rapidly developing, larger root volume when compared with the other barley cultivar. This character was associated with the ability to gather nutrients efficiently from a limited soil volume which was exploited by

both cultivars. This placed the cultivar with a small root volume under severe stress when both were dependent upon the same soil mass for nutrients. Andrews and Newman (1970) and Barley (1970) also showed the importance of a higher proportion of actively growing roots of a herbage species in determining its competitive superiority, especially in terms of nutrient uptake. Newman and Andrews (1973) correlated root density with potassium uptake of winter wheat, under competitive situations for potassium. Evans (1977) studied the comparative root morphology of pasture grasses and legumes and showed the presence of greater numbers of longer root hairs in grasses, which gave these roots a greater surface area. This difference in surface area of roots was considered advantageous to grasses in competition with clovers in terms of nutrient and water uptake, especially with less mobile elements like phosphorus. Competitive advantage of *Hordeum leporinum* over *Lolium rigidum* under conditions of low nitrogen was also expressed in terms of faster root growth of *Hordeum* which enabled it to utilize the available soil nitrogen more efficiently (Cocks, 1974).

Other characters of root growth conferring competitive advantage include the root density and greater actively absorbing root length. The importance of root density of a species in determining its superior competitive ability was illustrated by Andrews and Newman (1970). This becomes especially important in seedlings as all roots at this stage of growth are generally active and are able to take up nutrients. Harris (1967), and Olsen and Kemper (1968) reported the importance of the ratio of actively growing root length to root weight, while the significance of the length of root hairs in determining competitive success for nutrients and water was reported by Drew and Nye (1969) and Barley (1970).

Studies on the importance of root growth in terms of water uptake to determine successful establishment have also been reported. Plummer (1943) attributed the success or failure of establishment of twelve range grasses to total root development prior to onset of severe drought. McWilliam and Dowling (1970) and McWilliam et al. (1970) found that there were significant differences between different species of grasses and legumes in their rates of root elongation. The time required to obtain a

particular root length differed considerably due to differences in rates of germination and growth. Significant differences were also observed between species in their ability to germinate and obtain active root penetration under moisture stress. It has been suggested that these differences may be important under field conditions where root development is critical for good establishment, and this can also have a bearing upon competition under such conditions.

2.4.3.2 Growth and Development of the Shoot System

Rapid and more extensive shoot growth during establishment is commonly associated with competitive ability of herbage grasses (Rhodes, 1970). Plant height is considered a character associated with seedling vigour, which confers a competitive advantage on the taller species in gaining a greater share of the light incident on the plant canopy. In grasses, plant height is associated with leaf angle and orientation. The success of a plant within an association may result from the capacity of seedlings to avoid shade, which depends on height and inclination of the first leaves produced by the seedling. The importance of plant height in the competitive superiority of 'Manawa' ryegrass and 'Ruanui' ryegrass is reported by Harris (1968) and Eagles and Williams (1971) showed the importance of plant height and shoot growth form in the success of *Dactylis* cultivars growing in mixtures.

Leaf area has also been associated with competitive ability of grass species, especially in the early growth phase. Leaf area, along with plant height plays an important role in shading shorter plants with smaller leaf areas. The role of leaf area in pasture growth has been reviewed by Brown and Blaser (1968), and they illustrate its value in determining the performance of species in mixtures. Hill (1972) studied five genotypes of ryegrass and reported the superior competitive ability of long leaved genotypes. Studies on wheat by Smoliak and Johnston (1975) also present the superior competitive nature of the species with the greatest seedling leaf area and weight when grown in monocultures. The success of this species was related to its ability to compete successfully for light when associated with other species.

The most widely attributed and reported characteristic of seedlings in terms of competitive ability is the rate of tillering. The rate of

tillering of grasses was associated with aggressivity of species by Stapledon *et al.* (1927), and Davies (1928) stated that during the seedling year, a species was aggressive in proportion to its rate of tillering during the early growth period. Milthorpe (1961) reviewing published literature reported the similar embryo weights and relative growth rates of *Lolium perenne* and *Festuca pratensis*. However, under high densities, *Lolium* tended to suppress *Festuca* during the period of active growth and this was associated with the more rapid tillering rate of the former species. *Festuca* with fewer larger tillers was noted to succeed under hay conditions. Donald (1958) also concluded that faster tillering rates of *Lolium perenne* was a character which gave it a competitive advantage over *Phalaris tuberosa*. Tillering and its importance in herbage grasses has been studied and reviewed by many (e.g. Mitchell and Glenday, 1958; Langer, 1963; Evans *et al.*, 1964; Jewiss, 1972). These reports identify the importance of tillering in determining the productivity of a species as tillers are considered to be the vegetative growth units of herbage grasses. Thus rapid tillering during early growth enables a species to secure itself in a mixed stand, thereby developing a competitive advantage over its associates within that plant community.

2.4.4. GENERAL CONSIDERATIONS

Very little information is available on the characteristics of herbage plants, which are associated with competitive ability under the possibly modifying effects of cutting and grazing, variations in the edaphic environment and in relation to plant development (Rhodes, 1967). It is considered that competitive ability is associated with quantitative differences in characters governing the intake of essential growth factors at later stages of growth of the plant. A study by Norman (1960) indicated the importance of shading from surrounding plants in causing a species to adopt a more erect habit and thus lose a higher proportion of foliage when defoliated. Rates of recovery of species in relation to surrounding herbage and the effect of selective or preferential grazing has also been studied by Norman (1960). Thus as most reports indicate, characters governing competitive advantage in the seedling phase become important in determining subsequent performance of species in mixed swards. This is due to their ability to establish an early dominance in a competitive situation, which remains for a long

period unless modified by some external factor.

The principle of obtaining competitive advantage in a seedling association is based on the fact that the larger or earlier germinating seedling will be able to occupy and utilize the environment better and/or earlier. However, it will be able to modify the environment to the detriment of the smaller or the later emerging species only if its greater size or earliness gives it a mechanism by which it can compete. Thus seed size will not give an advantage to a species unless it gives superior root growth or plant height. It is generally accepted that competitive effects are most intensive when individuals of the same species or plants of similar growth habit such as grasses are grown together, due to similar needs of all species (Cocks, 1969; Haynes, 1980). Thus a superior growth characteristic of one species will begin a series of advantages to secure resources from the environment, thereby affecting the weaker species. This suggests that while competitive advantage may be due to one factor, the effect of all growth characteristics must be evaluated in determining the success of the aggressive species. In addition, the availability of resources for plant growth within the environment and external factors not used for plant growth have an important role in determining the superior performance of a species in a competitive situation. Thus such factors need to be taken into consideration when studying the competitive superiority of a herbage grass species.

2.5 ENVIRONMENTAL FACTORS AFFECTING COMPETITIVE ASSOCIATIONS IN HERBAGE PLANTS.

The emerging plant, developing from the seed obtains its requirements from the seed through physical links maintained for a limited time. After a period of time, the young plant either exhausts the food reserves or becomes independent and thereafter depends on its own ability to obtain growth requirements from the environment.

All environments do not contain abundant resources for plant growth, and thereby cause restrictions on the normal growth of plants. Furthermore, the presence of neighbouring plants can enhance the depletion of limited resources of the environment by their own consumption. Thus competition for these limited resources arises within plant communities even at early stages of growth, which thereafter becomes a phenomenon

that remains throughout the life cycle of the developing plant community.

Harper (1977) considered the consumable resources of the environment needed for plant growth as "Supply factors". In addition, other factors of the plant environment such as temperature, defoliation, presence of grazing animals on pastures and soil microbiological effects also have a great impact on the competitive ability of plants. These factors, which modify the plant's environment, but are not directly utilized by plants have been termed "Quality or Conditioning factors" (Harper, 1977). This classification (Harper, 1977) will be used in this section to identify factors affecting competitive interactions between herbage plants, with emphasis on pasture grasses.

2.5.1 "SUPPLY FACTORS" AFFECTING COMPETITION BETWEEN HERBAGE PLANTS

While animal ecologists have highlighted competition for space in terms of either movement or habitation within animal communities, similar research in plant ecology is rare. Donald (1963) reported competition for physical space in root crops as a factor affecting the growth and development of roots. Ross and Harper (1972) illustrated competition for space in terms of suitable germination sites for *Dactylis glomerata* seeds. While such situations do arise in grassland communities and have an effect on subsequent growth of species, plant populations are generally regulated by competition for resources needed for growth, which, as stated earlier have been identified as light, carbon dioxide, oxygen, water and nutrients (Donald, 1963). Amongst these resources, light and carbon dioxide are absorbed by leaves while the uptake of nutrients and water is generally limited to roots. Plants take up oxygen through both root and shoot systems.

Generally, one or more of these growth resources become limiting within a given environment, which has a bearing on the growth of the entire plant community. Competition develops among the species for the limiting factors, and the success or failure of a species within a community depends on its ability to obtain sufficient resources for its growth (Trenbath, 1976). However, it is difficult to isolate competitive effects in field situations into individual components (Donald, 1958; 1963) as observed competitive effects are a consequence of interactive processes. Thus de Wit (1960) grouped these resources as "Biological space" and identified competition between grasses, cereals and other crop combinations for "Biological space" within their plant

communities.

2.5.1.1 Environmental resources utilized by plant shoots

2.5.1.1.1 Light:- Harper (1977) states "The supply of light to an area of land is the most reliable of the environmental resources for plant growth. It's reliability lies in the regularity of diurnal and annual cycles of light intensity".

Light occurs as a stream of quanta, which if to be used in plant growth must be trapped by a photosynthetic structure and converted immediately to chemically bound energy. Thus competition for light becomes different from competition for other resources which have reservoirs from which competitors could obtain their requirements and which could also be stored and translocated within a plant (Donald, 1963).

Light energy is instantaneously available and thus needs to be intercepted by leaves immediately or it is lost as a source of energy for photosynthesis. Donald (1963) thus emphasized that the vital relationship in competition for light was one of physical position of leaves in a plant growing in an association of plants. The successful plant in a competitive situation is not necessarily that with more foliage, but the plant which has its leaves in an advantageous position relative to the foliage of its competitors for light. Stern (1962) highlighted the importance of canopy structure and other parameters associated with light interception and absorption. Much of the research and progress in the field of light energy and penetration, energy transfer and light interception and absorption by crop canopies has been recently reviewed by Anderson (1975).

Donald (1951) and Blackman and Black (1959) have suggested that there are many situations where light may be the only factor for which there is competition between plants. This occurs when adequate nutrients and water are supplied to crops and pastures. This situation arises in pastures as light intensity often falls to levels well below compensation point beneath dense swards. Thus species of short stature suffer due to shading effects of taller species. Even in situations where competition occurs for water and nutrients, light still remains a factor of major importance, as demonstrated by Donald (1958) in grass associations growing under low nitrogen levels.

Many researchers have demonstrated competition for light in pastures. Weaver and Flory (1934) found that on an upland prairie, light intensity at half the height of vegetation was about 25% and at ground level, this dropped to 5% of that above the sward, and reported the detrimental effect of this reduction on shorter species. Subsequent research and reviews including those of Blackman (1938); Donald (1951, 1961, 1963); Monsi and Saeki (1953); Brougham (1954a, 1958); Wilson and Peake (1956); Black (1957c); Norman (1960); Stern and Donald (1962); Edwards and Allard (1963); Harper and Clatworthy (1963); Wilkinson and Gross (1964); Anslow (1966); Alberda and Simba (1968); Harris (1972) and Pineiro and Harris (1978a) have demonstrated the importance of light and its utilization in competitive situations. More recently, Ludlow (1978) and Rhodes and Stern (1978) have comprehensively reviewed the light relations and competitive effects for light in pastures and illustrated the importance of light and competition for this resource in pastures.

Competition for light between associations of herbage grasses has also been demonstrated by many workers, which include among others, Donald (1958); Crocker and Martin (1964); Harris (1967); Rhodes (1968b, 1970, 1973); Eagles and Williams (1969); Risser (1969); Harris (1970a); and van den Bergh and Elberse (1970). Many others also have indicated the importance of light in studying other processes of interaction between grasses. Most studies show the importance of plant height and leaf orientation as major factors in determining competitive relationships between grasses for light. Rhodes (1968b) showed the ability of seedlings of *Lolium rigidum* planted at high densities to shade *Phalaris coerulescens* seedlings. Similar studies by Cocks (1969) show the ability of seedlings of *Hordeum leporinum* planted at high densities to shade seedlings of *Lolium rigidum*. Thus, plant height becomes an important character in competitive relationships between grasses, especially as success of establishment may result from the capacity of seedlings to avoid shade, which may be dependent on the time of emergence, plant height and degree of inclination of the first leaves produced by the plant. (Risser, 1969). In addition, small differences in plant height between species in grass communities are associated with large changes in light intensity, direction and quality, which can have great ecological significance to the competitive relationships between the species and also on pasture production (Donald, 1961; Grime 1966). The importance of light as a resource for plant growth is not limited to herbage production alone, and its importance as a resource for seed production of grass species has been shown by Lambert (1963).

The pattern of light interception and utilization by plant canopies has also been explained by models (e.g. de Wit, 1965; Duncan *et al.*, 1967; Baeumer and de Wit, 1968). These models show the importance of height, leaf area, structure and orientation of leaves within plant canopies to utilize the incident light. While most models have been developed for monocultures, (Rhodes and Stern, 1978), the model developed by Baeumer and de Wit (1968) incorporates methods of evaluating competitive relationships for light in mixed cultures.

2.5.1.1.2 Carbon dioxide (CO₂):- Studies conducted on CO₂ flux within crop canopies show that the concentration of CO₂ in the atmosphere away from a photosynthetic surface is about 300 ppm; which does not alter greatly from place to place. Studies on *Zea maize* show that CO₂ concentrations within crop canopies can be depleted greatly at times of maximum photosynthesis (Wright and Lemon, 1966). However, these scientists attributed this to a population effect as there is no evidence to show that CO₂ levels around a single isolated plant would depart significantly from that of the surrounding air. Thus if CO₂ levels are depleted within crop canopies, it may be attributed to the crop itself, poor air circulation within the canopy and the photosynthetic system of the crop (Harper, 1977).

Studies on plants having either C₃ or C₄ pathways of photosynthesis have not shown a depletion of CO₂ levels below that of a minimum required for photosynthesis, unless enclosed in chambers (Harper, 1977). Thus although competition for CO₂ between plants is theoretically possible, turbulence within plant canopies is usually sufficient to ensure adequate CO₂ (Kanemasu *et al.*, 1964). Thus, competition for CO₂ within plant associations, both crop and herbage species can be considered negligible (de Wit, 1965; Trenbath, 1976).

2.5.1.2 Environmental resources utilized by plant roots

2.5.1.2.1 Oxygen (O₂):- Generally, the mutual demands for oxygen by shoots of plants do not develop competitive situations, as the O₂ concentration is high and its mobility in the gaseous phase is also very high (Harper, 1977). In contrast, theoretically it can become limiting within a soil system. This arises as the diffusion rate of O₂ in water is much slower than in air, and thus the presence of waterfilms and hazardous

diffusion pathways can hinder O_2 movement. However, due to the high affinity of terminal oxidase systems for O_2 , the rate of aerobic respiration in roots is unlikely to be hindered unless O_2 concentrations near roots approach zero. Thus although O_2 is a resource consumed in large quantities by roots of growing plants (Lemon and Wiegand, 1962) no investigation clearly implicates the presence of competition for O_2 among plants, as diffusion of molecular O_2 seems to be sufficient to meet respiratory needs of roots, except in very wet soils (Greenwood, 1969; Harper, 1977).

2.5.1.2.2. Minerals:- Plants obtain their mineral requirements from reservoirs within the substrate which have local characteristic forces of supply and retention. Most soil minerals are retained by physical and/or chemical linkages with insoluble soil constituents and are made available to plant growth as ions through the soil solution. Thus, nutrient reservoirs are maintained within the soil system from which plants can draw their requirements. Due to the uptake of nutrients from these reservoirs by plants for either growth or storage within plant tissues, competition can develop between plants for one or more nutrients needed for plant growth.

Competition between plants for nutrients has been studied by many researchers. Publications on this subject include competition for nutrients in crop-weed associations (Zimdhal, 1980) and in cropping and pasture situations (e.g. Aberg *et al.*, 1943; Donald, 1963; Risser, 1969; Trenbath, 1976; Harper, 1977).

Three major aspects of competitive relationship for nutrients have been reported by Donald (1963), based on earlier experimental evidence of Drapala *et al.* (1961).

(i) In a situation where there is a finite supply of readily available nutrients, the competitive success of any plant can be governed by the number of individuals drawing on the supply and by the relative rates at which it is being used.

(ii) When nutrients are present in different forms, both chemically and physically, the competitive ability of different species may be determined by their capacity to make use of each of these forms.

(iii) The successful growth exhibited by one species due to the intake of nutrients can bring about a dominant effect to enable further successful utilization of available nutrients, which can affect other plants in terms of their requirement for the same nutrient and/or other growth factors.

Research on competitive interactions for nutrients in pastures has been extensively conducted and most reports have been concerned with grass-legume associations. These include reports by Blackman (1938); Blaser and Brady (1950); Gray *et al.* (1953); Walker *et al.* (1954); Mouat and Walker (1959); Snaydon (1962, 1971); Snaydon and Bradshaw (1962a); Jackman and Mouat (1972a,b); Hall (1974a,b); Harris and Hoglund (1977) and Andrews and Johansen (1978). All these publications highlight competitive interactions between grasses and legumes for different nutrients in many environment and under different management conditions. Recently Haynes (1980) reviewed all aspects of competitive relationships in grass-legume associations and highlighted the importance of competition for nutrients between these species.

Competition between grass species and cultivars has also received the attention of many scientists. Juska *et al.* (1955) reported the presence of competition for nutrients between Merion blue grass and creeping red fescue. Troughton (1956) found competition between *Lolium perenne* and *Phleum pratense* for nitrogen in pot trials. Donald (1958) also reported nutrient competition, especially for nitrogen between grass species. Evans (1960) showed that competition for nitrogen is a principle factor determining intraspecific competition between grasses. Similar studies on competition for nutrients in mixtures of grasses have also been reported by Welbank (1961, 1962, 1964); van den Bergh and Elberse (1962) while Bradshaw *et al.* (1958, 1960a,b, 1964) showed the response of different grasses to different nutrients and reported that nitrogen is a major nutrient affecting the performance of pasture species. Comprehensive studies and reviews by van den Bergh (1968, 1979) also present the importance of nutrient competition in determining competitive relationships between grass species in short and long term studies. Competition for nutrients was considered a dominant factor determining the success of establishing new grass plants within established swards (King, 1971). Research reports by Risser (1969); Eagles (1972); Evans

and Young (1972); Harris (1973); Cocks (1974); Fitter (1976); Mahmoud and Grime (1976); Remison and Snaydon (1978, 1980) and Gulmon (1979) also highlight the importance of competitive relationships for nutrients as a major factor determining the performance of grass species and cultivars in mixtures under different environments and experimental conditions.

Donald (1963) emphasized that competition for nitrogen was the most widespread form of nutrient competition affecting grasslands of the world. While the occurrence of competition for nitrogen can be attributed to its relative mobility within soil systems, research also highlights the importance of competition for other nutrients in determining the success of a grass growing in association with other species or cultivars (e.g. de Wit *et al.*, 1963; Baldwin, 1976).

Most of the recent studies investigating interference between species have concluded that "competition for nutrients is of greater importance than competition for light" (e.g. King, 1971; Snaydon, 1971; Eagles, 1972). Thus competition for nutrients can be considered a major factor determining competitive relationships between grass seedlings.

2.5.1.2.3 Water:- The supply of water to a given area of land is often the least reliable of all resources needed for plant growth (Harper, 1977). Thus water deficiency has been identified as a very common factor determining geographic limits of crop production.

Donald (1963) stated that "Competition for water occurs together with other forms of competition, especially for nitrogen and for light, but it is by no means of parallel intensity with these other forms". However, much work has been done on water deficiencies in economically important crops and pastures and has been reviewed by Risser (1969); Trenbath (1976); Turner and Begg (1978) and Zimdhal (1980).

Rummel (1946) measured the competitive effect of cheat grass on the establishment and growth of two cultivars of wheat grass at two moisture regimes and concluded that cheat grass was affected by lower moisture availability. Welbank (1961) studied the effect of nitrogen and water in competitive situations in *Agropyron repens* populations.

Although competition was observed for both factors, it was suggested that competition for water had a greater effect in limiting the productivity of the species. Harris (1967) showed the different root development patterns of *Bromus* species and *Agropyron* species under dry conditions in efforts to overcome water stress. Experiments of Harris and Lazenby (1974) highlight the ability of ryegrass to perform well and maintain competitive vigour when compared with paspalum under warm conditions with the provision of irrigation. This trend is reversed under dry conditions and paspalum becomes superior in the ryegrass-paspalum mixtures. Responses of other grass and pasture species to competitive stress for water have also been reported by Harris and Sedcole (1974) and Turner and Begg (1978).

Recently, Haynes (1980) in a review on competition between pasture species listed four important factors that determine the success of a plant in a competitive situation for water.

(i) The ability, rate and completeness with which plants can make use of the soil water supply.

(ii) The rate and extent of exploitation of the soil space.

(iii) The efficient use of water which is related to the plant's ability to regulate water loss.

(iv) The ability to exploit different parts of the soil system not used by roots of other species.

However, due to the close relationship between competition for water and nutrients (Donald, 1963; Turner and Begg, 1978) these characteristics can also be considered important in terms of competition for nutrients.

2.5.2 "CONDITIONING FACTORS" AFFECTING COMPETITION BETWEEN HERBAGE PLANTS

Competition, stress and disturbance are suggested by Grime (1974) to be the major determinants of vegetation. While competitive relationships develop between herbage species and cultivars for environmental resources, stress and disturbance are caused by conditioning factors which have an effect on the normal growth and competitive relationships

within a herbage association. Their effects on competitive relationships occur due to the ability of conditioning factors to alter the characteristics governing the uptake of growth requirements by plants. Many conditioning factors of the environment, which affect competition within herbage associations have been identified.

2.5.2.1 Density Effects

One of the most important concerns of the pasture researcher is the yield produced per unit area by a sown sward (Donald, 1951). Therefore, the effect of density on the performance of pasture species becomes an important parameter which has a deterministic effect on yield. As the density of a plant population is increased, individual plants are brought into close proximity which modifies their growth patterns. Thus Harper (1965b) stated that "The distance between two plants at which the two individual plants will show the result of such an interference is considered a function of the size of the plants and their age".

Intraspecific relationships between planting density and yield in terms of dry matter and seed yield have been well established for a wide range of crop and pasture plants by many scientists. This topic is comprehensively reviewed by Holliday (1960) and Harper (1977). Intraspecific relationships in terms of density and yield of pastures have also been reported by many workers including Donald (1951, 1954, 1963); Harper (1961); England (1965, 1968); Ross and Harper (1972). Studies by Donald (1951) illustrated a linear relationship between yield and density in annual pastures. Competition was evident at very early stages in the denser populations, while similar relationships became operative in populations with lower densities at later stages of growth.

Studies conducted on binary mixtures of grasses and other herbage species and cultivars combined in equal proportions show that the overall density of the population has very little effect on the final relationship between the two component species. However, increased density can induce the earlier onset of and enhance competitive effects between the two species (Davies, 1936; England, 1965, 1968; Fowler, 1982). This effect between grasses is highlighted by reports of England (1965, 1968) using cultivars of *Lolium perenne* and *Dactylis glomerata* and by Fowler (1982) using several grass species. These results also agree with those of Sandfaer (1954) and Sakai (1955, 1961) who reported

that increasing density tends to increase the magnitude of competitive effects, but does not alter the relative performance of the constituents of mixtures. Studies on legumes by Black (1960a) and Stern (1960) also show that irrespective of densities, competitive relationships develop within populations of similar plant types.

2.5.2.2 Temperature

Temperature is a major factor controlling the distribution and diversity of plants. The role of temperature assumes increasing importance within plant communities as it deviates above or below the general biological norm (McWilliam 1978). Temperature affects the morphology of the plant and influences its ability to adapt to altered temperature conditions or survive in competition with other members of the plant community. The dominant or aggressive nature of plants at high temperatures develops due to the ability to resist heat stress. In turn, the ability to resist heat stress relates to water retention within the plant and the ability to absorb water from the environment, which enhances competitive ability. On the other hand, resistance to cold temperatures by morphological and physiological changes facilitates the survival of plants and their successful uptake of growth requirements under cold conditions. This creates a dominant effect especially within plant communities in the temperate regions.

Temperature is considered an important determinant of the botanical composition of pastures (Fitzpatrick and Nix, 1970), due to differential responses of species. Since the work of Mitchell (1956a, 1956b) further reports on the response of pasture species to temperature have been presented (McWilliam, 1978). Effects of temperature on grasses and other pasture species and its effects on competitive interactions in mixtures have been reported by van den Bergh and de Wit (1960); Ennik (1960); Rhodes (1967); Eagles and Williams (1969, 1971); Eagles and Ostgard (1971); Harris (1972) and more recently by Harris *et al.* (1981a,b). These studies show that temperature and changes in temperature have an effect on the growth and productivity of pastures, and on competitive relationships in pasture mixtures. In addition, the effect of temperature on germination and early growth of pastures has been reported by Sprague (1943), while differential growth of several pasture swards in different seasons has been attributed to the differential response of component species to temperature changes (Baars, 1982). Harris and Lazenby (1974)

also showed the effects of temperature and water stress on competitive relationships in mixtures of temperate and tropical grasses.

2.5.2.3 Defoliation

A major parameter that acts as a disturbance to plant growth is defoliation, either by mechanical devices, grazing animals, cultivation, fire, treading, fouling of herbage or by extreme environmental conditions of frost, drought or wind (Harris, 1978). However, in pasture research, emphasis has been placed on defoliation of swards by cutting or by grazing animals. This aspect has received much attention (e.g. Brougham, 1954b; 1959; Mitchell and Glenday, 1958; Brougham and Harris, 1967; Harris and Brougham, 1968; Pineiro and Harris, 1978a,b), and these reports highlight changes in sward composition due to effects of defoliation. Studies have also been conducted on changes in the morphology and productivity of grass species due to different defoliation treatments (e.g. Anslow, 1967; Evans, 1973). More recently, a comprehensive review on defoliation by Harris (1978) highlights its importance as a determinant of growth, persistancy and composition of pastures.

The performance of a pasture plant in terms of dry matter productivity, and its competitive superiority as related to shoot growth is dependant upon the development of its growing points. This can be inhibited by poor light penetration into the plant canopy, in addition to limitations imposed by nutrient and water supply. Thus defoliation becomes an important factor in determining light relationships within the plant canopy. The intensity and frequency of defoliation also has a direct bearing on these light relationships within the canopy and thus affects the performance of plants within a sward (Harris, 1978).

Changes in competitive relationships in mixtures of grasses and legumes due to defoliation have been reported by many workers (e.g. Harris, 1974; Harris and Thomas, 1973). Similar studies on herbage grass mixtures have been reported by van den Bergh (1968); Scarisbrick and Ivins (1970); Harris (1970b, 1973); Harris and Thomas (1970, 1972); Harris *et al.* (1981b); Remison and Snaydon (1980) and many others. These reports illustrate the changes in plant performance and competitive ability of grasses as a response to different defoliation treatments, along with many other variables that affect competition within pasture swards.

2.5.2.6 Animal Factors

The productivity, botanical composition and interplant relationships in a pasture can be rapidly and substantially altered by grazing animals. This occurs as pasture species and cultivars differ in their response to defoliation, excretion, treading and seed dispersal processes by grazing animals (Sears, 1956).

The primary effect of the grazing animal on a pasture sward is that of defoliation. In addition to periodic removal of foliage, selective grazing can change the competitive balance existing between species. Selective grazing patterns are dependent upon the palatability, accessibility and the availability of the desired species. This aspect has been highlighted in research by many, including Langer (1973); Pineiro and Harris (1978b) and Sangster (1981). These studies illustrate the reduction of plant vigour and productivity of prairie grass under frequent grazing, due to its high palatability, height and low tillering habit. Thus continuous grazing either eliminates it or reduces its vigour and thus competitive ability. This creates difficulties in maintaining more palatable and preferred species within a continuously grazed sward (Pineiro and Harris, 1978b; Haynes, 1980). In contrast, some species such as *Phalaris arundinacea* are avoided by grazing animals (Marten and Jordan, 1974) which allows them to grow undisturbed and thereby gain competitive superiority within a sward.

In addition to grazing, treading and excretion by animals can also affect productivity, species balances and competitive relationships within a sward (Brougham, 1966; Edmond, 1970). Grass species such as *Lolium* and *Poa* are resistant to treading (Edmond, 1966; Watkin and Clements, 1978), which enhances their performance in a grazing situation. Excretion, especially urine of animals can depress the growth of pasture species, especially clovers and broadleaved components, thus decreasing their competitive ability. However, it has a stimulating effect on the growth of grasses, which gives them an advantage over other species in a sward.

Species and numbers of grazing animals also affect plant performance due to different feeding habits. All these effects build up to give certain species a competitive advantage in pastures. A comprehensive review on the effects of the grazing animal on pasture productivity, and composition has been presented by Watkin and Clements (1978), who highlight the impact of animals on pasture production.

In addition to the domestic grazing animal, insect pests of grassland species can have a bearing on plant performance and thus on competitive relationships between pasture species. In New Zealand, these include grass grub (*Costelytra zealandica*) Porina (*Wiseana* Spp.), Army worms, Argentine stem weevil (*Hyperdores bonariensis*) (Pottinger, 1973). These pests tend to show preference for certain grasses, which can affect competitive relationships. Although there is an extensive literature on the effects of pests on grass species, (e.g. Harris and Brock, 1972), it will not be reviewed as it is not relevant to the studies reported in this thesis.

2.5.2.5 Microbiological Effects

Soils under pasture contain some of the highest concentrations of roots of any agricultural system, with extensive microbiological activity (Barley 1970). Thus the rhizosphere of a pasture sward and its microbiological properties have a major effect on the growth and success of species in a pasture sward (Rovira, 1978).

Microorganisms which are external to the root can influence plant growth by affecting the growth and longevity of root hairs, release of growth promoting or inhibiting substances, the inhibition of nitrification, and in certain tropical grasses, by fixing nitrogen. Other organisms form invasive associations and are involved in symbiotic nitrogen fixation and more efficient extraction of nutrients, especially phosphorus, by forming endotrophic mycorrhizae (Barley, 1970; Rovira, 1978). In the process of competition between grasses, microbial effects are mainly seen in terms of nutrient utilization and to a lesser extent as harmful interactions. Influences of mycorrhizal infection on competition for phosphorus by *Lolium perenne* and *Holcus lanatus* have been shown by Fitter (1979) and the general concept of microbial effects on pasture plants has been presented by Rovira (1978).

2.5.3 GENERAL CONSIDERATIONS

Of the many factors of the environment, light, nutrients and water are considered the most important resources for plant growth. However, it becomes very difficult in practice to locate mechanisms of interference in plant mixtures. The existence of one limiting factor may well enhance the utilization of another factor to increase growth of a component species, which can conceal the actual process of interference (Donald, 1963). External factors other than growth requirements also affect

competition between pasture plants, which makes it more difficult to establish the actual mechanisms of competitive interaction.

Most experiments designed to discover causes of competition in pasture species and cultivars have been conducted with binary mixtures. Evidence from these experiments has emphasized the interactive effects between supplies of different growth resources. The development and use of partitioning techniques in competition studies (e.g. Donald, 1958; Aspinall, 1960; Rhodes, 1967; Cocks, 1969; and Snaydon, 1979) and the use of isotopes (Hall, 1974a,b) give an insight into the importance of competition between roots and shoots of species mixtures in determining the overall competitive relationship. These studies, especially the technique of Snaydon (1979) have strengthened the methods for isolating factors and the nature of competitive relationships in herbage mixtures. However, caution still needs to be taken in emphasizing the effect of a single factor or resource in determining competitive relationships in herbage mixtures, as interactive processes may still mask the actual mechanisms of interference between species.

2.6 NATURE OF COMPETITION WITHIN HERBAGE ASSOCIATIONS

Competitive interactions for a single growth requirement may occur in a specific situation, but generally competition between plants develops for many growth factors due to interactive effects (Donald, 1963). With the development of young seedlings in a species mixture, the roots intermingle. This initiates competitive interactions within the plant association before the leaves of the seedlings shade each other to develop competition for light. Thus in an establishing herbage community, root competition for either nutrients, water or both commences before competition for light begins (Weaver, 1926; Troughton, 1957; Donald, 1958; Aspinall, 1960; Rhodes, 1968b, 1970; Cocks, 1969). Subsequently, with the growth of the leaf canopy light becomes a factor of competition (Milthorpe, 1961).

It is reasonable to expect that neighbouring plants in an established sward may shade one another and thus develop a mutual or more generally a one-sided suppression of growth due to deprivation of light. These effects have been illustrated by many scientists, and more recently reviewed by Rhodes and Stern (1978). Similarly, the roots of competing

plants may draw on limited resources of nutrients and/or water from the soil and thereby affect the growth of each others root system (Harper, 1977). This development of competitive interactions between either the root systems, or shoot systems or both can be identified as aspects of competition between herbage species. The occurrence of such competitive effects within herbage mixtures has been demonstrated by many workers using partitioning techniques to separate shoot and root competitive effects (e.g. Donald, 1958; Schreiber, 1967; Lambert, 1968; Rhodes, 1968b; Cocks, 1969; King, 1971; Snaydon, 1971; Eagles, 1972; Barret and Campbell, 1973; Remison, 1978; Remison and Snaydon, 1980).

2.6.1 COMPETITION BETWEEN SHOOT SYSTEMS OF HERBAGE MIXTURES

Competition between shoot systems primarily occurs for light, as carbon dioxide is generally present in sufficient quantities for photosynthetic processes within the plant canopy (Donald, 1963; Harper, 1977). The reduction in photosynthetic capacity due to competition for light can impair the growth and development of plants when compared with plants growing under adequate light. The extent of damage caused by competition for light will depend on the stage of plant growth and the degree of shading, as overlapping of plant canopies does not shade plants uniformly (Rhodes and Stern, 1978).

Competitive relationships for light in herbage grasses have effects on both shoots and roots of species in mixtures. The effect of competition for light on the development of roots has been shown by Asher and Ozanne (1966). In terms of shoot growth, light and its intensity has an effect on tiller production, as reported by many, including Mitchell (1953a,b, 1954, 1955); Donald (1958); Patel and Cooper (1961); Langer (1963); Langer *et al.* (1964); Thomas and Davies (1978); King *et al.* (1979) and Alberda and Simba (1982). The effect of competition and mutual shading on tillering in herbage grasses has also been highlighted (e.g. Donald, 1958; Rhodes, 1968b; Kays and Harper, 1974; Ong, 1978; Ong *et al.*, 1978). The rate of leaf appearance in grasses is also affected by the reduction in light intensity within a grass canopy (Mitchell, 1953 a,b; Patel and Cooper, 1961; Anslow, 1966). Rhodes (1968a) found that all components of seedling shoot development, were affected to different degrees by competition. It was also seen that the rate of leaf appearance per tiller was less affected by competition

for light (Rhodes and Stern, 1978).

Trenbath (1976) reviewing published reports listed characters that confer competitive advantage for light. These were - rapid expansion of a tall canopy, large leaves to minimize penumbra effects, leaves horizontal under overcast conditions and plagiotropic under sunny conditions, leaves with C_4 photosynthetic pathway, a low transmissivity, leaves forming a mosaic leaf arrangement, a climbing habit, a high allocation of dry matter to building a tall stem and rapid stem extension in response to shading. These will hold true under general circumstances, but in specific plant combinations, such as populations of similar species or cultivars, more subtle differences in shoot morphology may confer a competitive advantage (Rhodes and Stern, 1978). While many publications are available on competition between pasture species for light (Risser, 1969), much less precise information is available on competitive relationships for light in grass associations. Competitive success of grass species in pasture populations have generally been attributed to tall and erect growth habits, as seen in reports by Lodge (1964); Grime (1966); McCown and Williams (1968); Eagles and Williams (1969) and van den Bergh and Elberse (1970).

In most situations, light alone does not give a significant competitive advantage to a species, due to the presence of competitive stress between root systems. This is often more important in the establishment phase (Rhodes, 1970). Thus caution needs to be taken in the interpretation of the results of competition experiments where emphasis is placed on competition for light, as most experiments with grass species differentiating shoot and root competition highlight the more important effects of root interactions in determining competitive relationships in mixtures (e.g. Donald, 1958; Rhodes, 1968b, 1970; Cocks, 1969; Eagles, 1972; Remison and Snaydon, 1980).

2.6.2 COMPETITION BETWEEN ROOT SYSTEMS OF HERBAGE SPECIES

When the seedlings of sown pastures are first emerging, their roots will be far apart and the uptake of resources by one root system will not interfere with supplies of growth requirements of its nearest neighbour. Within a short period of time, the root systems intermingle and as the soil becomes crowded, competition for supplies begins, before

shoot systems interact (Trenbath, 1976). This competitive effect between roots is further magnified as root surface areas may be over a hundred times greater than that of the shoot systems (Dittmer, 1937), which inevitably leads to crowding of roots in the soil. In experiments conducted in containers, this crowding effect can be expected to be magnified.

Early literature attributes the effects of competition on plant growth to both shoot and root interactions (e.g. Blackman and Templeton, 1938), but without any quantitative data to confirm the claim. Donald (1958) pioneered investigations of the relative roles of root and shoot systems in competitive situations. Thus, on the basis of evidence so far available, root competition is considered to be more important than shoot competition (Donald, 1958; Aspinall, 1960; Rhodes, 1968b; Cocks, 1969; Snaydon, 1971; Remison, 1978; Remison and Snaydon, 1980; Scott and Lowther, 1980).

2.6.2.1 Soil and Plant Factors Affecting Root Competition

The reaction of plants to mineral elements is a major determinant of their natural habitat and ability to survive and grow in ecosystems modified by man. Plants obtain their mineral and water requirements from the substrate which retains these resources and has local characteristics of retention and supply. Most soil minerals are held by some physical or chemical linkage to insoluble soil constituents and are in a rapid dynamic equilibrium with ions in the soil solution. The uptake of a nutrient by a root surface establishes a lower concentration within the vicinity of the root, which in turn develops a diffusion or concentration gradient towards the root by which the concentration is re-established (Nye, 1966; Dunham and Nye, 1974). The rate of flow of nutrients through diffusion or mass flow in water to the vicinity of the root and the uptake of these nutrients by roots varies with different nutrient ions. The more mobile ions (e.g. Nitrate) (Bray, 1954) are taken up at faster rates (Brewster and Tinker, 1970) than the relatively immobile phosphorus and potassium ions which are held in the soil colloidal system (Barley, 1970). Potassium is buffered as it is held within the soil colloids and local depletion by root absorption is made up by the release of this bound potassium (Nye, 1968). Thus

the zones of depletion around active roots for mobile nutrients enlarge faster and overlap more rapidly (Bray, 1954; Andrews and Newman, 1970). This overlapping of depletion zones around root systems of different species causes competition for nutrients within that plant association.

Depletion zones of mobile nutrients such as nitrates are very large, as these ions are carried passively in soil water and are rapidly taken up (Barley, 1970). Nutrients such as phosphorus, ammonium, calcium and potassium are strongly absorbed onto surfaces of soil particles and are in low concentrations in soil water, and only move by diffusion (Olsen and Kemper, 1968; Brewster and Tinker, 1970). Studies on depletion zones of nutrients show this aspect clearly. Bhat and Nye (1973) reported that phosphate depletion zones may extend only 0.7 cm from the root surface after one week, while water has been observed to start flowing towards root systems from 12 cms away in less than 6 days in a wet soil (Dunham and Nye, 1973).

Overlapping of depletion zones causes competitive effects for soil resources in a plant community by the interference of one species in another's absorption zone. This effect has recently been studied using electrical analogues (Nye and Tinker, 1969; Sanders *et al.*, 1970; Baldwin *et al.*, 1972, 1973). These studies show that competitive effects between plants are dependent upon rates of nutrient diffusion, nutrient absorbing power of roots and root volume and density. Studies by Cornforth (1968); Andrews and Newman (1970) and Newman and Andrews (1973) on nitrogen and phosphorus uptake by wheat plants with different root densities exemplify these theories.

If the narrowness of the depletion zones for nonmobile nutrients tends to prevent interference between individual roots except at very high densities, competition for these nutrients is also prevented (Baldwin *et al.*, 1972). Andrews and Newman (1970) highlight this aspect in terms of competition for phosphorus between wheat plants. However, competition for phosphorus in pastures which generally have high root densities has been reported by Donald (1963) and Snaydon (1971). As the principles that apply to competition between individual roots of a plant can be related to competition between plants, the distribution of roots in the soil and the relative volume of active roots of a plant or

species has a great influence on the intensity and outcome of competitive effects between plants. If the component species of a plant association have similar characteristics as in a grass or cereal mixture, the mobile nutrients in the soil where the roots overlap are shared in proportion to the active root length of the components present in that volume of soil (Andrews and Newman, 1970; Baldwin *et al.*, 1972). In addition, as the degree of overlap between root systems determines the intensity of competitive effects (Cable, 1969; Trenbath, 1975), a knowledge of the distribution characteristics and density patterns of roots of component species in plant associations becomes an important factor in studying root competition in mixtures. This is further emphasized by the good correlation often observed between root abundance and uptake activity for nutrients within a species (Nye and Foster, 1961; Barley, 1970).

Although the soil system retains nutrients required for plant growth in both soluble and insoluble forms, all nutrients are not available for plant utilization. Studies by Weirsum (1961) show that both pasture and crop plants do not utilize the available soil volume and thus all nutrients in the soil system are not made available for plant growth. Subsequent work by Hall (1974a) on the utilization of labelled nitrogen by mixtures of forage species in pot cultures, shows that while it is assumed that soil nitrogen will potentially be available for both species, the uptake of a given species will depend on its relative uptake ability, rate of root elongation and the number, size and efficiency of roots. In addition, a part of the total soil nitrogen is not available to plants (Hall, 1974a). Thus even under apparently adequate nutritional conditions, the quantity of nutrients available to plants may become limited. Thus competition will inevitably develop for this resource between species with different nutrient uptake and utilization capacities and active root volumes, even at an early stage of growth. This effect can be further accentuated in soils or rooting media with low nutrient holding capacities and in pot cultures where the restricted volume of soil limits the nutrient availability.

A process similar to luxury consumption of soil resources is also possible in plant associations. Excessive quantities of nutrients over immediate needs may be absorbed by a plant in its growing stage and be redistributed within the plant. Williams (1955) has shown that 90% of total nitrogen and phosphorus contents of mature plants of cereals are

taken up before the plant has reached 25% of its final dry weight. In addition to luxury consumption, the success of a species in competition for a soil factor usually leads to the enhanced consumption of other factors (Litav and Seligman, 1970; Hall, 1974b). If the availability of these required factors is low within the soil, competitive effects are enhanced. This is often encountered in mixed pastures, as shown by Blaser and Brady (1950); Walker and Adams (1958); Stern and Donald (1962); Trenbath (1976).

One of the most important factors determining root competition among plants is the soil volume exploited by the root system. Studies conducted on the effect of soil volume on plant growth show that both shoot and root growth are affected by reductions in soil volume (Stevenson, 1967). This reduction in growth is attributed to crowding effects developing between roots and thereby causing interference to the uptake mechanisms of resources for plant growth. The concept of "effective soil volume" (Stevenson, 1967) shows that in most situations and especially in pot cultures, the effective soil volume needed for unhindered plant growth is not reached. This leads to sub-optimal plant growth which magnifies competitive effects. Most of these studies have been reported on water uptake, but due to the intimate relationship that exists between water and nutrient uptake, similar theories can be developed for nutrient uptake (Stevenson, 1967). In addition, within a restricted soil volume, faster growing roots occupy a greater soil volume, which retards the growth and resource absorption by slower growing species. Theories and subsequent experimentation on root competition reported by Berendse (1979, 1981, 1982) show that intensive competition occurs within a given rooting zone for growth requirements by pasture plants. The faster growing species is seen to exploit the environment to its benefit, and gain at the expense of slower growing species, even at apparently adequate nutrient levels. When rooting depths differ, root competition is seen to have little effect in determining the performance of species in mixtures, as roots obtain their resources from different soil depths (Trenbath, 1976; Berendse, 1981).

Early research reviewed by Troughton (1957) illustrates that while considerable variation exists due to environmental conditions, root growth of herbage grasses is generally restricted to the surface layers of the soil. Similar results have also been reported by Burton (1943) and Gist and Smith (1948) in the United States of America and at Hurley,

England by Garwood (1966). Garwood (1966) stated that while the exact quantity of roots depended upon the supply of nitrogen and water, the proportion of roots in the top two inches of a 30 inch sample was between 60-80% of the total quantity. 50-60% of the root quantity was found in the top inch of a 6 inch sample. 40-50% of the roots of a pasture sward 6 months after sowing was also found in the top inch of a 6 inch sample. Techniques to study the spatial distribution using isotopes (e.g. Litav and Harper, 1967; Ellern *et al.*, 1970; Baldwin and Tinker, 1972) have demonstrated extensive intermingling of root systems in mixtures within the upper soil layers. Baldwin and Tinker (1972) also report the reduction of roots in one species due to the presence of others. Thus in grass mixtures, competition within the root zone becomes intense due to the similar rooting patterns, rooting zones and similar requirements for growth resources from the soil.

2.6.2.2 Importance of Root Competition in Herbage Associations

Competition between grass species in terms of root interactions has been studied by many scientists. Milthorpe (1961) suggested that the superior competitive ability of *Lolium* spp when compared with *Festuca pratensis* was associated with faster root growth of the former species, in mixtures of the two species. In studies of O'Brien *et al.* (1967), the advantage of a hybrid of tall fescue x ryegrass in competition with either parent was partly due to its ability to exploit water and nutrients from deeper regions of the soil. de Wit *et al.* (1963) reported theories of root competition for nutrients. Studies of Litav and Wolovitch (1971) show root competition to be the major factor governing the success of *Avena sterilis* when grown with *Oryzopsis holciformis*, and research of Eagles (1972) shows that root competition was the more important factor determining the performance of cocksfoot cultivars when grown in mixtures. Root interactions in terms of phosphorus uptake by *Lolium perenne* and *Agrostis tenuis* have been reported to affect their performance in mixtures (Fitter, 1976). Kujira and Kanda (1977) also studied competition in *Lolium perenne* from a viewpoint of root behaviour and reported that root competition in terms of physiological activity of the root system has a deterministic effect on the performance of two cultivars in mixtures. Recently, Remison and Snaydon (1978, 1980) highlighted the importance of root interactions in determining plant performance in grass mixtures and illustrated seasonal changes in root competitive ability in binary mixtures of grass species. The results of Newbery and Newman (1978) show that root interactions promote co-existence of species, especially in nutrient poor soils.

Root competition is also seen to be important in seed production of grasses, due to its effects on plant weight (Lambert, 1968). King (1971) has demonstrated root competition between established and establishing grasses. Harris (1967) and Harris and Wilson (1970) reported competitive effects between roots for water among grass seedlings, where *Bromus* species penetrated the soil before *Agropyron* species to utilize the available soil moisture under low moisture regimes.

Most reviews and experiments on herbage competition emphasize the importance of root interactions. These relationships have been explained in many ways, such as differential nutrient uptake, utilization of similar rooting zones, effective soil volumes and allelopathic effects. In addition, competition between roots has been reported to begin earlier than shoot competition due to the more rapid development of the root system. While most studies have been associated with nutrient relationships, due to the close affinity between nutrient and water uptake, similar situations will develop in competitive relationships for water (Stevenson, 1967; Trenbath, 1976; Harper, 1977). Thus it can be considered that root competition between similar species such as grasses growing in mixtures determines the outcome of competitive relationships to a large extent. This effect will be most prominent in the early stages of plant growth, when shoot systems do not overlap.

In established swards, frequent grazing allows light penetration, thus minimizing competition for light. However, due to intermingling of root systems, root competition can have an effect on the regrowth of the shoot system. Under conditions where pasture is conserved *in situ* and competition for light occurs over long periods, the effect of shoot competition may override the effect of root competition.

2.6.3 INTERACTIONS BETWEEN SHOOT AND ROOT COMPETITION

It has long been postulated that competition for each of two factors will develop interactive processes, so that the aggressive species will gain competitive advantages exceeding the sum of effects which occur when each factor operates alone (Clements *et al.* 1929). Chippendale (1943) and more recently Trenbath and Harper (1973) highlighted this effect. Trenbath (1976) cites many situations where interactions occur in competitive situations between species, due to smaller and less efficient roots having an effect on shoot growth or slower shoot development affecting root growth. Asher and Ozanne (1966) also indicate

effects of leaf shading on root development in grasses.

It is extremely difficult to study competitive interactions involving two or more factors under normal field conditions (Donald, 1963). Experiments can be designed to show the interaction of nutrients and water on grass growth. However, such studies take no account of the influence of these factors on the competitive relationship for light, which may be of prime importance in determining the outcome of competition between root systems. Due to these difficulties, Donald (1958) used partitions in his experiments, and this technique has subsequently been developed by Snaydon (1979). These experiments highlight the relative importance of root and shoot competition and their overall effect on the outcome of competition between pasture species.

The occurrence of competitive interactions for one growth factor between species in a mixture can develop a series of interactions between the component species. This can potentially affect most of the growth activities of the species and can develop into very complex situations which become difficult to identify. Donald (1958) presented these interactions clearly (Table 2.1), and as seen, these interactions determine the final outcome of competition between grass species in mixtures.

Table 2.1 The interactive process of competition between root and shoot systems of herbage plants

Effects	Competition for Light only	Competition for Nutrients only	Competition for both Light and Nutrients
Direct	(a) Intrusion of A into light environment of B <i>Reduced light supply for B</i>	(b) Intrusion of A into nutrient supply of B <i>Reduced nutrient supply for B</i>	B suffers: <i>(a) Reduced light supply (c) Reduced nutrient supply</i>
Indirect	(b) As a result of reduced light supply <i>B has reduced capacity to exploit its own nutrient supply</i>	(d) As a result of reduced nutrient supply <i>B has reduced capacity to exploit its own light supply</i>	<i>(b) Reduced capacity to exploit the nutrient supply (d) Reduced capacity to exploit the light supply.</i>
Interactions	Interactions of (a) and (b)	Interaction of (c) and (d)	Interactions <i>ab, ac, ad, bc, bd</i> and <i>cd</i> plus any higher order interactions

From Donald (1958)

2.7 MEASUREMENT OF PLANT COMPETITION

Many different types of competitive interactions between plants have been identified (Harper, 1977) and thus many methods of experimentation and analysis have been developed to study competitive relationships between plants. The complexity of the technique adopted to study competition depends on the complexity of the interactions seen in a particular situation. Thus in general ecological studies of natural vegetation, complex models are used, while more simple techniques are adopted to evaluate combinations of crops, pastures and weed-crop interactions (Spitters, 1979).

Experiments designed to evaluate competitive relationships measure plant performance in a given situation. Thus, these experiments identify the outcome of a competitive relationship in terms of a plant's reaction to a given situation.

In cultivated crops, yield-density relationships within a species or cultivar are well identified and documented (Harper, 1977). In mixed cropping, design of experiments to identify competition and techniques of analysis has been comprehensively reviewed by Mead (1979); Mead and Stern (1980); Mead and Riley (1981) and Spitters (1980). Spitters and van den Bergh (1982) have reviewed the methods of studying weed-crop competition.

Methods of studying competition in pastures, and the design of such experiments follow similar patterns to those of crop and weed-crop combinations. These designs have generally been developed to include two species or cultivars.

2.7.1 EXPERIMENTAL DESIGNS FOR STUDYING PLANT COMPETITION

Two major types of competition experiments have been developed to study interspecific competition (Harper, 1977; Spitters and van den Bergh, 1982). Many modifications of the initial designs are currently used both in ecological and agronomic research to study competition in crops and pastures.

2.7.1.1 Additive Experiments

In additive experiments, two species are grown together, and the density of one is maintained constant while that of the other is varied. The species of which the density is held constant is regarded as the

indicator. Thus, there is always a change in density of the overall plant population in these experiments.

Additive experiments are commonly used to study the relative aggressiveness of one or more species to a given indicator species. In the simplest form, additive experiments become phytometer experiments in which a single indicator plant is placed in a stand of a second species (Harper, 1977).

Additive experiments are generally used to study effects of weeds on crops, where a weed population is added to a given stand of crop plants (Spitters and van den Bergh, 1982). Studies of this nature have been reported by Trenbath and Harper (1973); Trenbath (1974b, 1975). Harper (1977) reviewing such studies states "Many examples of carefully designed additive experiments show that the order of aggressiveness of a group of species is independent of the test species; but it is probably dangerous to assume this as a general rule without further experiments".

The importance of the additive design lies in its ability to answer more directly the agricultural question "to what extent is the yield of a crop reduced by the presence of weeds?" However, the disadvantage of this method is the absence of adequate mathematical models to quantify competition effects and to make predictions on various competitive situations (Spitters and van den Bergh, 1982). In addition, the analysis of additive experiments becomes difficult as the proportional composition and the density of the mixture changes with the introduction of a species. These changes tend to completely confound the competitive effects (Harper, 1977).

Recently, Martin (1973), Veevers and Boffey (1975); Boffey and Veevers (1977); Veevers (1978) and Veevers and Zafar-Yaab (1980) have presented balanced designs for studying two component competition experiments. In these experimental designs, plants of the two species are arranged in a hexagonal grid, so that for plants of one species, the neighbouring plants of the second species vary between zero and six. These designs are considered suitable for many types of experiments - e.g. 'de Wit' replacement series, mixed cropping trials, two component plant breeding trials and density and/or spacing experiments, where competitive interactions have an effect on the performance of species

(Veevers and Zafar-Yaab, 1980).

2.7.1.2 Substitute (Replacement) Experiments

In most fields of competition research, the substitutive or replacement series experimental design is used. The main characteristic of this design is that the proportions of the two species A and B in a mixture are varied while the overall density (A+B) is maintained constant. Thus a range of mixtures is generated, beginning with the monoculture of species A, progressively replacing plants of species A by those of species B until a monoculture of species B is obtained. This experimental design was introduced by de Wit (1960) to study competition in cereal mixtures and now has been extended widely to accommodate cereal, cereal-legume, pasture and crop-weed mixtures.

The replacement series experiments developed by de Wit (1960) identify competition between two species for "biological space". The term "space" embraces all growth requirements for which plant species compete. However, due to the interactive nature of the process of competition for these factors, it becomes difficult to separate the components of competition by the method of the replacement series first suggested by de Wit (1960).

Competitive interactions occur both above and below ground, and the final outcome of competition between the two species is a result of both shoot and root competition. It is of value therefore, to separate root and shoot effects and experimental designs capable of achieving this have been developed.

Donald (1958) first developed a technique, where pots were partitioned both above and below ground. This allowed root systems of two species to exploit the same soil volume while their canopies were prevented from intermingling and shading each other or conversely the canopies to intermingle freely but the root systems were separated. Aspinall (1960) extended Donald's technique, but both these techniques were based on the additive experimental design used for competition studies, which is characterized by the addition of one species to a population of another. A similar technique was also used by Wilkinson and Gross (1964).

The most widely used experimental technique to study interspecific competition between two species is that of de Wit (1960), based on the replacement series principle. Thus Donald's technique was modified to allow either addition or substitution of component species (Schreiber, 1967; Snaydon, 1971). Furthermore, its modifications and improvements allowed a constant effective density across treatments and the collection of more information on the nature of competitive interactions.

Since the development of the improved techniques by Schreiber (1967) and Snaydon (1971), many studies have been conducted using this design to evaluate the relative importance of root and shoot competition in pasture mixtures, and to determine the nature of interspecific competition for particular growth requirements between pasture grasses (Lambert, 1968; Rhodes, 1968b; Cocks, 1969; Barret and Campbell, 1973; King, 1971; Litav and Wolovitch, 1971; Eagles, 1972; Remison, 1978; Remison and Snaydon, 1978, 1980). Similar studies have been carried out with legumes (e.g. Scott and Lowther, 1980). The major part of these competition studies was conducted with microwards established either in boxes or pots.

The use of populations planted in rows to study the response of plants to competitive situations within communities was a significant development, as the study of competition essentially involves the individual plant and its response to modifications of the environment by other plants (Black, 1966). Thus, Snaydon (1979) introduced a more effective method of partitioning to study the competitive relationship between plants. The most important advantage of this technique was the ability to vary the relative densities of interacting species, yet separating shoot and root interactions. In addition, the presence of partitions in all treatments gave a uniform environment to both mixtures and monocultures. This allowed the de Wit (1960) concept of competition for space to be separated into root and shoot components. Thus Snaydon's (1979) technique unified the complimentary experimental designs and analyses of Donald (1958) and de Wit (1960).

Partitions, especially above ground were reported to have a major effect on the micro environment (Warren and Lill, 1975), by shading and affecting plant growth (Rennie, 1974). This effect above ground

has been successfully reduced by the use of partitions with reflective surfaces. The successful use of 'sisalkraft' for this purpose has been reported by Remison (1978) and Remison and Snaydon (1978, 1980). Although other limitations of this partitioning technique have been cited by Snaydon (1979), it can be considered the best currently available method for partitioning plant competition into root and shoot components.

2.7.2 METHODS OF ANALYSING PLANT COMPETITION

The literature on plant competition shows that only a limited range of experimental designs have been used in the study of plant interactions and competition. However, many methods of analysis and interpretation are observed (Trenbath, 1978).

2.7.2.1 Qualitative Evaluation

The earliest studies of competition between plants were qualitative and the data was presented in tables without further analysis, or a graph was used to present the data. This is illustrated by the studies of Sakai (1955). Subsequently the methods of presenting data in a graphical form were developed to evaluate plant growth in species mixtures, and to assess intercropping methods and competitive relationships (Pearce and Gilliver, 1979).

2.7.2.2 Analytical Models

In addition to factorial designs and models which have been used by agricultural scientists from very early times, competition experiments are also analysed with either "additive" or "proportional" models (Trenbath, 1978; Spitters, 1979).

2.7.2.2.1 Factorial Models:- The technique of analysis of variance is used in competition experiments to evaluate the performance of a species in a mixture relative to its monoculture. In partition experiments it is used to evaluate the effects and importance of shoot and root competition. This technique provides a method of differentiating between treatments, including experimental error. It also becomes important in establishing the significance of interactions between each of the treatments, as seen in studies reported by Williams (1962) and Langer (1973). The general use of this technique for experimental data analysis is well described by Cochran and Cox

(1957), Snedecor and Cochran (1967) and Steel and Torrie (1981), and these principles can be used for competition experiments.

More specifically, analysis of variance has also been used by McGilchrist and Trenbath (1971) and Gleeson and McGilchrist (1978) to evaluate competitive indices.

2.7.2.2.2 Additive Models:- Trenbath (1978) described the additive model thus - "It is based on the expectation that the gain of per-plant yield by the aggressor (e.g. genotype i) in the mixture ij over that in its monoculture is equal to a corresponding loss by the subordinate (genotype j) in the mixture compared with its monoculture". Mathematically, this can be expressed as

$$Y_{ij} - Y_{ii} = -(Y_{ji} - Y_{jj})$$

where Y_{ij} is the yield per plant of i in mixture with j and Y_{ii} and Y_{jj} the yield per plant of i and j in monoculture.

Spitters (1979) grouped the diverse additive models into three classes according to the experimental design.

(A) Fitness experiments - The term "fitness" is generally defined as the ability to produce fertile "descendants". These models are basically devised to study natural selection, and thus are considered not appropriate to describe competition effects (Spitters, 1979).

(B) Replacement series experiments - These are substitution series of two components, which are represented by two monocultures and a number of intermediate mixtures, all at equal density. In these experiments, the response of a given species to different numbers of the associate species is considered to be additive (Spitters, 1979), and generally the performance per plant is regressed against the number of plants of the other component in the mixture (Sakai, 1955, 1957). In such regressions, a positive slope presents the superior performance of the component evaluated. This performance is enhanced by increasing numbers of the associate species, and hence this species can be regarded as a strong competitor. A negative slope indicates weak competitive

ability and a deviation of the regression from linearity shows a departure from additivity (Spitters, 1979).

(C) Competition diallels:- This technique is generally used to explore the manner in which plants interact. Thus sets of genotypes are grown in all possible pair combinations, together with monocultures (Trenbath, 1974a). In addition, competition diallels are considered the most appropriate designs to estimate and to test the additive effects and effects indicating deviation from simple additivity (Spitters, 1979). To achieve these objectives, a uniform plant density is adopted in all treatments and the proportions of the genotypes in mixtures is in the ratio of 1:1.

Yield data from mixture diallels provide information on aggressiveness and productivity of plants of each genotype studied. Estimates of average aggressiveness are used to test hypotheses concerning fitness and to identify morphological or physiological components of competitive advantage and predict likely shifts in components of sown pasture swards (Trenbath, 1978). Competition diallels are also used to evaluate "general and specific combining abilities" of mixture components (Trenbath, 1978; Spitters, 1979).

Many methods of analysis have been developed for competition diallels, and the "genealogy" of the development of techniques has been presented by Trenbath (1978). The techniques used by researchers include additive models in combination with analyses of variance to test the significance of competitive effects and departures from additivity, as in studies by Williams (1962). Another method of competition diallel analysis in terms of genetic parameters, is the regression of array covariance on array variance, which is used by Durrant (1965); England (1965); Harper (1965); Norrington-Davies (1967, 1968, 1972); Hill and Shimamoto (1973) and Wright (1975). Analyses based on a linear regression of yield of each genotype on an environmental index is seen in studies of Wright (1971); Breese and Hill (1973) and Hill (1973). Similar studies have also been reported by Harris (1977) and Harris and Sedcole (1974). More recently, Gleeson and McGilchrist (1978, 1980) developed a technique to analyse plant competition data from incomplete mixture diallels and mixture diallel exper-

iments with unequal proportions of genotypes. The technique of diallel analysis in competition studies is comprehensively reviewed by Hill and Shimamoto (1973); Trenbath (1978) and Spitters (1979).

2.7.2.2.3 Proportional Models:- Trenbath (1978) defined proportional models thus - "The proportional model is based on the expectation that the proportional gain of per plant mixture yield in the aggressor is equal to a corresponding proportional decrease in the subordinate, compared in each case with per plant yields in the genotypes' own monoculture".

It is expressed mathematically as

$$\frac{Y_{ij} - Y_{ii}}{Y_{ii}} = \frac{-Y_{ji} - Y_{jj}}{Y_{jj}}$$

where Y_{ij} is the yield per plant of i in mixture with j and Y_{ii} the yield per plant of i in monoculture. This model is seen to be appropriate for a wide range of competition experiments (Spitters, 1979).

The first use of a proportional model to determine competitive ability is considered to be that of Stadler 1921 (cited by Spitters, 1979). However, the most comprehensive proportional model developed is that by de Wit (1960). This model is considered appropriate to a diversity of competition experiments such as binary mixtures and multi-component blends of species, and the replacement series where the relative frequency of species composition varies (Spitters, 1979). The theory of de Wit's model was subsequently extended to accommodate the concept of Relative Yield Total (RYT) by de Wit and van den Bergh (1965). Dynamic simulation of the process of competition with time was also presented by Baeumer and de Wit (1968) and de Wit (1970).

Many types of models, both additive and proportional have been developed to analyse plant competition. The different types of models reported in the literature include those of Hill (1973); Leon and Tumpson (1975); Baldwin (1976); Torssel and Nichols (1976); Jagannath (1978); Smith et al. (1981) in addition to those cited earlier. Thomas and Stepler (1970) also reported a method of presenting plant competition as population pressure upon a plant. Theoretical models to simulate plant competition have also been developed (e.g. Trenbath, 1974c).

Trenbath (1978) and Spitters (1979) extensively reviewed many types of competition models. These reviews show that both additive and proportional models become essentially the same for 1:1 binary mixtures, when monocultures do not differ in yield. The incorporation of the relative yield concept in the proportional model removes any errors in the interpretation of results that are due to differences in yield of the two species grown in a mixture. Thus it is concluded that a strictly proportional model is adequate in the analysis of competition between genotypes belonging to the same or related species (Trenbath, 1978; Spitters, 1979).

2.7.3 THE DE WIT MODEL

De Wit (1960) developed this model to obtain a quantitative description and assessment of competition, based on experiments with oats and barley sown in mixtures. Subsequently the model was extended to analyse competition in grasses (de Wit, 1960; de Wit and van den Bergh, 1965). Van den Bergh (1968); Spitters (1979) and Brakhekke (1980) have subsequently reviewed this model extensively. Trenbath (1978) suggests that for ecological work, statistical analyses should be based on the rational model of de Wit (1960). Both experimental and simulated data show the importance of the de Wit model in providing a sound basis for analysing replacement series experiments. The value of using the de Wit model to analyse competition experiments is also highlighted by Spitters (1979).

The model developed by de Wit (1960) is based on the assumption that in a mixture of two genotypes, the 'biological space' occupied by the species is related to their seed frequency and competitive ability. The results of such substitutive experiments with two species, where the overall density is kept constant is best illustrated by a replacement diagram. Both absolute and relative yields can be plotted in replacement diagrams, against the relative seed frequency or plant composition in the mixture. Replacement diagrams based on yields of the species can take one of four forms (Figures 2.2 A-D) and can be illustrated in terms of per plant yields (Figure 2.2 E).

The Figure 2.2 A represents a situation, where the growth of two species in a mixture results in each contributing to the total yield in direct ratio to its proportion in the sward. Thus the two species do

not interfere with the growth of each other, or have similar intra and interspecific competitive effects. The situation presented by Fig 2.2 B (i and ii) is one where one species has a suppressing effect on the other, and both species utilize the same environmental resources. Thus interspecific competition is seen in this situation. The Figure 2.2C presents a situation where the species inhibit each other's growth due to mutual antagonism, thereby neither species contributing its expected share to the yield of the mixture. In contrast, the ability of both species to complement each other's growth and escape some measure of interspecific competition is seen in Figure 2.2 D. The replacement diagram where the per plant yield is plotted against the relative frequency of the plants of the other genotype is indicated in Figure 2.2 E. The more aggressive plant (I) is seen to yield better with increasing numbers of the other genotype.

The importance of replacement diagrams in highlighting competitive effects has been reported by many workers (e.g. de Wit, 1960; van den Bergh, 1968; Hall, 1974 a,b; Trenbath, 1978; Spitters, 1979). Wildin and Hall (1980) have extended the use of replacement diagrams to highlight trends in treatment responses, thereby allowing some comparison of responses between plant frequencies.

In competition experiments, the performance of a species in a mixture is related to its competitive ability. De Wit assumed the ratio of the yields of the species to be proportional to the ratio of the initial plant frequencies and the ratio of the monoculture yields. The proportionality coefficient K was termed the Relative Crowding Coefficient. Thus, as suggested by de Wit (1960) this relationship can be expressed as:-

$$O_{ab}/O_{ba} = (Z_a/Z_b) \cdot (M_a/M_b) K_{ab}$$

Where M_a and M_b are the monoculture yields of species A and B; O_{ab} the yield of species A in a mixture with B and O_{ba} the yield of species B in a mixture with species A; the relative frequencies of the species being Z_a and Z_b respectively. K_{ab} is the relative crowding coefficient of species A in relation to species B.

The relationship between yield of a species in a mixture and a monoculture, the proportions of both species in a mixture and the relative crowding coefficient are best expressed by the following equation.

$$O_{ab} = K_{ab} Z_a (K_{ab} Z_a + Z_b)^{-1} M_a \quad \text{for species A}$$

$$O_{ba} = K_{ba} Z_b (K_{ba} Z_b + Z_a)^{-1} M_b \quad \text{for species B.}$$

using the same symbols as above. However, if it is assumed that $K_{ab} \cdot K_{ba} = 1$ (de Wit 1960), where species compete for the same environmental resources, then

$$O_{ba} = Z_b (K_{ab} \cdot Z_a + Z_b)^{-1} M_b.$$

The relative crowding coefficient has also been termed 'competitive power' of a species (Bakhuis and Kleter, 1965). If the product of the relative crowding coefficients of two species exceeds unity, it indicates a situation where the species do not compete for the same space (i.e. - occupy different niches) or competition has very little effect on the outcome of the yield of the mixture. A value less than unity indicates a mutual antagonism between the two species.

The relative crowding coefficient determines the curves of the replacement diagrams. The k values depend on the experimental conditions and if the species have different growth rhythms, on the total plant density (de Wit, 1960).

Relative crowding coefficient is used in most competition studies, to indicate the competitive ability of a species. Due to its wide applicability, Thomas (1970) developed a model using least squares estimates to calculate the relative crowding coefficients of two interacting species. This model has been widely used (e.g. Harris, 1973, 1974; Harris and Thomas, 1970, 1972, 1973; Harris *et al.*, 1981b; and Ivens and Mlowe, 1980). More recently, Machin and Sanderson (1977) developed a different model to calculate the relative crowding coefficient by the theory of maximum likelihood estimates, and this has also been used in competition studies (e.g. Rossiter and Palmer, 1981; Burdon *et al.*, 1981).

The concept of relative yield introduced by de Wit and van den Bergh (1965) indicates the productivity of a species in a mixture in relation to its monoculture at similar densities. Thus in a mixture, the relative yield of a species presents a value for its relative performance when compared with the other species, thereby indicating the ability of the species to gather resources from the environment for its growth. Thus the relative yield becomes analogous to the relative crowding coefficient. The sum of relative yields of two species is termed the Relative Yield Total (de Wit and van den Bergh, 1965), which is similar to the product of the relative crowding coefficients. The concept of relative yield total is well described by van den Bergh and Braakhekke (1978).

The interpretation of relative yield total is similar to that of the product of relative crowding coefficients of species growing in a mixture. A RYT equal to unity indicates either overlapping ecological niches, competition for the same environmental resources or absence of competition. In such a situation where competition is seen, the reduction in the relative yield of one species is complemented by the increase in relative yield of the other. A RYT less than unity presents a situation of inhibitory effects where the resources of the environment are used less efficiently, and the reduction in the relative yield of one species is not compensated by the increase of the other. A RYT greater than one is indicative of the opposite situation where the species together exploit the environment more efficiently than either of the monocultures.

The relative performance of species in mixtures and the concept of relative yield total in different competitive situations can best be illustrated by replacement diagrams, as presented in Figure 2.3. Van den Bergh and Braakhekke (1978) and Braakhekke (1980) highlight the importance of studying competition by these techniques due to their ability to illustrate different competitive situations.

The calculation of relative yield total by de Wit and van den Bergh (1965) was based on the yield of monocultures (Y_{ii} and Y_{jj}) and the yield components of the two species in the mixture (Y_{ij} and Y_{ji}), thus

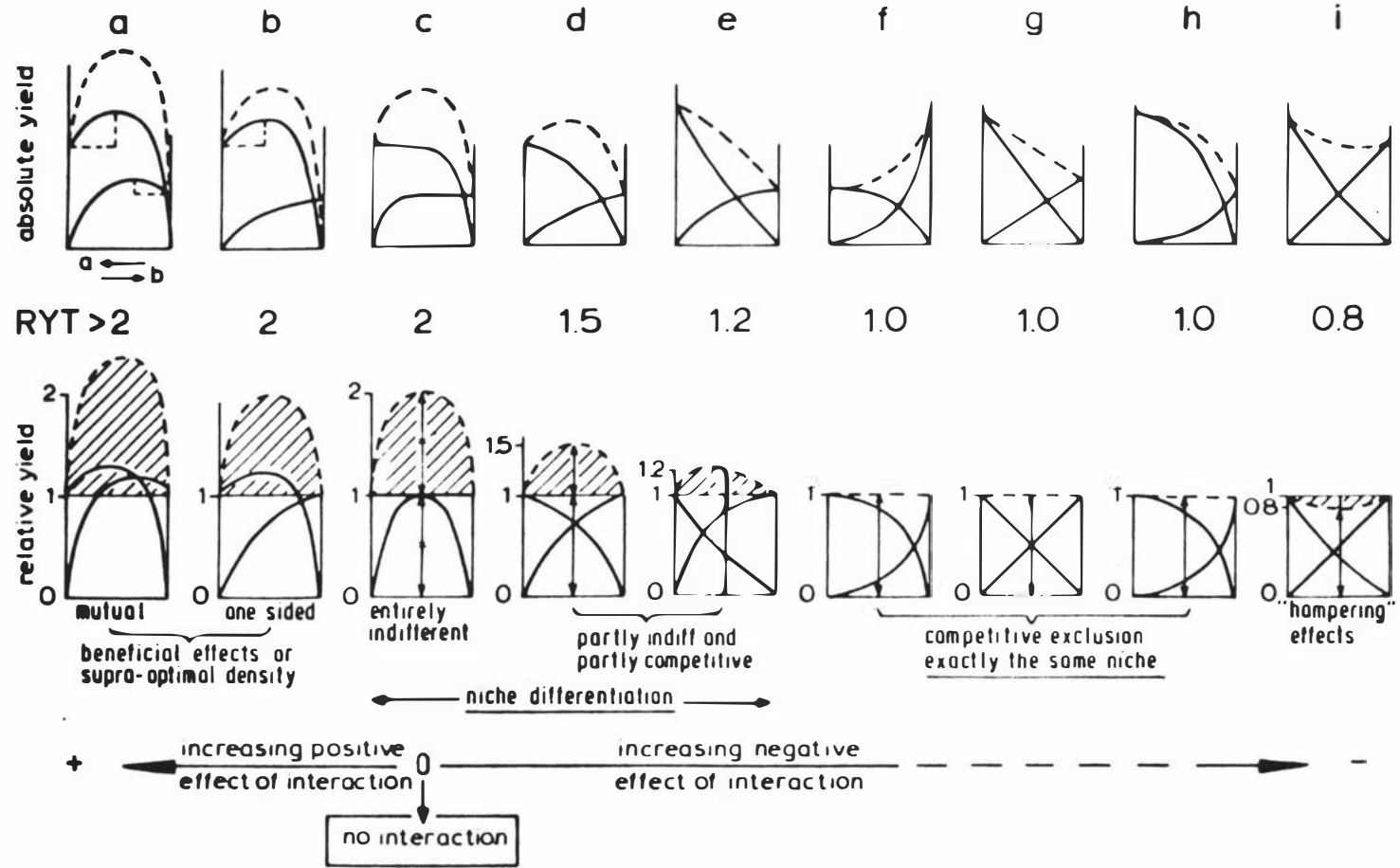


Figure 2.3 Relative Yield Totals and corresponding replacement diagrams illustrating different competitive situations (Braakhekke 1980).

$$\text{Relative Yield Total (RYT)} = \frac{Y_{ij}}{Y_{ii}} + \frac{Y_{ji}}{Y_{jj}}$$

The concept of using yields to determine relative yield total was later modified by McGilchrist and Trenbath (1971) to include per plant performance data such as dry matter production and tillering as a basic measure of mixture productivity. Thus the calculation of relative yield total based on McGilchrist and Trenbath (1971) was

$$\text{Relative Yield Total} = \frac{1}{2} \left| \frac{Y_{ij}}{Y_{ii}} + \frac{Y_{ji}}{Y_{jj}} \right|$$

where Y_{ii} and Y_{jj} are per plant productivity of the two species in monocultures and Y_{ij} and Y_{ji} the per plant productivity of each species when grown with the other.

McGilchrist and Trenbath (1971) also developed a measure to indicate the aggressivity of a species relative to another when both are grown in a mixture. This aggressivity index is also based on relative performance of a plant in relation to its monoculture, which removes any bias due to differences in monoculture performance of the two species. Thus using the same notations of relative yield, McGilchrist and Trenbath (1971) proposed the aggressivity index as

$$\text{Aggressivity} = \frac{1}{2} \left| \frac{Y_{ij}}{Y_{ii}} - \frac{Y_{ji}}{Y_{jj}} \right|$$

Thus the relative aggressivity of one species in relation to the other can be considered to be half the difference between the relative per plant performance of the two species when grown in a mixture.

Relative crowding coefficient, relative yield total and aggressivity are all indices which are derived from measurements at a given time. However, de Wit (1960) also developed indices to measure changes in competitive ability with time. These include the relative replacement rate (de Wit, 1960; van den Bergh, 1968), ratio diagrams (de Wit, 1960) and relative reproductive rates (de Wit, 1960; de Wit and van den Bergh, 1965).

The relative replacement rate of a species at a given time is evaluated with reference to an index harvest. If the yield of species I in the presence of equal numbers of itself is i_i and its yield in the presence of equal numbers of species J is i_j , the relative yield of I in mixture is $\frac{i_j}{i_i}$. Thus over a time interval m - n , the change in the two species in a mixture can be expressed as

$$f_{ij} = \frac{r_i^n / r_j^n}{r_i^m / r_j^m}$$

A gain by species I in the time interval between the m^{th} and n^{th} harvest is expressed by the relative replacement rates (f) being greater than one.

De Wit (1960) and van den Bergh (1968) cite two important considerations in terms of changes in density and composition of species over the time period of study. Harper (1977) also reviews these considerations and indicates caution in using relative replacement rates in that the yield of a mixture should have reached a ceiling yield and that relative yield total should equal unity. Nevertheless the relative replacement rate has been used successfully to demonstrate competitive effects and changes (de Wit, 1960, de Wit *et al.*, 1966 and van den Bergh, 1968).

The use of ratio diagrams and relative reproductive rates have been highlighted in literature (e.g. de Wit and van den Bergh, 1965; van den Bergh, 1968; Braakhekke, 1980) but are not used as frequently as the other indices.

De Wit's model, initially developed for cereal mixtures has been widely used in pasture research to determine competition between species. The wide applicability of the original model and its subsequent modifications encompass competitive situations in stands of single species, related species and also between species of different families. Amongst the many indices developed by the model, relative crowding coefficient and relative yield total have been widely used in competition studies in pastures. Aggressivity has also been used to determine competitive ability (e.g. Remison, 1978; Remison and Snaydon, 1978, 1980).

One of the basic assumptions of the de Wit (1960) model is that plants compete for the same "biological space", which is indicated by the product of relative crowding coefficients and the relative yield total being equal to unity. Most competition studies between cultivars of the same species or cultivars of related species show that in mixtures the component species generally compete for the same environmental resources. Studies on cereals by Sandfaer, (1970-quoted by Spitters, 1979), Blijenburg and Sneeep (1975) and Spitters (1979) indicate no significant departure of relative yield total from unity. Trenbath (1974a, 1978) reviewing literature found that the mean relative yield total for biomass production of 572 graminaceous mixtures was $1.027 \pm .006$, and concluded that under the conditions used, competition occurs for the same environmental resources. This concept was also highlighted by a simulated diallel model (Trenbath, 1978).

Due to the wide applicability of the de Wit model, it is considered to be the best suited to study competition effects between similar species such as grasses. Its importance and usefulness is highlighted by its wide use as a technique to study interplant competition.

2.8 CONCLUSION

Competitive effects between herbage species are seen to have a significant influence during the establishment and early growth phase of the sward. The outcome of such effects in the early growth phase is carried over into later stages of growth, as competitive hierarchies in general tend to be persistent (Harper, 1977), unless changed by major influences of environmental and/or external factors. Thus a knowledge of such competitive relationships between species growing in mixtures in the early growth stages will be of assistance in obtaining successful establishment and performance of pastures. A knowledge of these relationships would further enable the use of correct proportions of seeds of the desired species for pasture establishment, and the adoption of relevant management practices during early growth to obtain the required composition and balance in the established pasture.

To obtain an insight into competitive relationships between grasses, the component species must be grown in different combinations. Thereafter causal factors and the nature of competition that help establish such relationships need to be ascertained. This is done by

studying individual plants under competitive situations, and for this purpose such mixtures are grown in simplified environments. Thus the investigations presented in this thesis were developed to identify such competitive relationships, the causal factors and the nature of competition in binary mixtures of three grass species commonly used in New Zealand pastoral agriculture. Emphasis was placed on the early growth phase of the species due to its importance in determining subsequent production, and the de Wit model was used to identify competitive relationships between the selected species and to determine their competitive abilities.

CHAPTER 3. COMPETITIVE EFFECTS ON PLANT GROWTH AND THE YIELD OF GRASS MIXTURES DURING THE ESTABLISHMENT PHASE.

3.1 GENERAL INTRODUCTION

Competition between grass species has been identified in both establishing and established pasture swards (Donald, 1963; Rhodes, 1970). Many workers cite the importance of the competitive ability of species in the early establishment phase (Rhodes, 1967, 1970; Cocks, 1969), which has a deterministic effect on the performance of the mixed swards at later stages of growth (see Chapter 2).

Competitive ability of species during early growth is attributed to many factors including seed size, germination rates and growth rates of both roots and shoots. The superior competitive ability of one species over another is a combination of one or more of these inherent characters, which can be expressed differently under different environments and management conditions. The ability to survive changes in environmental conditions also becomes very important, as inherent competitive advantages can be masked by external factors of the environment.

Reviews on competition between grass species growing in mixtures indicate that such species combinations compete for the same environmental resources (Trenbath, 1974a, 1978), which can be attributed to similar growth characteristics and demands of these species.

Successful establishment and performance of newly sown pastures becomes an important factor in maintaining a profitable livestock industry. Seed mixtures used for establishing pastures generally contain several grass species and cultivars (Harris, 1968; Levy, 1970; White, 1973), combined in different proportions. These mixtures are used in an endeavour to obtain greater and sustained yields of pasture under changing environmental and management conditions. Thus competition between species becomes an important criterion in determining the successful performance of the sown species.

This chapter presents three experiments conducted to identify the competitive relationships and effects between three grasses commonly used in New Zealand's pastoral industry (Section 1.2). Emphasis was placed on the establishment and early growth phase due to its effects on both growth and productivity of the species and swards.

3.2 EXPERIMENT 1.* A FIELD STUDY ON THE EFFECTS OF COMPETITION ON PLANT PERFORMANCE AND THE YIELD OF BINARY MIXTURES OF GRASS SPECIES DURING THE ESTABLISHMENT PHASE FROM SEED, AND SUBSEQUENT GROWTH OF THE ESTABLISHED SWARDS.

3.2.1 INTRODUCTION

Pastures in New Zealand generally consist of a complex mixture of improved and unimproved grass and legume species (Palmer, 1970; Brougham, 1973; Lancashire and Harris, 1977), with a greater number of grass species than legumes. Due to the frequent dominance and complexity of the grass component in these swards and incorporation of more grass species and cultivars in pasture seed mixtures, emphasis was placed in this study on the competitive effects between selected grass species.

Much research is reported on competitive effects between pasture grasses, and a major proportion of these experiments have been conducted either in boxes or pots, under fully or partially controlled environmental conditions. Thus a field study was undertaken to evaluate the inherent competitive abilities and relationships of the grass species when grown as mixtures, under uniform defoliation treatments.

In general, the easier environments of New Zealand offer a greater flexibility of time of sowing, while the colder and drier climates restrict times of sowing to either spring or autumn (Brougham, 1969; White, 1973). This study was conducted with a spring sown pasture. While it evaluated the competitive relationship during the establishment phase, dry matter yields were monitored during the second year to observe effects of competition during early growth on subsequent performance of species.

* Part of this experiment was published as "Competition between 'Nui' ryegrass, 'Matua' prairie grass and 'Apanui' cocksfoot during establishment and early growth" in *Proceedings of the New Zealand Grasslands Association* 43: 133-138; 1982.

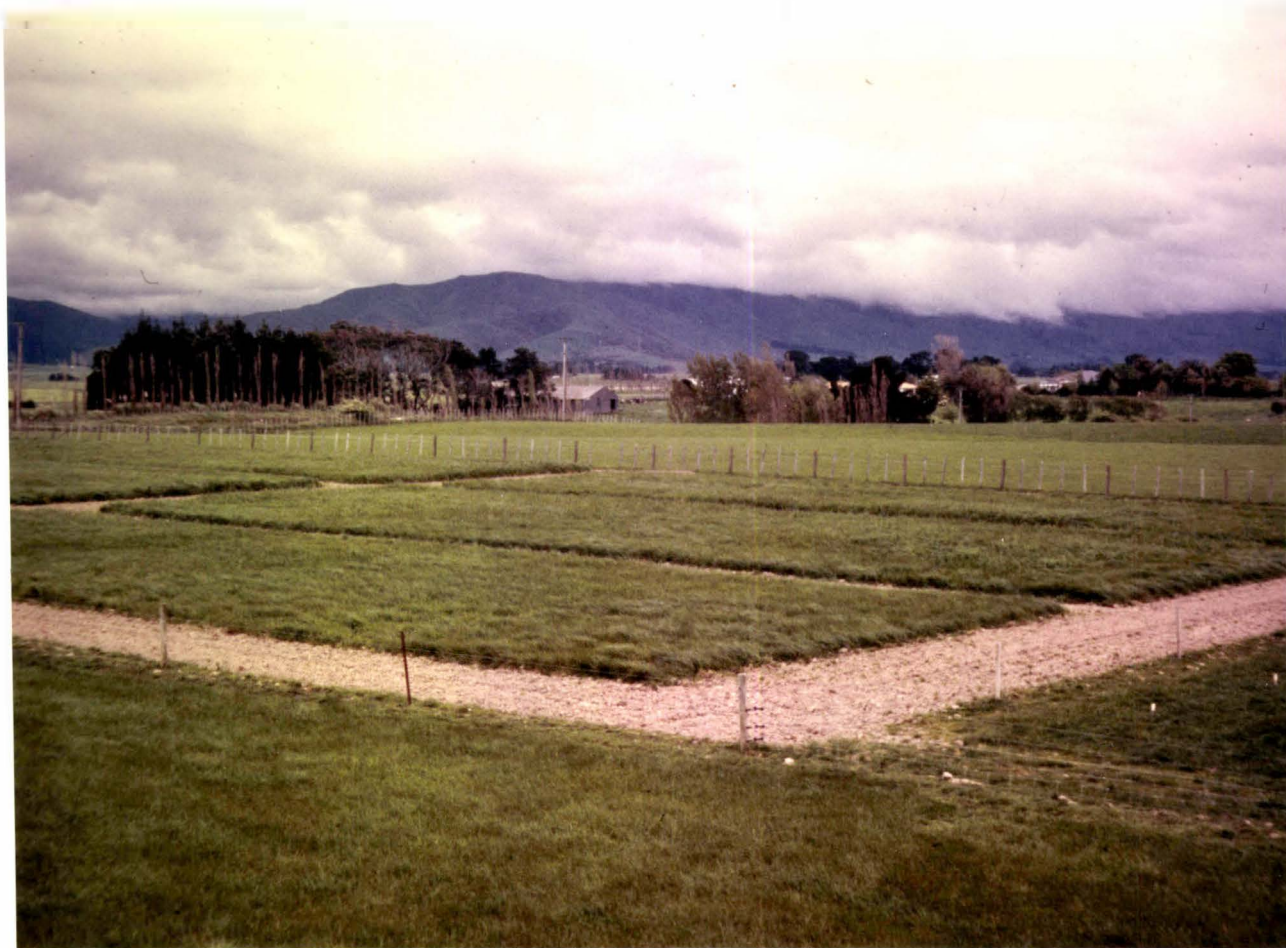


PLATE 1. A general view of the field trial (Experiment 1).

3.2.2 EXPERIMENTAL PROCEDURE

3.2.2.1 The site

The study was conducted on the Pasture and Crop Research and Development Unit, Massey University, situated 1.0 km from the Campus (Plate 1). The soil type of the experimental site was Tokomaru silt loam (an Aeric fragiaqualf) of medium fertility (Pollok, 1975; Scotter et al. 1979a), well drained and regularly topdressed.

Soil moisture tension determinations of the top 20 cm of the soil were made, using replicated gypsum blocks at 5, 10 and 20 cm below the soil surface. The gypsum blocks were sited randomly in all replicates.

3.2.2.2 Pasture Mixtures

The pasture grasses used for the study were "Grasslands Nui" perennial ryegrass (*Lolium perenne* L.) (Ref No NZ 3996A); "Grasslands Matua" prairie grass (*Bromus catharticus* Vahl) (Ref No. NZ 0507A) and "Grasslands Apanui" cocksfoot (*Dactylis glomerata* L.) (Ref No. 6048A). These species were combined in binary mixtures according to the replacement series principle of de Wit (1960), in the proportions of 1.0:0.0; 0.75:0.25; 0.50:0.50; 0.25:0.75 and 0.0:1.0. Thus nine mixtures and three monocultures were sown - namely

100% R; 75R:25P; 50R:50P; 25R:75P
 100% P; 75P:25C; 50P:50C; 25P:75C
 100% C; 75C:25R; 50C:50R; 25C:75R

These abbreviations (R = ryegrass, P = prairie grass and C = cocksfoot) are used as convenient notations throughout this thesis.

3.2.2.3 Pasture Establishment

Following ploughing, cultivation and top dressing with a basal fertilizer (12:10:10:8 - N:P:K:S) at the rate of 400 kg/ha, the different seed mixtures were broadcast on the 6th November 1979, behind a V ring roller and then lightly harrowed. Seeds were graded for uniform weight prior to making the seed mixtures and the 1000 seed weights of the graded seeds were: 2.07g, 9.73g and 0.89g for ryegrass, prairie grass and cocksfoot respectively. Seed rates were calculated to obtain approximately 400 plants per square metre, which is considered to be similar to normal pastoral conditions (Hill and Shimamoto, 1973).

3.2.2.4 Experimental Design

A randomized complete block design with 3 replicates was used for this study. Individual plot size was 3.5 x 13.5 metres.

3.2.2.5 Management of the Pastures

Broad leaved weeds and legumes, especially white clover (*Trifolium repens* L.) were controlled during the experimental period of November 1979 - March 1980, by three sprayings of M.C.P.B. and Dicamba at 1.5 kg active ingredient per hectare at regular intervals. Hand weeding was also adopted regularly to remove broad leaved weeds. Fertilizers were applied at a rate of 300 kg of 12:10:10:8 N.P.K.S per hectare after each harvest over the period November 1979 - November 1981, to overcome any nutrient deficiencies.

3.2.2.6 Measurements

(A) Establishment phase

Seedling emergence rates of each species in all treatments were measured by making seedling counts daily up to 21 days after sowing on two randomly sited quadrats (0.1m²) per plot. Seedling establishment and survival was assessed four weeks after sowing on the same quadrats.

Vegetative growth of the species was determined by removing two 0.1m² quadrats from each plot in the 5th, 6th, 7th and 8th weeks after planting. The roots were washed and plant height, root depth and tiller numbers per plant were determined for each species. The shoots and roots of the plants were separately dried at 80°C for 24 hours to determine dry matter accumulation of the species over this period.

The superficial cover of the different sward types was determined at weekly intervals during this period and prior to every harvest in the first season, by analysing 100 points along a fixed transect as described by Levy and Madden (1933).

Dry matter yields of the swards were obtained by mowing a central strip of 1.5 m in each plot to a height of 2.5 cm above ground level. Prior to each harvest two randomly selected quadrats were cut to the same height to obtain data on the botanical composition of the sward types and dry weights per plant. If the quadrats fell within the central strip,

the data was adjusted to take this effect into consideration. All plots were harvested on three occasions, at 9, 13 and 17 weeks after planting.

(B) Second Year

During autumn and winter 1980, the trial was grazed on two occasions, in June and September, approximately 4-5 days after the average light interception measured across all treatments around solar noon was 95%. A "Li-Cor" light meter, with a quantum sensor (Lambda Instrument Corp; Nebraska, USA) was used for these measurements. This technique was adopted to allow the species to compete for light and to measure the yielding ability of the mixtures and the productivity of each species at the time of maximum photosynthetic activity and hence maximum rates of growth (Brougham, 1956). In addition, this light interception technique, which is based on morphological characters of the species was adopted rather than a regular time interval during the second year, as it allows for changes in the environment such as periods of dry weather and high and low temperatures (Sheard and Winch, 1966).

Pasture productivity was measured during the period November 1980 - November 1981, by mowing the swards to 2.5 cm above ground level, on 6 occasions, namely November 1980, January, April, June, September and November 1981. All harvests were taken at approximately 95% light interception. Prior to harvesting, two randomly sited quadrats were cut to the same level to determine the botanical composition of the sward. This analysis was done to assess the competitive relationship between the species over this period and to relate the competitive effects of the establishment phase to those obtained in these later harvests.

3.2.2.7 Statistical Treatment

Analyses of variance were done by using the statistical computer programme "Genstat" (Alvey *et al*, 1977 - Rothamstead Experimental Station), available on the Massey University Burroughs 6700 computer. The performance of each species in various mixtures was compared with that of its monoculture, and in all analyses, unless otherwise stated, the following symbols used:-

NS = Non significance at 5% level of probability

* = P. \leq 0.05

** = P \leq 0.01

$\bar{x} \pm y$ where " $\pm y$ " represents the standard error of mean " \bar{x} ". Where the term "statistical significance" or "significance" is used, it refers unless otherwise stated, to the 5% level of probability.

Competitive interactions and the nature of competition between species were analysed using three indices - namely Relative Yield Total (RYT) (de Wit and van den Bergh, 1965); Aggressivity (McGilchrist, 1965; McGilchrist and Trenbath, 1971), and Relative Crowding Coefficient (de Wit, 1960).

Relative yield totals were calculated based on the botanical composition of species in mixtures, by the model of de Wit and van den Bergh (1965), based on the formula

$$RYT = \frac{Y_{ij}}{Y_{ii}} + \frac{Y_{ji}}{Y_{jj}}$$

where Y_{ii} and Y_{jj} are the yields of the monocultures and Y_{ij} being the yields of the i th species grown in combination with the j th species and Y_{ji} being vice versa.

The relative yield totals based on plant characteristics such as tiller numbers and plant weight were calculated using the model of McGilchrist and Trenbath (1971) presented as

$$RYT = \frac{1}{2} \left(\frac{Y_{ij}}{Y_{ii}} + \frac{Y_{ji}}{Y_{jj}} \right)$$

where Y_{ij} is the performance per plant of species i grown in combination with species j , Y_{ji} being vice versa and Y_{ii} and Y_{jj} indicating the performance per plant of species i and j in monocultures.

Subsequently, these RYT values were tested for departure from unity at the 5% significance level.

The analysis of "Aggressivity" (McGilchrist and Trenbath, 1971), which measures proportional changes in plant performance rather than

arithmetic changes was also used to measure the relative competitive ability of species growing in different combinations. Aggressivity of the i th species is expressed as

$$A_{ij} = \frac{1}{2} \left(\frac{Y_{ij}}{Y_{ii}} - \frac{Y_{ji}}{Y_{jj}} \right)$$

using the same notations as RYT based on per plant performance.

The competitive ability of each species in relation to the other species was analysed by the competition model of de Wit (1960), using the concept of relative crowding coefficients. These relative crowding coefficients (K_{ij} and K_{ji}) were calculated as

$$K_{ij} = \frac{Y_{ij} \cdot Z_j}{(M_i - Y_{ij}) Z_i}$$

$$K_{ji} = \frac{Y_{ji} \cdot Z_i}{(M_j - Y_{ji}) Z_j}$$

where M_i and M_j are the mono-culture yields of species i and j , Y_{ij} and Y_{ji} the yields of species i and j grown in combination, Z_i and Z_j the relative plant frequencies.

Two computer models based on the competition model of de Wit (1960) have been developed using the least squares estimate method (Thomas, 1970) and by computing the maximum likelihood estimates (Machin and Sanderson, 1977). The Thomas (1970) model has been more widely used in competition studies (e.g. Harris, 1973; Harris and Thomas, 1970, 1972; Ivens and Mlowe, 1980; Harris et al. 1981b) and as the programme for this model was available on the PDP 11/45 computer at the D.S.I.R., Palmerston North, it was used in the present study (Appendix 1). In addition, the residual values obtained from this model were checked for normality by plotting probability curves (Bhattacharya and Johnson, 1977) using the computer programme "Minitab" (Ryan, 1981) on the Prime 750 computer at Massey. The significance levels of the correlation coefficients of the residual values of species growing in combinations were also tested using the above programme.

As these tests indicated that the residual values were normally distributed and in general were not correlated significantly, it was assumed that both models (Thomas 1970, and Machin and Sanderson, 1977) would give similar values for the relative crowding coefficients (Arnold, Nicholls, pers. comm). This further substantiated the use of the readily available programme for the Thomas (1970) model for this study.

3.2.3 RESULTS

3.2.3.1 Climate and Soil Moisture

Before presenting the results in detail, it is pertinent to appreciate the climatic conditions during the experimental (establishment and early growth) period.

TABLE 3.1. Meteorological measurements, D.S.I.R. - Palmerston North
(Approximately 1.5 km from the experimental site)

	Oct'79	Nov	Dec	Jan'80	Feb	March	April
Rainfall (mm)	96	105	114	61	36	137	97
1928-1980 mean (mm)	88	78	94	79	67	69	81
Mean temperature ($^{\circ}$ C)	12.7	13.3	15.9	17.7	17.8	15.5	13.3
1928-1980 mean ($^{\circ}$ C)	12.4	14.2	16.1	17.3	17.6	16.4	13.9

As shown in the table, the experimental period was generally wetter and cooler than average, thereby ensuring adequate moisture for pasture growth.

Regular determinations of soil moisture potential also indicated an adequate supply of moisture for pasture growth except for very limited dry periods as reflected in the top 5 cm of the soil (Appendix 2A). In addition soil moisture levels monitored by rainfall and pan evaporation (Scotter *et al.* 1979 a,b) indicated similar results except for a sharp drop in soil moisture levels in February and early March, which may have inhibited pasture growth (Scotter, pers. comm.) (Appendix 2B). However, soil moisture was generally considered adequate for pasture growth over the establishment and early growth period (Table 3.1).

3.2.3.2 Seedling Emergence and Establishment

Ryegrass and prairie grass achieved 75% emergence within 7 and 9 days respectively, while cocksfoot seedlings emerged in 14-15 days (Table 3.2).

TABLE 3.2 Time of emergence of species (Days)

Species	Time to 75% emergence (days)
Ryegrass	7.4
Prairie grass	8.9
Cocksfoot	14.4
\bar{Sx}	0.21
CV%	6.0%

Plant counts of the sown species taken at four weeks from sowing did not deviate significantly from the required populations (per 0.1 m²) in the respective mixtures (Table 3.3).

TABLE 3.3 Plant counts of species taken 28 days after sowing (No. plants per 0.1 m²).

Proportion of species in mixture	Expected no. of plants	Ryegrass	Prairie grass	Cocksfoot
100%	40	38.6±1.2	39.0±1.2	36.7±1.8
75%	30	28.2±1.2	28.3±0.7	28.0±0.9
50%	20	19.5±1.4	19.0±0.6	18.2±0.8
25%	10	9.2±0.9	9.7±0.3	8.7±0.6

3.2.3.3 Vegetative Characters

3.2.3.3.1 Shoot Characters:-

(A) Plant height

The plant heights of all three species of grasses in mixtures did not differ significantly from that of their respective monocultures until after the first total defoliation 9 weeks after planting (Appendix 3). However, subsequent measurements indicated that all three species, when sown in mixtures with 25% of the companion species, were taller than plants in their respective monocultures. In addition, prairie grass plants growing in combination with the other species, were taller than

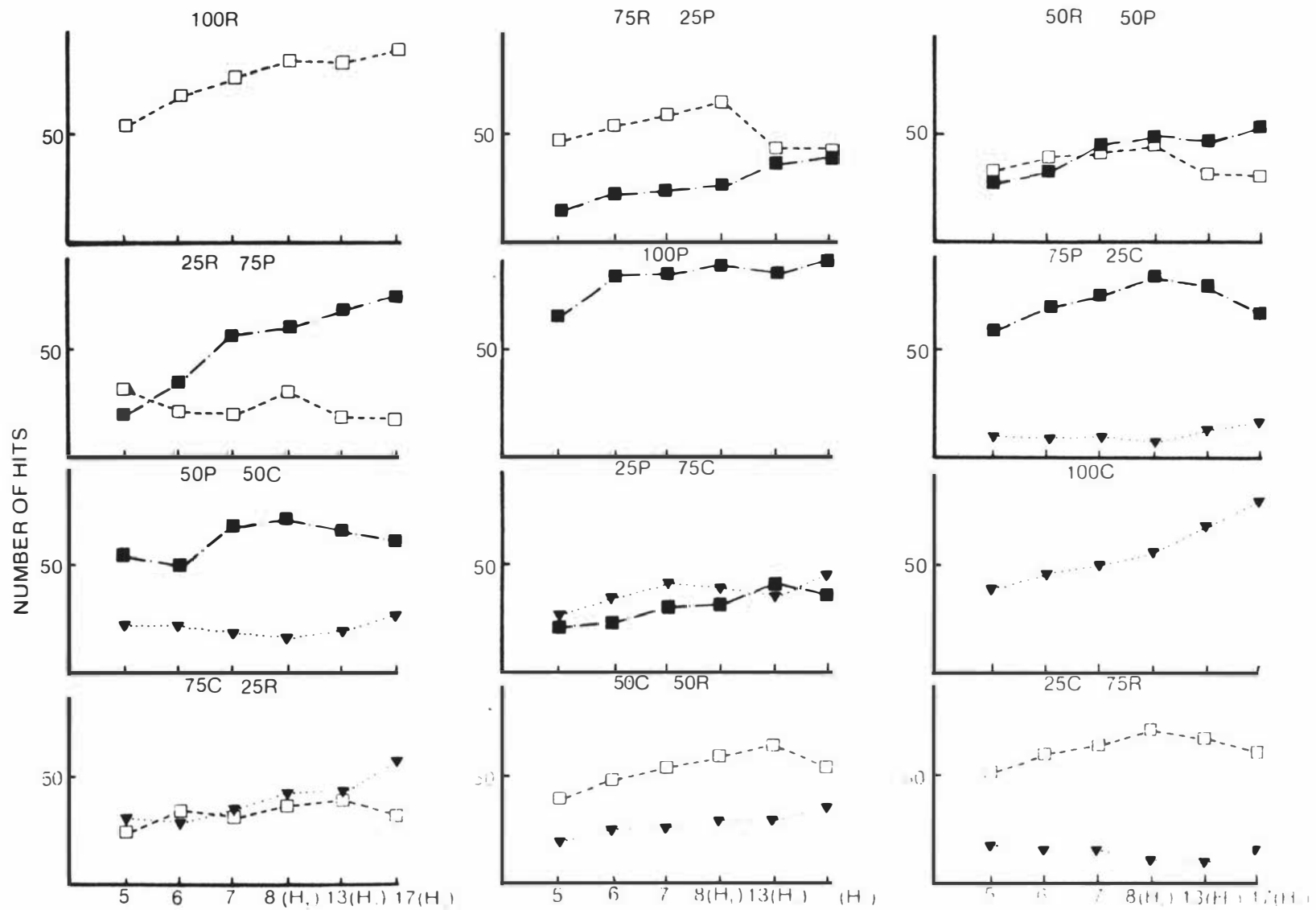


Figure 3.1: Point analysis (number of hits of each species) Along a fixed transect across all treatments

plants in its monoculture.

The canopy cover of the swards obtained from 100 points taken along a fixed transect showed that both prairie grass and ryegrass occupied a relatively greater surface cover than its proportions in the mixture, when grown with cocksfoot (figure 3.1). Cocksfoot occupied a greater surface cover than the proportion of cocksfoot seed in the mixture only in its 75% combination with ryegrass. In the ryegrass-prairie grass mixtures, ryegrass occupied a greater surface cover only in the 75R 25P mixture. Generally, prairie grass was the tallest species and thus dominated the surface cover of the canopy, which reflected its potential to intercept more incident light energy and shade the other species in the mixtures.

(B) Tiller Numbers

An evaluation of tiller numbers per plant during early growth is presented in table 3.4. Ryegrass had the highest and cocksfoot the lowest number of tillers per plant throughout the experimental period.

The effects of the presence of one species on the growth of the other is highlighted by the tiller numbers per plant. Generally, all species when combined with 25% of another species had a greater number of tillers per plant than their monocultures, thus reflecting a greater intraspecific than interspecific competitive effect at this planting density. This effect was most prominent in ryegrass and prairie grass.

More specifically, the tiller numbers of cocksfoot were greatly depressed in its 25% and 50% combinations with ryegrass and prairie grass, at all harvests. In addition, prairie grass reduced the tiller numbers of cocksfoot to a greater extent than ryegrass. The tiller numbers of ryegrass were similarly affected by 75% and 50% prairie grass and to a lesser extent by 75% cocksfoot. The tiller numbers of prairie grass were markedly depressed in its combination with 75% ryegrass.

Prairie grass plants also had greater tiller numbers than in its monoculture when combined with 50% of the other species. Ryegrass plants in the 50C 50R mixture also had greater tiller numbers than in its monoculture.

TABLE 3.4. Mean tiller numbers per plant of species grown in mixtures and monocultures during early growth

(A) RYEGRASS	Monoculture	75R with 25P	50R with 50P	25R with 75P	75R with 25C	50R with 50C	25R with 75C	Significance	\bar{Sx}
Week 5	5.7	5.9	5.2	5.2	6.3	6.3	5.5	**	0.17
Week 6	6.9	7.2	6.4	6.4	7.5	7.3	6.8	*	0.18
Week 7	12.2	12.7	11.6	11.2	13.5	13.1	12.2	*	0.36
Week 8 (H ₁)	18.3	18.6	16.8	15.5	19.7	19.2	17.8	**	0.23
Week 13 (H ₂)	19.4	20.3	19.2	18.5	20.4	19.8	18.7	*	0.31
Week 17 (H ₃)	17.7	17.9	17.6	17.3	18.4	18.0	16.9	**	0.19
(B) PRAIRIE GRASS	Monoculture	75P with 25R	50P with 50R	25P with 75R	75P with 25C	50P with 50C	25P with 75C	Significance	\bar{Sx}
Week 5	4.2	4.5	4.4	4.0	4.7	4.6	4.2	*	0.13
Week 6	5.9	6.2	6.1	5.7	6.9	6.6	5.9	**	0.15
Week 7	7.0	7.7	7.3	6.8	8.0	7.7	7.1	**	0.13
Week 8 (H ₁)	8.5	10.3	9.3	7.9	10.3	9.7	8.6	*	0.33
Week 13 (H ₂)	8.0	8.3	8.2	7.7	8.8	8.4	7.7	*	0.37
Week 18 (H ₃)	8.5	8.7	8.6	8.3	9.5	8.9	8.1	**	0.13
(C) COCKSFOOT	Monoculture	75C with 25R	50C with 50R	25C with 75R	75C with 25P	50C with 50P	25C with 75P	Significance	\bar{Sx}
Week 5	2.9	3.0	2.6	2.6	2.9	2.6	2.4	*	0.11
Week 6	3.5	3.6	3.1	2.9	3.5	2.9	2.8	**	0.09
Week 7	4.5	4.5	4.1	4.0	4.5	4.1	3.9	*	0.10
Week 8 (H ₁)	5.9	6.0	5.5	5.4	5.9	5.3	5.0	*	0.13
Week 13 (H ₂)	6.9	7.1	6.7	6.4	6.7	6.4	6.2	*	0.13
Week 17 (H ₃)	5.9	6.1	5.8	5.5	6.0	5.5	5.4	**	0.10

(C) Weight of shoots

Prairie grass had the highest and cocksfoot the lowest dry weight per plant at all harvests. The differences between the species increased with time (Table 3.5).

The effect of one species on the growth of another in grass species mixtures is again reflected in the dry matter accumulation patterns of the three species. As shown in table 3.5, the increase in dry weight per plant of the major species in the mixture (i.e. 75%) was generally greater than in their respective monocultures and in the mixtures when present as an equal or minor component (i.e. 50% or 25%). This again reflects greater intraspecific competition within a species than interspecific competition at this density. This effect is again minimal in the 75% combinations of cocksfoot with either ryegrass or prairie grass.

The changes in dry weights of shoots are similar to those observed in the tiller numbers. In addition to their 75% combinations, ryegrass and to a greater extent prairie grass affect the growth of cocksfoot in their 50% mixtures with cocksfoot. While causing a decrease in the shoot weight of cocksfoot in these mixtures, both ryegrass and prairie grass plants accumulate greater dry matter than in their monocultures. The growth of ryegrass plants is affected when combined with 75% and to a lesser extent with 50% prairie grass, compared with the ryegrass monocultures. The dry weights of ryegrass shoots are reduced when grown with 75% cocksfoot.

The presence of ryegrass and cocksfoot did not greatly reduce the shoot weights of prairie grass when compared with its monoculture. Prairie grass had a greater effect on the growth of cocksfoot plants than on ryegrass plants.

(D) Root characters

Both root depth (length from base of plant to tip of the longest root) and root weight per plant were determined for the first four samplings by removing 0.1 m² quadrats (Appendices 4 and 5). In spite of the inevitable difficulties that arose in obtaining complete root systems of individual plants under field conditions, it is interesting to note that the results show trends similar to those obtained in measurements of tiller numbers and shoot weights of the three species. Prairie grass had the largest root system (in terms of root depth and

TABLE 3.5. Mean weights of shoots (g) per plant of species grown in mixtures and monocultures during early growth

(A) RYEGRASS	Monoculture	75R with 25P	50R with 50P	25R with 75P	75R with 25C	50R with 50C	25R with 75C	Significance	\bar{Sx}
Week 5	0.114	0.119	0.108	0.106	0.123	0.121	0.114	*	0.004
Week 6	0.284	0.287	0.274	0.270	0.294	0.290	0.283	*	0.005
Week 7	0.510	0.513	0.503	0.494	0.518	0.511	0.508	*	0.004
Week 8 (H ₁)	0.672	0.692	0.601	0.545	0.729	0.714	0.648	*	0.023
Week 13 (H ₂)	0.568	0.610	0.576	0.532	0.621	0.572	0.548	*	0.018
Week 17 (H ₃)	0.542	0.570	0.536	0.512	0.579	0.550	0.521	**	0.009
(B) PRAIRIE GRASS									
	Monoculture	75P with 25R	50P with 50R	25P with 75R	75P with 25C	50P with 50C	25P with 75C	Significance	\bar{Sx}
Week 5	0.148	0.153	0.151	0.145	0.164	0.160	0.149	*	0.002
Week 6	0.391	0.403	0.397	0.390	0.406	0.401	0.393	*	0.006
Week 7	0.680	0.689	0.681	0.677	0.710	0.694	0.682	*	0.005
Week 8 (H ₁)	1.079	1.258	1.174	1.017	1.219	1.193	1.010	**	0.040
Week 13 (H ₂)	1.064	1.114	1.040	0.984	1.117	1.135	1.002	*	0.036
Week 17 (H ₃)	0.997	1.051	1.019	0.951	1.068	1.078	0.973	*	0.030
(C) COCKSFOOT									
	Monoculture	75C with 25R	50C with 50R	25C with 75R	75C with 25P	50C with 50P	25C with 75P	Significance	\bar{Sx}
Week 5	0.092	0.093	0.085	0.084	0.092	0.084	0.081	*	0.003
Week 6	0.115	0.115	0.110	0.109	0.114	0.108	0.107	*	0.003
Week 7	0.165	0.166	0.160	0.159	0.164	0.156	0.152	*	0.004
Week 8 (H ₁)	0.404	0.411	0.363	0.358	0.412	0.357	0.350	**	0.011
Week 13 (H ₂)	0.369	0.380	0.365	0.323	0.383	0.341	0.331	**	0.009
Week 17 (H ₃)	0.329	0.338	0.336	0.299	0.333	0.305	0.303	*	0.014

weight) and cocksfoot the smallest root system.

3.2.3.4 Total Dry Matter Production

(A) Establishment phase

The results presented in this section refer to the pasture dry matter yields of the different monocultures and mixtures, measured at nine weeks after sowing and thereafter on 2 occasions at four weekly intervals, during the establishment period. The pure stand of prairie grass was more productive than the other monocultures and all mixtures at every harvest. By comparison, the pure stand of cocksfoot was the least productive and the pure ryegrass stands were intermediate in yield. (Table 3.6). The yields of all mixtures lay between those of the respective monocultures.

TABLE 3.6. Dry matter yields (g/m^2) of grass mixtures and monocultures at each harvest during the establishment phase.

Treatment	H ₁ (9 weeks after sowing)	H ₂ (13 weeks after sowing)	H ₃ (17 weeks after sowing)
100R	111.3	137.6	93.9
75R25P	123.0	114.5	106.8
50R50P	131.2	124.1	117.3
25R75P	146.1	136.8	134.2
100P	152.3	143.8	141.3
75P25C	140.2	134.2	129.3
50P50C	119.9	115.9	110.4
25P75C	104.0	100.5	94.5
100C	86.0	86.5	79.1
75C25R	93.3	91.0	83.6
50C50R	98.5	96.5	86.4
25C75R	107.1	103.4	92.9
Significance	**	*	**
\bar{Sx}	4.22	9.65	2.76

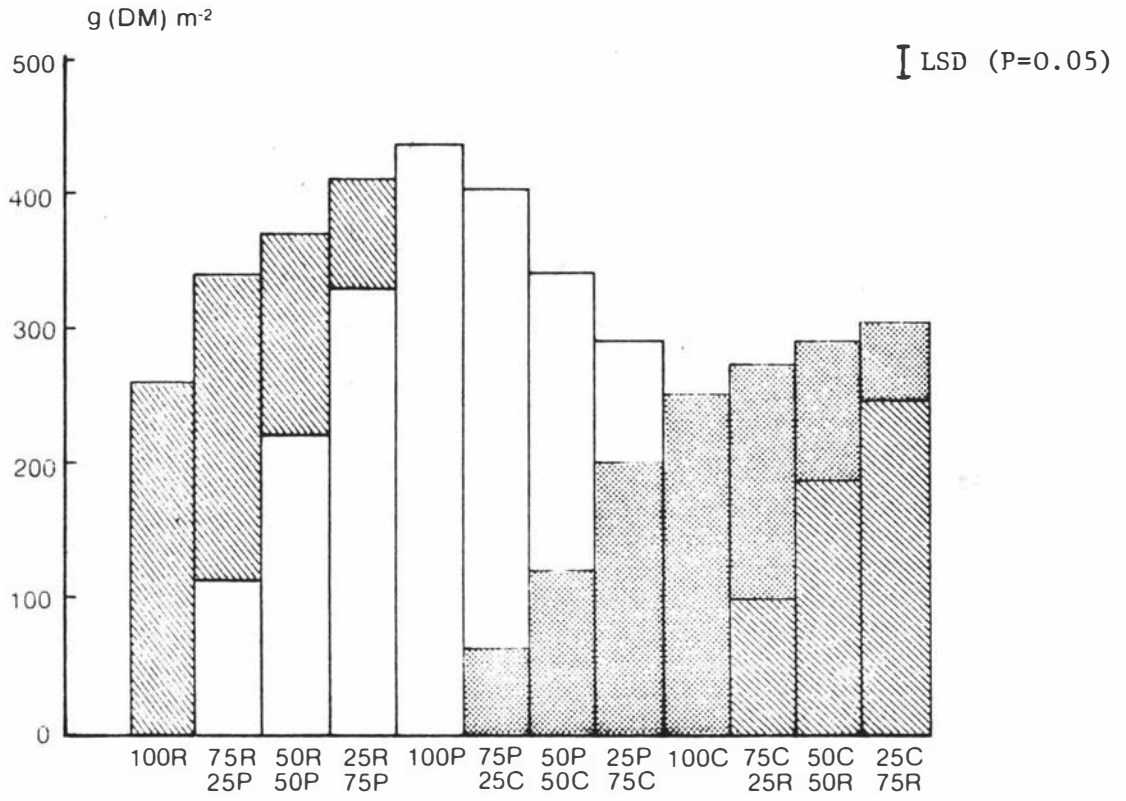


Figure 3.2: Cumulative dry matter yields (g.m⁻²) of grass mixtures and monocultures during the establishment phase.



Mixtures containing prairie grass and ryegrass generally produced greater amounts of dry matter than mixtures with cocksfoot. The contribution of prairie grass to the total yield of mixtures was greater than the proportion of seeds in the mixtures over this period (figure 3.2). Ryegrass also showed a similar effect when combined with cocksfoot. The performance of both ryegrass and to a greater extent cocksfoot was depressed by the presence of prairie grass in the mixtures.

(B) Second year of growth

All plots were harvested on 6 occasions over the period November 1980-November 1981, to measure the yields of the mixtures. Prairie grass outyielded all other mixtures and monocultures at every harvest (Table 3.7) and over the entire period (Figure 3.3). The yield of ryegrass was greater than that of cocksfoot. Although the trend in these yield relationships is uniform at every harvest, changes in yields with climatic and seasonal variations can be identified in the results. For example, the yields of cocksfoot increase during summer and early autumn harvest, while winter harvests show a higher yield in prairie grass.

TABLE 3.7 Dry matter yields (g/m²) of grass mixtures and monocultures at each harvest during the second year

Treatment	H ₁ (November 1980)	H ₂ (January 1981)	H ₃ (April 1981)	H ₄ (June 1981)	H ₅ (September 1981)	H ₆ (November 1981)
100R	311.0	243.7	332.0	175.6	248.7	303.3
75R25P	329.0	259.0	334.7	204.6	278.0	324.0
50R50P	344.7	276.3	378.7	230.3	304.0	338.3
25R75P	368.7	287.0	394.7	246.3	328.3	356.3
100P	381.0	304.7	406.3	268.3	350.3	370.0
75P25C	339.3	277.7	362.0	231.6	288.3	319.0
50P50C	280.7	235.3	277.3	186.0	234.7	239.7
25P75C	203.0	195.7	199.7	129.6	134.3	187.0
100C	126.7	151.3	116.7	77.6	59.0	189.3
75C25R	173.0	173.0	184.3	108.0	107.7	163.0
50C50R	225.0	193.3	236.7	140.6	164.0	204.0
25C75R	261.0	222.0	302.7	159.0	207.3	256.7
Significance	*	**	**	**	**	**
\bar{S}_x	19.77	19.21	22.65	8.28	16.70	18.89

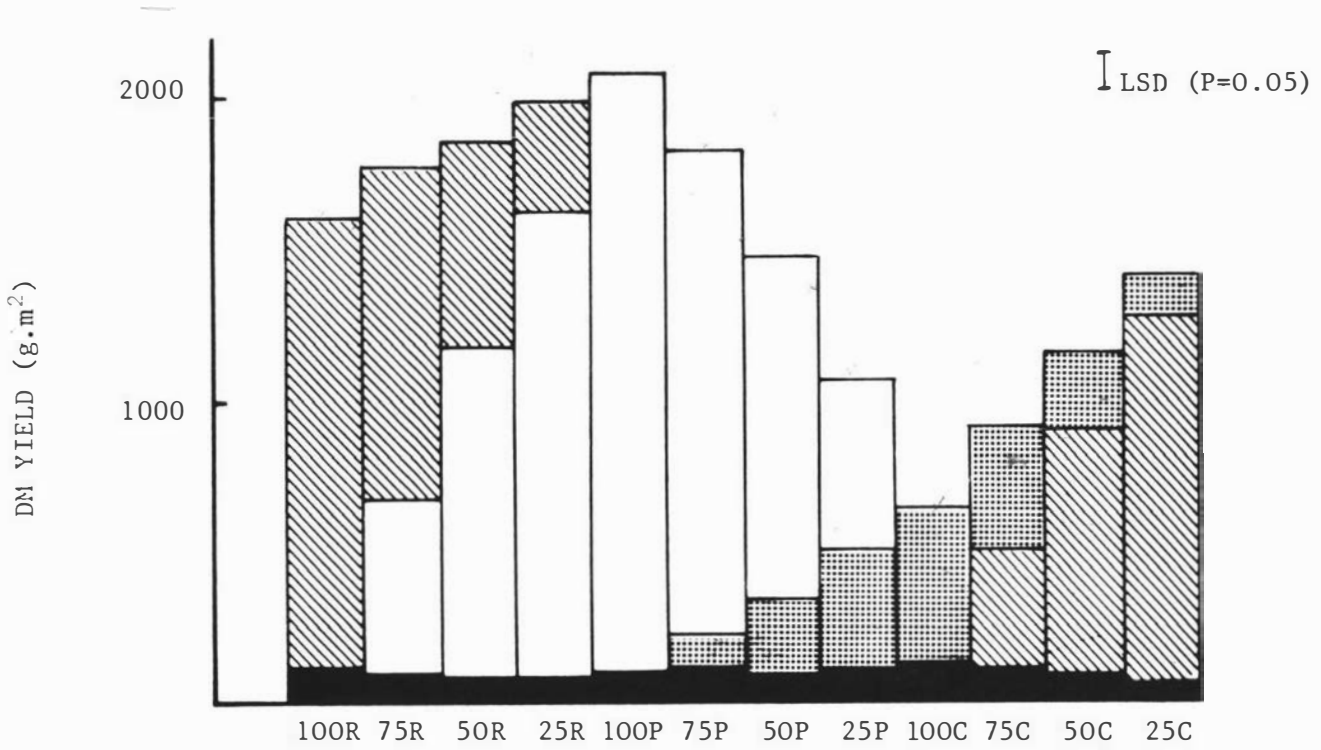


Figure 3.3 Cumulative dry matter yields (g.m⁻²) of grass mixtures and monocultures during the second year.



Ryegrass



Prairie Grass



Cocksfoot



Weeds and other Species

The yields of mixtures lie between the individual monocultures at every harvest, although the differences tend to be less prominent than in the establishment period. The contribution of each species to the total yield of the mixtures also follow a similar pattern to that of the establishment phase (figure 3.5 A,B,C).

3.2.3.5 Competition Effects

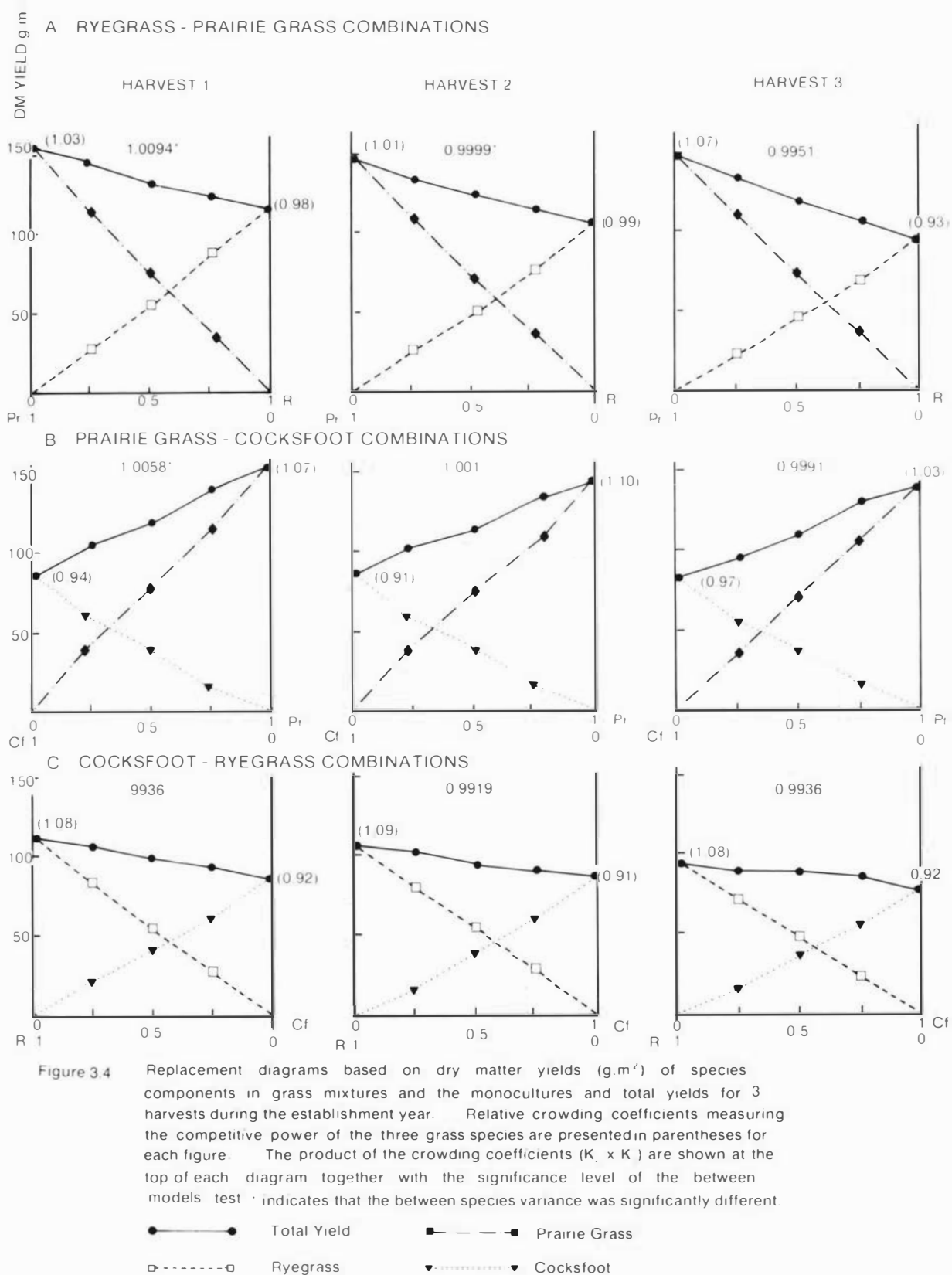
Three major parameters were used to evaluate competition effects between the species and the competitive ability of the species.

(A) Replacement diagrams and relative crowding coefficients

The replacement diagrams drawn from fittings obtained from the Thomas (1970) model for the yield components of the three species over the establishment phase and the second year are presented in figures 3.4 and 3.5 respectively.

In most instances, the between-species variance test (4 parameter model of Thomas 1970) was not significant, thus enabling the application of the between models (3 parameter model) test in both time periods. In addition, as the products of the relative crowding coefficients were close to unity in all mixtures at all harvests, it was concluded that these three species compete for the same 'biological space' (de Wit 1960) under the conditions of this experiment.

The relative crowding coefficients of the three species indicate the superior competitive ability of prairie grass over the total experimental period; and cocksfoot was the weakest competitor (figures 3.4, 3.5). While competitive abilities of the species do not change greatly with successive harvests during the establishment phase, changes can be seen in the different harvests during the second year (Table 3.8).



A RYEGRASS - PRAIRIE GRASS COMBINATIONS

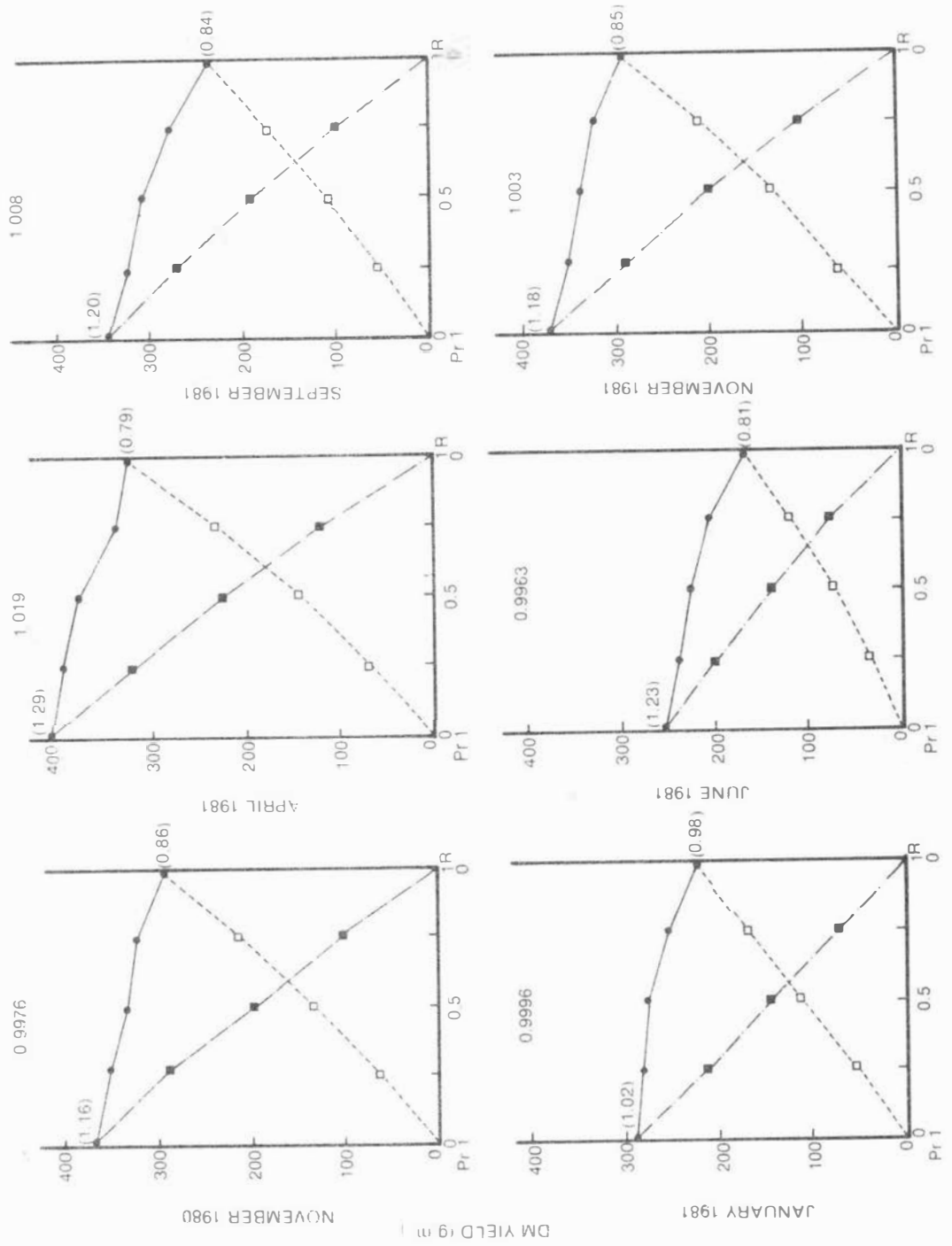
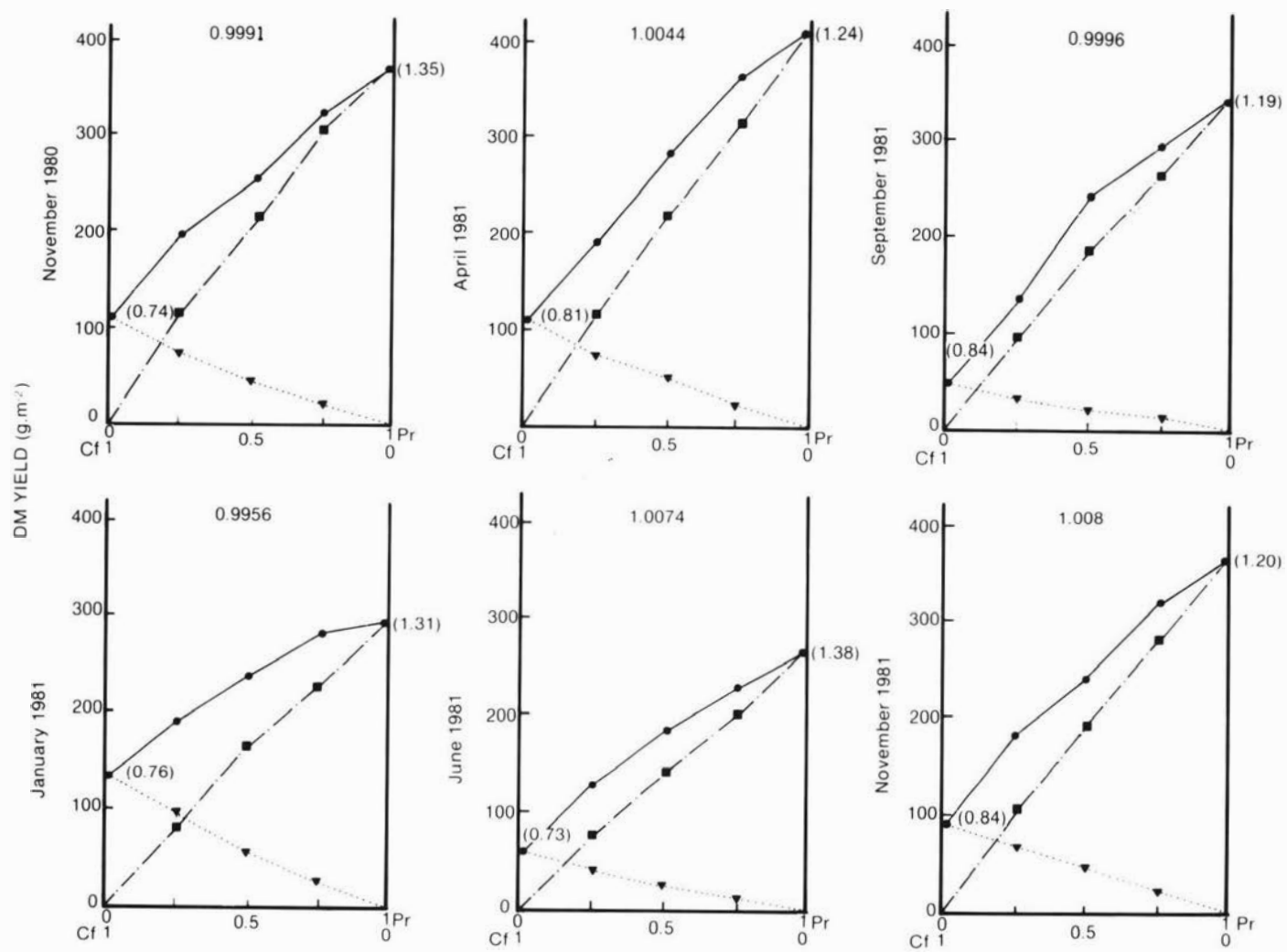


Figure 3.5: Replacement diagrams based on dry matter yields ($\text{g}\cdot\text{m}^{-2}$) of species in mixtures and monocultures and total yield at every harvest during the second year. Symbols and conventions as for Figure 3.4.

B PRAIRIE GRASS - COCKSFOOT COMBINATION



C COCKSFOOT - RYEGRASS COMBINATIONS

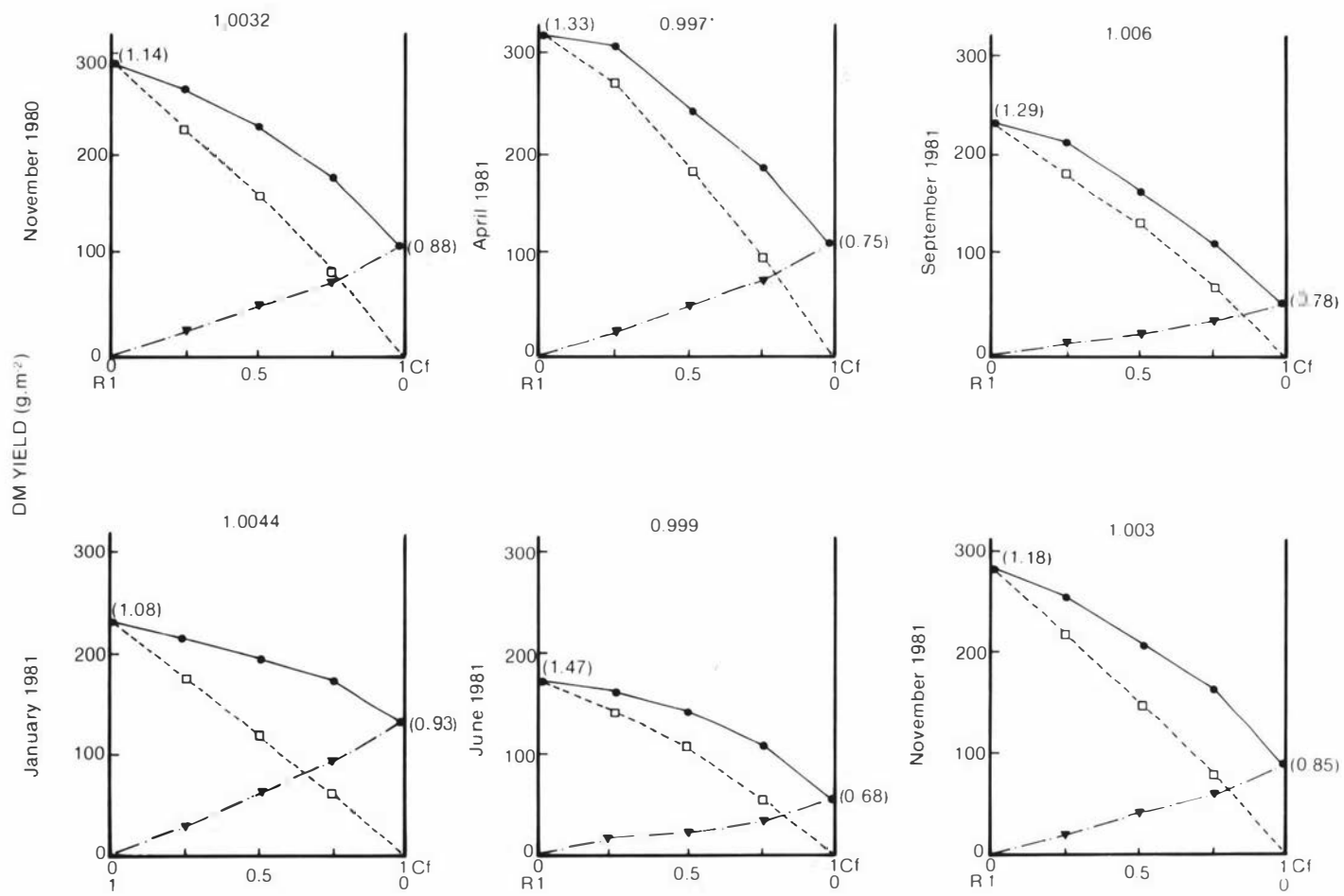


TABLE 3.8 Relative crowding coefficients of binary combinations at every harvest during the second year

Harvest date	Ryegrass-Prairie grass combination		Prairie grass-Cocksfoot combination		Cocksfoot-Ryegrass combination	
	Ryegrass	Prairie grass	Prairie grass	Cocksfoot	Cocksfoot	Ryegrass
November 1980	0.86	1.16	1.35	0.74	0.88	1.14
January 1981	0.98	1.02	1.31	0.76	0.93	1.08
April 1981	0.79	1.29	1.24	0.81	0.75	1.13
June 1981	0.81	1.23	1.38	0.73	0.68	1.47
September 1981	0.84	1.20	1.19	0.84	0.78	1.29
November 1981	0.85	1.18	1.20	0.84	0.85	1.18

A comparison of the yields of the three species over this period (Table 3.7) and the relative crowding coefficients (Table 3.8) indicate similar changes. The relative crowding coefficients tend to increase and decrease with the yielding ability of the three species at different harvests in the second year.

(B) Relative Yield Totals (RYT)

The RYT values can be calculated for both vegetative characters of the species and yield components at every harvest. Calculations based on both types of growth parameters in all combinations revealed no significant differences between RYTs of the three different combinations of each pair of species (namely 0.75:0.25; 0.50:0.50; 0.25:0.75). Thus the three RYT values were averaged to obtain an overall value for each species combination, and are presented in Tables 3.9 and 3.10.

TABLE 3.9 Relative yield totals based on vegetative characters of the species over the establishment phase

Vegetative character	Species combination	Time of harvest (weeks after sowing)					
		Week 5	Week 6	Week 7	Week 8(H ₁)	Week 13(H ₂)	Week 17(H ₃)
Tiller number	Ryegrass-Prairie grass	0.996±.006	0.997±.005	1.001±.004	0.989±.002	0.995±.003	0.999±.002
	Prairie grass-Cocksfoot	0.998±.002	0.989±.003	0.992±.005	0.997±.006	0.985±.002	0.994±.003
	Cocksfoot-Ryegrass	0.995±.007	0.988±.004	0.995±.005	0.988±.003	0.992±.003	0.995±.004
Root weight	Ryegrass-Prairie grass	0.992±.004	0.990±.002	0.997±.002	0.998±.001		
	Prairie grass-Cocksfoot	0.998±.001	0.993±.004	0.996±.001	0.997±.001		
	Cocksfoot-Ryegrass	0.993±.005	0.992±.004	0.997±.001	1.001±.001		
Shoot weight	Ryegrass-Prairie grass	0.993±.005	0.995±.003	0.994±.002	0.989±.007	0.996±.003	1.003±.002
	Prairie grass-Cocksfoot	0.995±.008	0.990±.003	0.987±.002	0.991±.004	1.003±.009	0.998±.009
	Cocksfoot-Ryegrass	0.994±.004	0.991±.004	0.990±.003	0.985±.002	0.996±.004	0.991±.004

TABLE 3.10 Relative yield totals based on yield components

I. Establishment year

Species combination	Harvest Number		
	H ₁	H ₂	H ₃
Ryegrass-Prairie grass	1.008±.004	1.005±.002	0.999±.004
Prairie grass-Cocksfoot	1.003±.007	0.993±.006	0.997±.003
Cocksfoot-Ryegrass	0.998±.006	1.001±.003	1.004±.003

II. Second Year

Species combination	Harvest Number					
	H ₁	H ₂	H ₃	H ₄	H ₅	H ₆
Ryegrass-Prairie grass	1.012±.014	1.010±.007	1.006±.007	1.000±.007	1.005±.009	1.008±.008
Prairie grass-Cocksfoot	1.007±.008	1.011±.011	1.007±.006	1.005±.012	1.012±.005	1.014±.008
Cocksfoot-Ryegrass	1.006±.008	1.014±.012	1.007±.006	1.008±.006	1.009±.004	1.006±.004

In all instances, the RYTs were not significantly greater or less than one. This implies that these species generally competed for the same environmental resources, and occupied the same biological niche during the period of this experiment. This is also expressed by the products of the relative crowding coefficients.

(C) Aggressivity effects

The measurement of aggressivity indicates the cumulative effects of competition at every harvest or sampling in terms of plant characteristics. Thus the aggressivity indices based on shoot weights and tiller numbers were calculated by the method of McGilchrist and Trenbath (1971), at every harvest during the establishment phase (Table 3.11).

TABLE 3.11 Aggressivity indices of the more aggressive species based on plant characters in the establishment phase.

Time of measurement (weeks)	Aggressivity of Prairie grass						Aggressivity of Prairie grass						Aggressivity of Ryegrass												
	when grown with Ryegrass						when grown with Cocksfoot						when grown with Cocksfoot												
	75R	25P	50R	50P	25R	75P	Signif	+ S.E.	75P	25C	50P	50C	25P75C	Signif	+ S.E.	75C	25R	50C	50R	25C	75R	Signif	+ S.E.		
1. Shoot weight	5	-0.035	0.031	0.048	*	0.013		0.110	0.083	0.004	**	0.009	-0.004	-0.002	0.085	NS	0.034								
	6	-0.008	0.024	0.038	*	0.007		0.051	0.040	0.003	NS	0.013	-0.009	0.013	0.043	NS	0.012								
	7	-0.014	0.032	0.075	NS	0.027		0.081	0.060	-0.005	NS	0.020	-0.004	0.016	0.027	*	0.005								
	8	-0.044	0.097	0.178	**	0.022		0.131	0.110	-0.041	**	0.005	-0.026	0.042	0.098	NS	0.032								
	13	-0.068	0.017	0.055	*	0.029		0.105	0.071	-0.046	**	0.014	-0.033	0.009	0.108	**	0.014								
	17	-0.049	0.016	0.055	**	0.012		0.075	0.077	-0.018	**	0.014	-0.031	-0.017	0.080	*	0.015								
2. Tiller numbers	5	-0.037	0.067	0.088	**	0.015		0.153	0.111	0.045	NS	0.029	-0.091	0.116	0.115	*	0.029								
	6	-0.039	0.051	0.062	**	0.014		0.184	0.142	-0.007	**	0.005	-0.016	0.091	0.129	**	0.012								
	7	-0.037	0.040	0.076	**	0.012		0.131	0.089	0.007	**	0.012	-0.004	0.087	0.114	**	0.006								
	8	-0.017	0.071	0.145	**	0.003		0.164	0.118	0.012	*	0.020	-0.022	0.066	0.088	**	0.007								
	13	-0.047	0.010	0.032	**	0.014		0.093	0.063	0.013	**	0.005	0.029	0.031	0.065	*	0.014								
	17	-0.014	0.005	0.019	**	0.004		0.077	0.045	-0.025	**	0.007	-0.042	0.019	0.054	**	0.007								

In general, prairie grass was the most aggressive species over this period, and ryegrass was more aggressive than cocksfoot. However ryegrass was more aggressive than prairie grass in the 75R25P mixture, while cocksfoot indicated a similar effect on ryegrass in the 75C25R mixture. The aggressivity of cocksfoot increased over prairie grass at later samplings in the 75C25P mixtures.

The aggressivity indices change significantly with changes in species proportions in the different mixtures of a given binary combination, thus implying great changes in the competitive ability of a species with a 25% change in the species proportion.

3.2.4 DISCUSSION

The emergence of seedlings from soil depends on the interaction of many factors, among which soil factors such as moisture, crust strength and oxygen diffusion rates play a major role (Hanks and Thorpe, 1956; Arndt, 1965; Barley and Greacen, 1967; Brock, 1973). In addition, seed factors such as rapidity of germination and water imbibition properties of species also determine the rate and success of seedling germination and emergence (McWilliam and Dowling, 1970). Data collected in this study indicate differences in emergence rates of the species, especially cocksfoot (Table 3.2). As the seed bed was well prepared and as rainfall during the first 7-10 days after sowing ensured adequate available moisture near the soil surface, it can be considered that environmental factors had little effect on the emergence rates of the three species. As these germination rates were similar to those obtained under laboratory conditions, the differences in emergence rates can be considered a species characteristic of the grasses used in this study.

Analysis of competition between the three species over the experimental period indicates that they compete for the same environmental resources ("biological space" - de Wit, 1960). This is expressed by the RYT values and the products of the relative crowding coefficient being close to unity (Tables 3.9, 3.10, Figures 3.3, 3.4) (de Wit, 1960; Bakhuis & Kleter, 1965; van den Bergh, 1968). These results also conform to the theory of Trenbath (1974a, 1978) that grass species grown in binary combinations generally compete for the same environmental resources. In addition, competition for the same environmental resources by grass species can be expected to occur during establishment and early growth, as grasses generally have similar morphological characters and growth patterns (Barnard, 1964; Jewiss, 1966).

While competing for the same environmental resources within a given environment, the grasses establish a dominance hierarchy from the early stages of growth. The relative crowding coefficients computed on yield components (Figures 3.3, 3.4) and the aggressivity indices during the early growth stage (Table 3.11) indicate this dominance hierarchy as being prairie grass > ryegrass > cocksfoot.

The superior competitive ability of prairie grass over the other

species and of ryegrass over cocksfoot is well illustrated by the growth characteristics during the establishment phase (e.g. Tables 3.4, 3.5, Appendices 4,5). The magnitude of these growth characteristics in the more aggressive species is increased when grown with a weaker species, especially in the mixture containing 25% of the weaker species. As mentioned earlier, this indicates a greater intra-specific competitive affect within the species at the plant density used in this study, where a weaker species offers less resistance to the growth of a more aggressive species than plants of its own species. Due to this effect, the more aggressive species can utilize more of the environmental resources, and thus exhibit superior growth in comparison to its monoculture. This is highlighted in most vegetative characters in the 75% and 50% combination of prairie grass with other species and in similar combinations of ryegrass with cocksfoot. However, this effect is not clearly illustrated by plant height (Appendix 3) until the swards are defoliated. The inability of plant height to express competitive relationships clearly can be related to limited light penetration patterns within a sward, and thus in order to compete with the taller species, shorter species (e.g. cocksfoot in prairie grass-cocksfoot swards) grows taller. This process of etiolation of the shorter species which masks the competitive relationships is removed when the plants are defoliated, giving a better light distribution to the regrowing plants within the sward, until a good cover is established again by the taller species.

The present study shows that both ryegrass and prairie grass establish more rapidly than cocksfoot (Table 3.1), which gives these species an initial advantage. In addition, greater and more extensive dry matter production per plant by these species (Table 3.5) will utilize a greater share of the environmental resources, hence limiting their availability for the growth of cocksfoot plants, especially as the species compete for the same environmental resources. Thus the competitive advantage attained by both ryegrass and prairie grass over cocksfoot in this study can be attributed to both earlier emergence and faster and greater growth of the more competitive species. This is in agreement with results published by many scientists, which have highlighted the importance of early emergence and/or faster growth rates as major determinants of successful competitive ability in pasture grasses (e.g. Stapledon and Davies, 1928; Arens, 1962; Cullen, 1964;

England, 1965, 1968; Harris, 1967; Risser, 1969; Harris, 1973; Bebawi and Naylor, 1981; Harris *et al.* 1981, a,b). Further emphasis can be placed on these causal factors of competitive advantage of prairie grass and ryegrass over cocksfoot as Cullen (1964) states that such effects are more pronounced during establishment due to the interaction of early emergence and faster growth.

Ryegrass emerges 2-3 days earlier than prairie grass, although the latter has a faster initial growth rate, as illustrated by greater dry matter production (Table 3.5). Thus the larger prairie grass plant can be expected to utilize a greater proportion of the limited environmental resources due to its larger root and shoot systems (Appendices 3 and 4); thereby affecting the growth of ryegrass plants in ryegrass-prairie grass mixtures. Thus, these results highlight the importance of more extensive and rapid early growth rates rather than speed of germination in determining the competitive hierarchies between ryegrass and prairie grass. These competitive relationships do not change over the early growth phase, as indicated by the vegetative and yielding characteristics of the species in mixtures.

The effect of competitive dominance during establishment on subsequent performance can be evaluated by studying the RYTs and relative crowding coefficients based on yield components at every harvest during the second year. Neither the RYTs nor the products of the relative crowding coefficients depart significantly from unity (Table 3.10, Figure 3.4) thus illustrating competition for the same environmental resources by the component species. This effect does not differ from the first season, and can be expected as similar plants can generally be assumed to utilize similar biological environments. The competitive abilities of the species based on relative crowding coefficients also show the superior competitive ability of prairie grass over the other species and ryegrass over cocksfoot during the second year (Table 3.8). This trend appears to be independent of seasonal changes, and the relationships are similar to those of the establishment phase (Figure 3.3). Thus it is clear that competitive relationships established in the early growth phase of grass swards are extended to later stages of growth, especially if similar management practices are adopted throughout the lifespan of the sward. This observation is in agreement with reports of other workers (e.g. Rhodes, 1967; Harris, 1973).

Major changes in management practices and/or environment can effect changes in competitive relationships due to differential responses of grass species to such treatments, as illustrated by many researchers (e.g. England, 1965, 1968; Harris and Thomas, 1970, 1972; Harris *et al.*, 1981a,b; Remison and Snaydon, 1978, 1980). These effects could well change the competitive relationships observed in this study. For example, prairie grass, which is susceptible to heavy and consistent grazing pressure (Pantall, 1961; Langer 1973), may lose its competitive dominance under such conditions. In terms of climatic variations, if the seasonal changes, especially the warm dry periods of summer had lasted longer, bringing conditions of water stress, cocksfoot, which has been identified and used as a high producer under warm dry climatic conditions (Langer, 1973), may well have shown increased aggressivity reversing the observed inferior relationship with ryegrass and prairie grass. These factors need to be considered in the practical farming situation, where both environmental and management conditions are subject to considerable variability.

"Grasslands Matua" prairie grass has been identified as a superior winter growing species (Wilson, 1977; Vartha, 1977; Rumball, 1974; Lancashire, 1982). "Grasslands Nui" ryegrass is considered a good spring and autumn producer with abilities to produce even under dry conditions in summer (Armstrong, 1977; Harris *et al.*, 1977; Ritchie, 1975; Baars *et al.*, 1976; Sheath and Greenwood, 1982). "Grasslands Apanui" cocksfoot is identified as a good summer producing species (Langer, 1973; Vartha, 1975; Sheath and Greenwood, 1982). These seasonal growth characteristics of these grass species can be identified during the second year (Table 3.7). These are also illustrated in the yield component data and the relative crowding coefficients obtained in the second year (Figure 3.4, Table 3.8); which was considered an average year in terms of climatic variation across seasons. Although prairie grass shows overall dominance, the yields and the relative crowding coefficients of cocksfoot increase during warmer periods, while that of prairie grass decreases. This effect is reversed in winter. Ryegrass exhibits an increase in the relative crowding coefficient values in spring and autumn. These variations highlight the relationships between yielding ability and competitive ability under conditions suitable for the growth of the three species. They also illustrate the importance of competitive dominance established during early growth in maintaining similar relationships at later stages in pasture grass mixtures, especially under conditions of uniform management.

Van den Bergh (1968) working on grass mixtures concluded that "The problem of sowing grasslands is the choice of the highest yielding species under the prevailing conditions, rather than the highest yielding mixture". Many grass species and mixtures have been studied under different environmental conditions and the yields of mixtures lay between the monoculture yields, and slightly exceeded the mean yields of the pure stands (Donald, 1963; England 1968). Subsequently, Trenbath (1974a, 1978) reviewed a large number of experiments on both grass and cereal mixtures and concluded that yields of mixtures generally lie between the yields of the respective monocultures.

In terms of dry matter production, the results of this study largely supports the above findings. The dry matter production of mixtures do not exceed those of the respective monocultures, at any harvest (Tables 3.6, 3.7), and cumulative yields of the second year (Figure 3.3) also show the same effect. In contrast to these findings, Whittington and O'Brien (1968) indicated increased productivity of grass mixtures over the higher yielding monoculture at later stages of growth. Such conditions were reported by these authors in the third year of growth, especially under "grazing management". The results of Whittington and O'Brien's trials over the early growth phase conform to the general pattern of intermediate yields of mixtures, which is more prominent under "hay management" with infrequent harvests more akin to the present experiment and results. Closer evaluation of the RYT_s (Table 3.10) and the products of the relative crowding coefficients (Figure 3.4) in the second year show that all of the former and a major proportion of the latter exceed unity (although not significantly). This suggest a slightly superior performance of species in mixtures than in monocultures during later growth, and they may begin to compete for space which is not exactly the same (de Wit, 1960; van den Bergh and de Wit, 1965). Thus further evaluations of yields and competition indices over longer periods may present variations from that observed, as indicated by Whittington and O'Brien (1968), especially due to different growth periods of the species.

The yields of mixtures lying between the respective monocultures is termed "non transgressive yielding" by Trenbath (1974a) who has described its causal mechanisms. Competition for the same resources by species in mixtures is a major factor causing this "non transgressive yielding". In the context of mixtures yielding non transgressively,

it seems that there is no real advantage to the farmer in sowing a mixture of grass species if his aim is to maximize dry matter production under ideal conditions. However, this becomes valid only if the farmer knows in advance which species will yield most under the proposed management system (Harper, 1977). Thus, if uncertainty prevails, mixtures are believed on average to give higher yields than pure stands (Remison and Snaydon, 1980).

3.2.5 CONCLUSIONS

The results of this trial indicate that the grasses used compete for the same environmental resources, and the superior growth of one species is offset by the inferior performance of the companion species. Competition occurs between grass species in the establishment phase and these relationships and effects have a bearing upon later production and species relationships in grass mixtures, especially under uniform management. Amongst the grasses selected, prairie grass indicates potential as a good producing species and a more aggressive species than ryegrass or cocksfoot, and ryegrass than cocksfoot under the management conditions of this study. This overall superior performance of species can be related to early germination and emergence, and more extensive growth during the seedling stage. This enables the faster germinating and extensively growing larger species to establish and obtain more of the growth resources within the environment, thereby, inflicting a detrimental effect on the growth of the later emerging and/or the smaller species.



Plate 2. A general view of the box experiment.

3.3 EXPERIMENT 2. A STUDY ON THE EFFECTS OF COMPETITION ON PLANT PERFORMANCE AND THE YIELD OF BINARY MIXTURES OF GRASS SPECIES DURING THE ESTABLISHMENT PHASE FROM SEEDLINGS OF THE SAME AGE.

3.3.1 INTRODUCTION

Much research has been published on the importance of early emergence as a factor which provides a species with a distinct advantage when sown in a mixture. Studies by Stapledon and Davies (1927), Rummel (1946), Chippendale (1949), Blaser *et al.* (1956), Harris (1968) and many others (Section 2.4) have illustrated this in many grass species in different environments.

Experiment 1 (Section 3.1) illustrated the suppressive effect of prairie grass and ryegrass over cocksfoot during early growth stages, and this effect persists even at later stages of growth. As both prairie grass and ryegrass germinate and emerge earlier than cocksfoot, this was considered a contributory factor to the competitive advantage of the former species. Thus an experiment was designed to identify the competitive effects between the selected grass species, when the germination and emergence phase was excluded from the competitive relationships between the species, by transplanting seedlings of the same age, in binary mixtures.

3.3.2 EXPERIMENTAL PROCEDURE

3.3.2.1 The Site

The experiment was conducted at the Seed Technology Centre, Massey University, during the period January - June 1980. The boxes containing the micro swards were placed outdoors on a concrete floor and exposed to normal climatic conditions.

3.3.2.2 The Boxes

The microswards were established in boxes (30 x 30 x 18cm) (Plate 2). The soil used for the trial was a Tokomaru silt loam, collected from the site of the field trial (Section 3.2). The soil was passed through a 4 mm sieve to remove stones and the boxes were completely filled and left for one week for the soil to settle and then topped up.

3.3.2.3 Grass Species and Combinations

The same species and combinations used in the previous study were again used in this experiment.

3.3.2.4 Sward Establishment

Samples of the graded seed (Section 3.2) of the three species were germinated in plastic trays filled with perlite in a temperature controlled glasshouse (25^o/15^oC). After 21 days, the seedlings were placed near the experimental site for two days to harden the plants prior to planting.

A basal dressing of 25 g of 12:10:10:8 (N:P:K:S) fertiliser was watered into each box two days prior to planting, to prevent the development of possible nutrient deficiencies.

The seedlings of the three species were transplanted according to the replacement series principle of de Wit (1960) (Figure 3.6). A single seedling was planted at each point at a distance of 5 cm, in order to obtain an overall density of 400 plants per square meter, which was similar to that adopted in the field study. Within each species, the seedlings were selected for uniformity of size. At the time of planting, prairie grass had the largest seedling with 2-3 leaves, while cocksfoot had the smallest seedling with 1-2 leaves. Ryegrass seedlings had 3-4 leaves at the time of planting, although they were smaller than prairie grass seedlings.

3.3.2.5 Experimental Design

A randomized block design with three replicates was used for this study, with each box containing 30 plants making up one treatment within a replicate.

3.3.2.6 Management

The plants were watered during dry periods in order to provide adequate water for plant growth. There were no problems with diseases and pests during the experiment and emerging weeds were removed manually. All boxes were fertilized after each harvest with a uniform application of 20 g of Urea (43%N) per box, which was watered in.

3.3.2.7 Measurements

Plant height (the height from the soil level to the tip of the youngest leaf) and tiller numbers were measured from 4 weeks after establishment of seedlings, for a further four weeks. Thereafter, the swards were cut on 4 occasions to a height of 2 cm above soil level. At each harvest, plant height, tiller numbers and leaf area per plant was measured prior to drying the samples at 80°C for 24 hours to obtain dry matter production per plant and total dry matter production per box.

3.3.2.8 Statistical analysis

A similar procedure to that reported in section 3.2.2.7 was adopted for this experiment.

3.3.3 RESULTS

3.3.3.1 Vegetative Characters

The measurement of vegetative characters of plant growth, namely tiller numbers, shoot dry weights and leaf area are presented in Tables 3.12; 3.13 and 3.14 respectively. Plant height is presented in Appendix 6. The results show that the performance of all species is enhanced in comparison to their monocultures when grown with 25% of another species. This illustrates a greater intraspecific competitive effect within monocultures than interspecific competition between the species at the planting density used in this study. The enhanced growth of plants in a 75% mixture is least prominent in cocksfoot, especially when grown with prairie grass.

TABLE 3.12 Mean tiller number per plant of the grass species during early growth and prior to every harvest, when grown in mixtures and monocultures

Species mixtures	Mean tiller number						
	Time of measurement (wks after transplanting)						
	4	5	6	7 _(H1)	12 _(H2)	16 _(H3)	20 _(H4)
(A) RYEGRASS							
Monoculture	6.7	10.8	14.7	16.7	14.5	13.2	12.2
75R with 25P	7.1	11.3	15.0	16.7	14.6	13.7	13.1
50R with 50P	6.0	10.1	14.1	16.1	13.8	12.5	11.8
25R with 75P	5.5	9.8	13.9	15.6	13.4	11.9	11.3
75R with 25C	7.3	11.8	15.3	17.5	15.2	13.5	12.8
50R with 50C	7.0	11.3	15.0	17.0	14.7	13.3	12.6
25R with 75C	6.6	10.8	14.7	16.6	14.5	12.9	11.9
Significance	**	**	**	**	**	**	**
\bar{Sx}	0.05	0.10	0.05	0.06	0.06	0.07	0.04
(B) PRAIRIE GRASS							
Monoculture	3.0	5.9	8.7	12.2	12.0	11.6	10.8
75P with 25R	3.1	6.5	9.2	12.8	12.7	12.6	11.6
50P with 50R	2.9	6.2	8.9	12.4	12.4	12.3	11.1
25P with 75R	2.8	5.6	8.4	12.0	11.8	11.2	10.1
75P with 25C	3.0	6.6	9.3	12.9	12.7	12.4	11.5
50P with 50C	2.9	6.2	8.9	12.6	12.4	12.3	11.2
25P with 75C	2.7	5.8	8.6	12.1	12.0	11.7	10.5
Significance	**	**	**	**	**	**	**
\bar{Sx}	0.03	0.05	0.05	0.04	0.08	0.09	0.05
(C) COCKSFOOT							
Monoculture	3.0	5.0	6.9	9.3	8.7	8.0	7.6
75C with 25R	3.1	5.0	6.9	9.4	8.6	8.1	8.0
50C with 50R	2.9	4.7	6.6	9.0	8.4	7.9	7.5
25C with 75R	2.8	4.4	6.4	8.8	8.1	7.7	7.4
75C with 25P	3.0	5.0	6.9	9.4	8.6	8.0	7.7
25C with 50P	2.9	4.7	6.5	8.9	8.2	7.7	7.4
25C with 75P	2.7	4.3	6.3	8.6	7.9	7.6	7.3
Significance	**	**	**	**	**	**	**
\bar{Sx}	0.03	0.07	0.03	0.05	0.06	0.04	0.04

TABLE 3.13 Mean shoot weight per plant (g) of the grass species at every harvest, when grown in mixtures and in monocultures

Species mixture	Mean shoot weight per plant (g)			
	H ₁	H ₂	H ₃	H ₄
<u>A RYEGRASS</u>				
Monoculture	0.743	0.688	0.658	0.649
75R with 25P	0.774	0.707	0.676	0.661
50R with 50P	0.706	0.666	0.651	0.644
25R with 75P	0.684	0.634	0.642	0.625
75R with 25C	0.821	0.720	0.678	0.666
50R with 50C	0.775	0.709	0.671	0.659
25R with 75C	0.734	0.688	0.655	0.638
Significance	**	**	**	**
\bar{S}_x	0.009	0.004	0.009	0.007
<u>B PRAIRIE GRASS</u>				
Monoculture	1.496	1.293	0.998	0.906
75P with 25R	1.634	1.373	1.031	0.928
50P with 50R	1.584	1.339	1.017	0.918
25P with 75R	1.444	1.247	0.983	0.901
75P with 25C	1.700	1.374	1.012	0.937
50P with 50C	1.629	1.336	1.008	0.926
25P with 75C	1.485	1.298	0.999	0.907
Significance	**	**	**	**
\bar{S}_x	0.012	0.004	0.007	0.005
<u>C COCKSFOOT</u>				
Monoculture	0.654	0.648	0.618	0.595
75C with 25R	0.657	0.649	0.617	0.601
50C with 50R	0.620	0.616	0.598	0.580
25C with 75R	0.583	0.606	0.592	0.570
75C with 25P	0.655	0.647	0.619	0.597
50C with 50P	0.604	0.617	0.605	0.583
25C with 75P	0.562	0.611	0.599	0.571
Significance	**	**	**	**
\bar{S}_x	0.008	0.027	0.012	0.017

TABLE 3.14 Leaf area (cm²) per plant of the grass species at every harvest

Species combination	H ₁	H ₂	H ₃	H ₄
<u>(A) RYEGRASS</u>				
Monoculture	14.94	11.31	11.08	9.94
75R with 25P	15.11	11.23	11.24	10.59
50R with 50P	11.87	9.01	8.92	9.56
25R with 75P	12.85	8.33	9.18	8.76
75R with 25C	15.44	11.42	11.42	10.18
50R with 50C	16.06	13.61	12.61	11.04
25R with 75C	14.48	10.81	10.81	9.63
Significance	**	**	**	**
\bar{S}_x	0.143	0.102	0.072	0.113
<u>(B) PRAIRIE GRASS</u>				
Monoculture	27.07	21.41	20.57	19.66
75P with 25R	28.22	23.56	21.72	20.42
50P with 50R	30.81	25.72	22.63	20.51
25P with 75R	26.21	21.76	19.44	18.24
75P with 25C	28.74	23.06	21.81	21.12
50P with 50C	31.00	24.47	22.52	22.70
25P with 75C	26.81	22.68	21.20	19.08
Significance	**	**	**	**
\bar{S}_x	0.118	0.343	0.071	0.229
<u>(C) COCKSFOOT</u>				
Monoculture	13.37	9.81	9.60	9.06
75C with 25R	13.56	9.67	9.70	9.24
50C with 50R	10.51	7.36	7.36	7.02
25C with 75R	11.84	8.98	8.98	8.28
75C with 25P	13.30	9.60	9.52	9.16
50C with 50P	10.37	7.59	7.76	6.86
25C with 75P	10.92	7.41	7.93	7.26
Significance	**	**	**	**
\bar{S}_x	0.113	0.078	0.367	0.855

Generally, a higher proportion of the more competitive species has a greater suppressive effect on the growth of the weaker species in mixtures. This is illustrated in the 75% and 50% mixtures of prairie grass with the other species and in similar combinations of ryegrass with cocksfoot.

The more competitive species also increases its growth in comparison with its monoculture, when combined with less or equal proportions of the weaker species. Generally, the plants in 75% mixtures with 25% of the weaker species show greater growth rates than in their 50:50 mixtures. This is illustrated by both tiller numbers and shoot dry weights of prairie grass in combination with the other species and ryegrass with cocksfoot. In contrast, the leaf area of prairie grass is greater in its 50% combinations than in its 75% combinations with the other species. A similar effect is seen in ryegrass in the 50C:50R mixture.

Although prairie grass has a suppressive effect on the growth of the other species and ryegrass on cocksfoot in their 75% and 50% mixtures, the weaker species have an adverse effect on the growth of the more aggressive species in their 25% combinations with 75% of the weaker species. Ryegrass reduces the growth of prairie grass in the 75R:25P mixtures, when compared with the prairie grass monoculture. The adverse effect of cocksfoot on prairie grass in the 25P:75C mixture is minimal. However, cocksfoot has a greater adverse effect on ryegrass in the 75C:25R mixtures.

All these effects do not change over the experimental period, and plant height, tiller number and shoot weight relationships are similar to those observed in the field experiment during the establishment period.

The results also highlight the superior growth of prairie grass in terms of height, leaf area and dry matter production. Although ryegrass has a greater tiller number per plant than prairie grass, in competitive situations, the growth of ryegrass is affected and thus the tiller numbers are reduced by the presence of prairie grass plants in either equal or greater proportions (i.e. in 25R:75P and 50R:50P mixtures). Prairie grass increases its tiller numbers in these mixtures when compared with its monoculture. Cocksfoot is the smallest and the

weakest of these three species and is affected by the presence of the other species in mixtures.

The growth of cocksfoot is affected by prairie grass more than by ryegrass. This effect is seen in all vegetative characters and does not change with time.

3.3.3.2 Dry Matter Production

The results presented in this section indicates the total yield accumulated per box at each harvest.

Swards of prairie grass produced the highest yield at every harvest during this period, and mixtures containing a major proportion of prairie grass outyielded all other mixtures (Table 3.15). The yield of cocksfoot was the lowest, while ryegrass yields were in-between the other two monoculture yields.

TABLE 3.15 Dry matter yields (g/box)* of mixtures and monocultures at each harvest

Treatment (Weeks after planting)	Dry matter yield (g/box)			
	7 weeks (H ₁)	12 weeks (H ₂)	16 weeks (H ₃)	20 weeks (H ₄)
100R	14.95	11.31	11.08	9.94
75R 25P	17.92	13.89	13.31	12.53
50R 50P	22.34	17.36	16.77	15.70
25R 75P	24.77	19.82	18.63	17.54
100P	27.07	21.41	20.57	19.65
75P 25C	24.34	19.19	18.38	17.69
50P 50C	21.69	16.97	16.11	15.78
25P 75C	17.08	12.89	12.46	11.66
100C	13.34	9.81	9.60	9.06
75C 25R	13.82	9.98	10.00	9.36
50C 50C	13.62	10.48	10.48	9.56
25C 75R	14.57	10.83	10.81	9.70
Significance	**	**	**	**
\bar{S}_x	2.161	1.232	1.082	1.495

* Conversion factor to g/m² = yield per box x 11.11

The yields of all mixtures lay between the monoculture yields of the component species at all harvests. The contribution of prairie grass to the yields of mixtures was greater than its seed proportion in all mixtures. Ryegrass showed a similar trend in the ryegrass-cocksfoot mixtures (Figure 3.7). In general, the yielding pattern of the treatments did not change with time, although a decrease in dry matter production was noted with successive harvests. *My.*

3.3.3.3 Competitive Indices

Relative yield totals based on vegetative characters and yield components did not deviate significantly from 1 (Tables 3.16 and 3.17). In addition, most graphs obtained from the Thomas (1970) model (Figure 3.7) did not show a significant departure from the between-models test, and the products of the relative crowding coefficients were also close to unity.

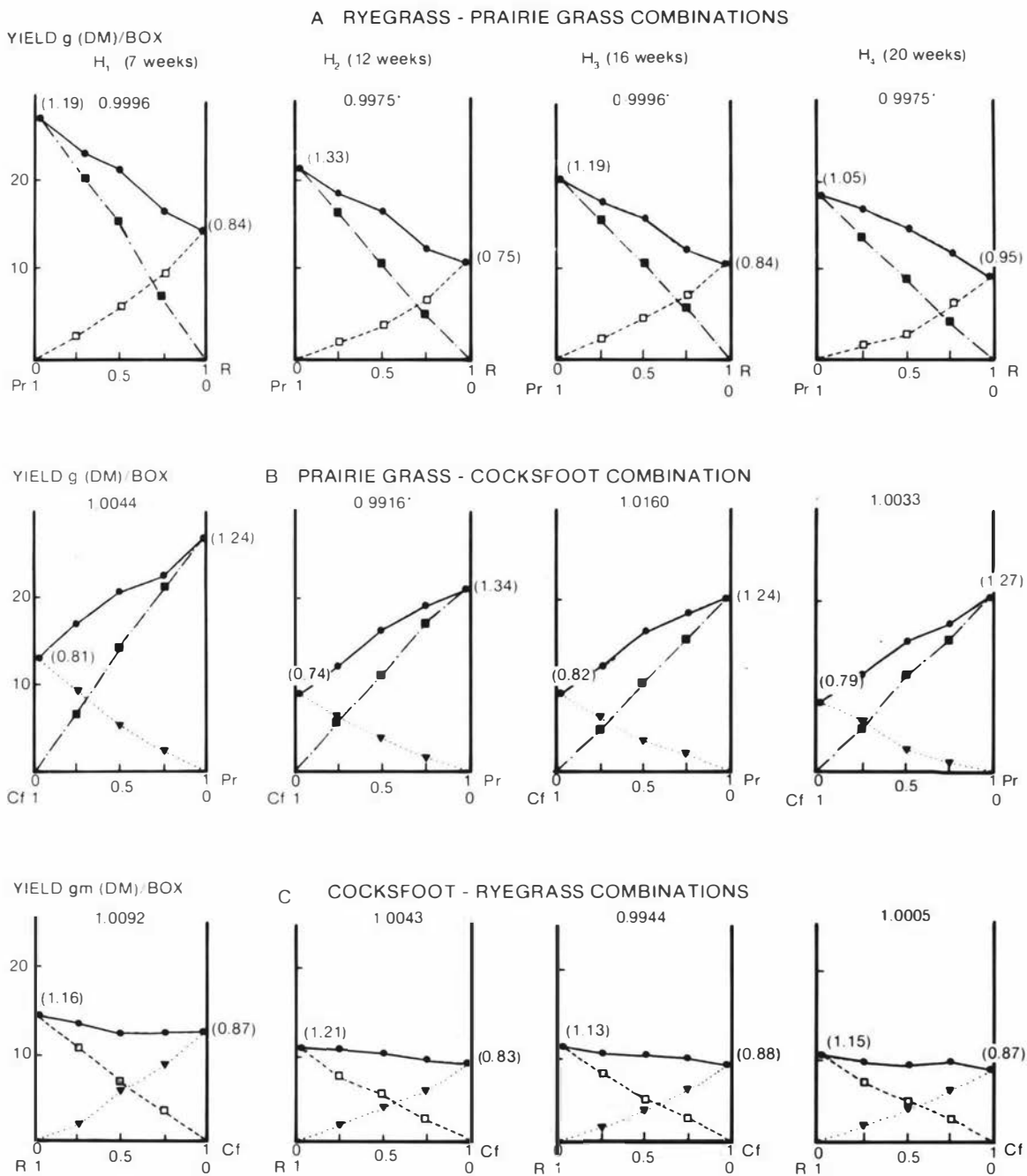


Figure 3.7 Replacement diagrams based on dry matter yields (g/box) of species components in grass mixtures and monocultures and the total yields at each harvest. Symbols and notations are similar to those of Figure 3.4.

TABLE 3.16 Relative yield totals based on vegetative characters of the 3 species - Experiment 2

(A) Tiller numbers per plant

Species combination	Weeks	4	5	6	7	12	16	20
Ryegrass-Prairie grass		0.995±.003	0.998±.006	0.996±.003	0.992±.003	0.995±.002	0.998±.002	0.999±.003
Prairie grass-Cocksfoot		0.995±.006	0.994±.004	0.992±.004	0.995±.002	0.993±.002	1.006±.004	1.001±.002
Cocksfoot-Ryegrass		1.005±.003	0.990±.005	0.995±.005	0.005±.005	0.992±.004	0.993±.003	1.008±.003

(B) Shoot weight per plant

Species combination	Weeks	7	12	16	20
Ryegrass-Prairie grass		1.005±.003	0.996±.002	1.005±.002	0.999±.003
Prairie grass-Cocksfoot		1.001±.002	0.998±.003	0.997±.002	0.999±.002
Cocksfoot-Ryegrass		0.996±.004	0.994±.003	0.995±.001	0.995±.003

TABLE 3.17 Relative yield totals based on yield components at each harvest - Experiment 2

Species combination	7 12 16 20 weeks after planting			
Ryegrass-Prairie grass	1.002±.002	1.003±.003	0.999±.009	1.003±.004
Prairie grass-Cocksfoot	0.999±.002	1.001±.002	1.003±.003	1.006±.004
Cocksfoot-Ryegrass	1.006±.003	1.005±.007	1.003±.004	1.002±.005

The relative competitive abilities of the species were examined by evaluating the relative crowding coefficients of each species at every harvest (Figure 3.7). Prairie grass consistently maintained a greater relative crowding coefficient than the other species, and the values were greater than one, which implied its superior competitive nature. The relative crowding coefficients of cocksfoot were always less than unity, illustrating its poor competitive ability in comparison with the other species. Ryegrass exhibited a superior competitive ability over cocksfoot. There was no change in the competitive abilities of the species with time.

Analysis of aggressivity of the three species also indicates the significantly superior competitive ability of prairie grass over the other species and ryegrass over cocksfoot (Table 3.18). While prairie grass was generally more aggressive than cocksfoot and ryegrass in its 75% and 50% mixtures, ryegrass demonstrated greater aggressivity than prairie grass in the 75R:25P mixture (denoted by the negative aggressivity index of prairie grass). The greater effect of cocksfoot on the competitive ability of ryegrass than on prairie grass in its 75% mixtures with those species is highlighted by the aggressivity indices.

Although the aggressive nature of prairie grass over the other species and of ryegrass over cocksfoot did not change over the experimental period, the aggressivity indices of the more competitive species declined over time. This effect is clearly seen in the aggressivity indices based on shoot weights. The aggressivity indices of prairie grass and ryegrass decrease with successive harvests when grown with cocksfoot and that of prairie grass when grown with ryegrass. The results also show that ryegrass has a greater effect on the growth of prairie grass than cocksfoot, as the aggressivity indices of prairie grass are less when combined with ryegrass than when combined with cocksfoot (Table 3.18).

TABLE 3.18 Aggressivity indices of the more aggressive species based on the vegetative characters of the 3 species - Experiment 2.

Time of measurement		Treatment combinations																							
<u>(A) Tiller Numbers</u>		Aggressivity of Prairie grass in combination with Ryegrass					Aggressivity of Prairie grass in combination with Cocksfoot					Aggressivity of Ryegrass in combination with Cocksfoot													
		75R	25P	50R	50P	25R	75P	Signif	+SE	75P	25C	50P	50C	25P	75C	Signif	+SE	75C	25R	50C	50R	25C	75R	Signif	+SE
Wk	4	-0.050	0.105	0.171		**	0.014	0.092	0.049	-0.005	*	0.016	-0.024	0.033	0.072	*	0.013								
	5	-0.044	0.059	0.099		**	0.012	0.134	0.063	0.000	*	0.018	0.005	0.060	0.103	*	0.019								
	6	-0.026	0.029	0.056		**	0.007	0.076	0.037	-0.008	**	0.008	0.000	0.031	0.062	**	0.007								
	7	-0.009	0.028	0.055		**	0.005	0.060	0.041	-0.005	*	0.005	-0.002	0.027	0.055	**	0.006								
	12	-0.010	0.044	0.071		**	0.009	0.073	0.046	0.008	*	0.010	0.002	0.025	0.059	**	0.005								
	16	-0.039	0.052	0.092		**	0.012	0.063	0.054	0.004	NS	0.014	-0.014	0.013	0.034	**	0.006								
	20	-0.023	0.034	0.075		NS	0.025	0.054	0.031	-0.021	*	0.012	-0.037	0.021	0.042	**	0.003								
<u>(B) Shoot Weight</u>																									
Wk	7	-0.036	0.054	0.085		*	0.019	0.134	0.082	-0.005	**	0.007	-0.009	0.046	0.105	**	0.011								
	12	-0.031	0.034	0.070		**	0.006	0.059	0.041	-0.007	**	0.009	-0.002	0.039	0.055	**	0.006								
	16	-0.022	0.015	0.028		**	0.007	0.022	0.015	-0.001	*	0.006	-0.002	0.026	0.036	**	0.002								
	20	-0.011	0.011	0.024		*	0.007	0.037	0.021	-0.002	*	0.006	-0.013	0.021	0.033	**	0.009								

3.3.4 DISCUSSION

The primary objective of this experiment was to evaluate the competitive relationships that develop among the selected grass species when established as mixtures from seedlings of the same age. This was done to overcome any advantageous effects that may develop due to earlier emergence by one species.

The results of this study are similar to those of the field trial, where pasture swards were established from seed. The dominant affect of prairie grass over the other species is illustrated in all vegetative characters measured, and by the relative crowding coefficients. The superior competitive affect of ryegrass on cocksfoot is also illustrated by the results. Thus the absence of the effect of early emergence of both ryegrass and prairie grass over cocksfoot does not seem to have made a great impact on the competitive hierarchies established between the species.

A larger initial size and more rapid growth ensures the success of a seedling by obtaining a greater share of the environment in terms of growth requirements. The larger area occupied by the initially larger and extensively growing species gives it a greater capacity to exploit its surroundings, thereby depriving the smaller and slower growing species of growth resources. The results present this situation, as prairie grass and ryegrass seedlings are bigger and also grow more extensively than cocksfoot seedlings. Thus, the superior competitive ability of these species over cocksfoot during the early growth phase can be attributed mainly to their initially larger seedling sizes, larger plant forms and extensive growth patterns, rather than any differences in time of emergence, which was also considered an important factor in the earlier experiment. In addition, these studies are in accordance with many studies which have illustrated the importance of a larger initial seedling and more rapid growth on successful plant establishment and competitive advantage (e.g. Stapledon and Davies, 1927; Blaser *et al.*, 1952b, 1956; Cullen, 1964; Harris, 1968; McKell, 1972 - see section 2.4).

Later emerging species often offset this drawback if they have a larger seedling and more rapid growth rates, by being more efficient in absorbing growth resources from the environment and using them to

produce dry matter (Trenbath *et al.*, 1977). The superior competitive ability of prairie grass over ryegrass can again be attributed to this factor, as although ryegrass emerges 2-3 days earlier (Section 3.2), prairie grass has a larger seedling which grows faster.

Although the superior growth patterns of the more aggressive species decrease with increasing proportions of the weaker species, leaf area of both prairie grass and ryegrass increases in these 50:50 mixtures with the weaker species. This effect is not observed in plant dry weights and was not noticed in the field trial. However, such a phenomenon may be possible due to greater light infiltration into the canopy leading to greater leaf expansion due to the reduction in the number of plants of the same species in this particular mixture, when compared with either its monoculture or the 75% mixtures.

As the relative yield totals and products of the relative crowding coefficients are close to unity, it can be concluded that the species compete for the same environmental resources under the conditions of the experiment (de Wit, 1960; Trenbath, 1974a). This can be attributed to the growth forms of the grass species during this early period, which are generally similar (Langer, 1972). Due to competition for the same environmental resources, the more aggressive species obtains a greater share of the growth resources within that environment due to its larger plant form and more rapid growth rate, even in situations when slower in emergence. This reduces the availability of resources to the weaker species and thus affects its growth. This competitive effect will be further accentuated in this experiment as the plants are grown in boxes, which inevitably limits the soil environment available for root growth.

The yields of the mixtures lie between those of the respective monocultures, conforming to the general trend among grass species (Trenbath, 1974a). Thus, as reported by Remison and Snaydon (1980), in the short term, there does not seem to be an advantage in growing a mixture of grasses under ideal management conditions, if the highest yielding species in that environment can be identified.

The reductions in yields of the swards and shoot weights with successive harvests may have resulted from the limited size of the soil environment available for root growth. The reduction in aggressiveness indices of the species, especially as seen in values calculated from shoot weights may also be a result of this restrictive size of the soil environment, as restrictions on root growth affects shoot growth (Davidson, 1978).

3.3.5 CONCLUSIONS

The competitive hierarchy established between prairie grass, ryegrass and cocksfoot is dependent to a great extent upon the initial seedling size, and more extensive and rapid initial growth rates. This is best illustrated by the superior competitive nature of prairie grass over ryegrass. However, early emergence can give an additional advantage to a rapidly and extensively-growing species such as ryegrass or prairie grass enabling it to successfully establish and secure growth resources from the environment before the later emergence of an associated species (e.g. cocksfoot).

The species examined generally compete for the same environmental resources. The depressed growth of the weaker species is compensated by a proportional increase in productivity of the more aggressive species, thus indicating a compensatory competitive nature, which results in relative yield totals being close to unity and mixtures yielding in-between the respective monocultures.

3.4 EXPERIMENT 3. A STUDY ON THE EFFECTS OF COMPETITION ON PLANT PERFORMANCE AND THE YIELD OF BINARY MIXTURES OF GRASS SPECIES DURING THE ESTABLISHMENT PHASE FROM SEEDLINGS OF SIMILAR GROWTH STAGE, AND THE EFFECT OF TEMPERATURE ON THEIR RELATIONSHIPS.

3.4.1 INTRODUCTION

The superior competitive abilities of prairie grass and ryegrass over cocksfoot, and of prairie grass over ryegrass have been attributed to their relatively larger initial seedling size and more rapid growth rates. These characteristics are assisted by relatively earlier emergence of both ryegrass and prairie grass when compared with cocksfoot. As growth rates and forms of species are inherent characters, it was desired to evaluate the competitive relationships between the selected species when the initial advantage of a larger seedling of the more competitive species was minimized. Thus, the experiment was designed to use seedlings of a similar growth stage to construct the microwards.

New Zealand pastures are generally established in spring or autumn (Levy, 1970; White, 1973), and these seasons have different temperature regimes. Such differences may affect the competitive relationships between the selected grass species in the establishment period, as temperature is reported to have a bearing upon competitive relationships between pasture species (e.g. van den Bergh and de Wit, 1960; Eagles and Williams, 1969, 1971; Harris *et al.* 1981b); and on the botanical composition of pastures (Fitzpatrick and Nix, 1970). Thus it was considered desirable to evaluate the effect of simulated spring and autumn temperature regimes on the competitive interactions between the three species, during the early growth stages, using controlled climate facilities.

3.4.2 EXPERIMENTAL PROCEDURE

3.4.2.1 Environmental Conditions

The experiment was carried out in the controlled environment rooms at the Plant Physiology Division, Department of Scientific and Industrial Research, Palmerston North, during the period May - August 1980. The temperature was controlled at 14^oday/6^oC night \pm 0.5^oC in one room and at 20^oC day/10^oC night \pm 0.5^oC in the other. The lower temperature regime was considered to represent the mean sward temperature of the autumn months from March - May, while the higher temperature represented the spring months from September to November. The temperature regimes

were established using a 50 year average of the mean monthly maximum and minimum screen temperatures of 32 stations of the New Zealand meteorological service in the central region of the country, ranging from Waikato to Canterbury. In using the monthly mean maximum and minimum temperatures, it was accepted that these temperatures were not sustained over long periods. However, this effect was assumed to be largely compensated as screen maxima are generally as much as 3°C-5°C lower than canopy maxima and grass minima are as much as 3°C lower than screen minima. Similar assumptions have been made by Harris *et al.* (1981a).

The water vapour pressure deficit in both rooms was 10/2 mb (day/night) representing relative humidities of 37.4% RH day/78.6% RH night \pm 5% RH at 14°/6°C and 65.2% RH day/83.7% RH night \pm 5% RH at 20°/10°C. The diurnal temperature and humidity changeover occurred over 2 hours, the 12 hours photoperiod beginning and ending half way through the changeover. The mean photosynthetic irradiance at standard trolley height in each room was 155 W.M.⁻² provided by a combination of 4 x 1 kw "metal arc" high pressure discharge lamps and 4 x 1 kw tungsten iodide lamps, filtered through a 3 cm water thermal barrier.

3.4.2.2 Cultural

The seeds of the three species were sown into germination trays containing sand, and placed in a heated glasshouse (25°/15°C). As seedlings of the same growth stage were required to establish the micro-swards, cocksfoot seeds were sown 8 days prior to the other species as it takes a longer time interval to germinate. When the seedlings of the three species reached the 2-leaf stage (i.e. approximately 14 days after emergence) they were transplanted into plastic containers (18 x 18 x 18 cm) containing approximately 4 litres of Opiki peat loam:sand (70:30 v/v) potting mixture. The seedlings were transplanted at one per each of the 16 locations on a 5 cm equally spaced matrix (i.e. 400 plants per sq. metre, which was similar to that of the earlier studies). Although all three species had reached the 2 leaf stage, prairie grass seedlings were taller and larger than ryegrass, and cocksfoot. The pot size containing 16 plants was considered adequate to observe treatment differences between species, based on studies reported by Rogers and Lazenby (1966).

The plants in the containers were arranged in a replacement series

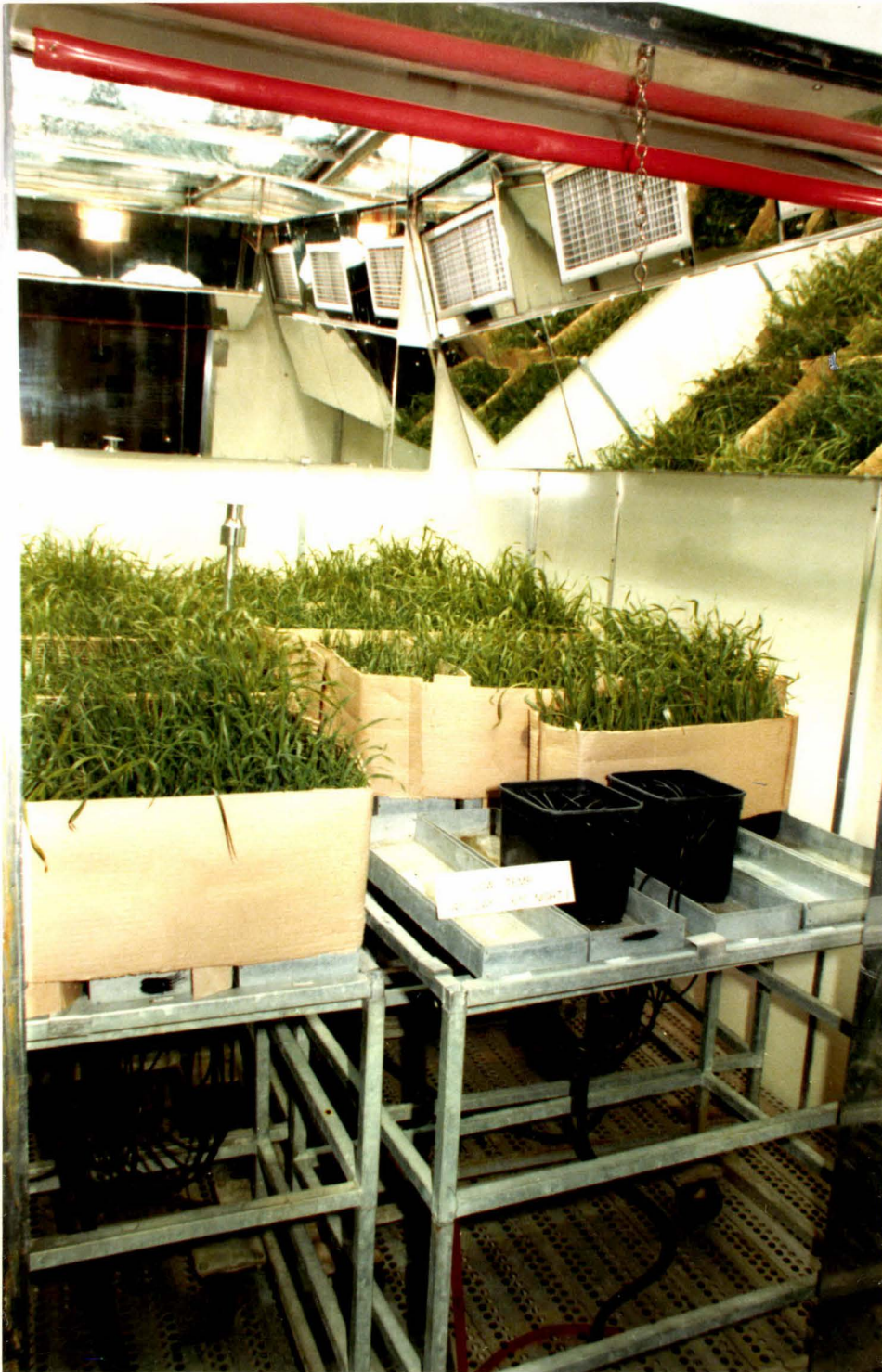


Plate 3. The layout of the experiment in the controlled environment rooms.

to obtain the nine mixtures and three monocultures used in previous experiments.

The transplanted seedlings were kept for 7 days in the glasshouse prior to being placed in the controlled environment rooms. While the pots were in the glasshouse, 100 ml of $\frac{1}{2}$ strength modified "Hoaglands-A" mineral nutrient solution and 100 ml of water was added to each pot daily. In the controlled environment rooms all pots received 2 x 100 ml applications of the above mineral nutrient solution daily, metered through an automated microtube system.

3.4.2.3 Experimental Layout

Each treatment contained 3 pots placed adjacent to each other, giving a total of 48 plants per treatment. The treatments were replicated three times and the pots were placed on 8 trolleys in each room. To prevent different species mixtures shading each other and to limit light entering the plant canopies laterally, cardboard shields were placed between the sward types. As the plants grew, the shields were moved upwards to surround the plant canopies to about 2/3rds of their maximum height (Plate 3).

The experimental design used was a randomised block design.

3.4.2.4 Measurements

In order to overcome differential responses of species to environmental conditions, all measurements were made at an average of 50% and 95% light interception across all swards. Light interception was measured using a "Li-Cor" quantum meter, as described in the first experiment (Section 3.2.2).

Plant height (measured from the base of each plant to tip of youngest leaf) and tiller numbers were measured at 50% and 95% light interception on three occasions.

The plants were harvested approximately 5 days after the swards reached an average light interception of 95%, thus allowing full interactive effects to occur between plant canopies in terms of competition for light. The plants were cut to a height level to the rim of the pot (about 2 cm above soil level). Three harvests were made from each

of the two temperature regimes. At every harvest, the leaf area of each plant was measured, prior to drying at 40°C in a vacuum oven for 24 hours to obtain dry matter production per plant and per pot.

3.4.2.5 Statistical Analysis

The techniques used were similar to those reported earlier (Section 3.2.2.7).

3.4.3 RESULTS

The microswards in the lower temperature regime took a longer time to reach 95% light interception. While the swards in the warmer temperature regime reached the harvesting stage within 4 weeks of moving the pots to the climate rooms, those in the lower temperature room reached this stage 7-10 days later. This pattern continued throughout the experiment.

Both temperature regimes produced large succulent plants due to the controlled environmental conditions. However, the overall trends of interaction did not change from those observed in the field or box trial.

The growth of all species in the high temperature regime was greater in terms of all characters studied. There was no overall change in relationships between the species with changes in temperature, thus implying that the selected temperatures had little effect on the competitive relationships between the species.

3.4.3.1 Vegetative Characters

All characters measured again highlighted the overall superior growth and competitive ability of prairie grass over the other species and ryegrass over cocksfoot.

Prairie grass was the tallest species (Appendix 7) while cocksfoot was the shortest. The height of every species in its 75% mixtures was greater than their respective monocultures. The height of associated species in these mixtures were significantly reduced when compared with their monocultures.

Prairie grass affected the growth of the other species and ryegrass affected cocksfoot in their 75% and 50% mixtures. However, cocksfoot

in turn had a detrimental effect on associated species in its 75% mixtures. This is clearly illustrated by tiller numbers (Table 3.19), leaf areas (Table 3.20) and plant dry weights (Table 3.21).

TABLE 3.19 Mean tiller numbers per plant of the grass species at high and low temperatures, measured at an average light interception of 50% and 95% across all treatments

Species mixture	50% LI		95% LI (H ₁)		50% LI		95% LI (H ₂)		50% LI		95% LI (H ₃)	
	High T ^o	Low T ^o	High T ^o	Low T ^o	High T ^o	Low T ^o	High T ^o	Low T ^o	High T ^o	Low T ^o	High T ^o	Low T ^o
(A) Ryegrass												
Monoculture	10.1	6.6	15.8	14.2	9.8	8.9	13.4	12.6	8.2	8.2	12.8	12.2
75R with 25P	11.0	7.1	16.6	14.6	10.3	9.8	14.2	12.9	9.0	8.8	13.6	12.8
50R with 50P	9.6	6.5	15.6	14.0	9.5	8.7	13.3	12.4	8.0	7.9	12.5	11.9
25R with 75P	9.1	6.0	15.0	13.7	9.0	8.2	12.8	12.1	7.2	7.5	12.1	11.7
75R with 25C	10.7	7.1	17.0	14.5	10.1	9.5	14.3	13.3	9.3	8.6	13.2	12.6
50R with 50C	10.5	6.8	16.1	14.4	9.6	8.9	13.8	13.0	8.3	8.3	13.2	12.3
25R with 75C	9.6	6.5	14.9	13.7	9.4	8.1	12.6	12.1	7.1	7.6	12.3	11.9
Significance	**	**	**	**	**	**	**	**	**	**	**	**
S _x	0.26	0.15	0.31	0.22	0.31	0.25	0.27	0.13	0.35	0.21	0.24	0.26
(B) Prairie grass												
Monoculture	6.1	4.3	10.3	8.6	6.0	4.3	9.6	7.9	5.2	4.3	8.5	6.9
75P with 25R	6.4	4.7	10.7	9.1	6.6	4.7	10.2	8.2	5.8	4.6	8.9	7.3
50P with 50R	6.4	4.4	10.4	8.8	6.1	4.5	9.8	8.2	5.3	4.4	8.7	7.3
25P with 75R	5.6	3.9	9.6	8.1	5.4	4.0	8.9	7.6	4.6	3.8	7.7	6.6
75P with 25C	6.5	4.8	11.1	9.1	6.5	4.6	10.3	8.6	5.8	4.6	9.1	7.7
50P with 50C	6.5	4.6	10.8	8.8	6.5	4.4	9.9	8.4	5.5	4.5	8.7	7.3
25P with 75C	5.9	4.3	9.7	8.4	5.6	4.2	9.1	8.0	4.9	4.0	7.8	6.5
Significance	**	**	**	**	**	**	**	**	**	**	**	**
S _x	0.21	0.12	0.22	0.16	0.20	0.15	0.26	0.20	0.22	0.14	0.23	0.18
(C) Cocksfoot												
Monoculture	7.3	4.6	11.7	9.0	6.6	6.2	11.0	8.7	6.0	5.4	9.2	7.7
75C with 25R	7.9	4.7	12.6	9.2	7.2	6.4	11.7	9.1	6.7	5.9	9.7	8.0
50C with 50R	7.0	4.5	11.3	8.8	6.6	6.1	10.6	8.2	5.8	5.3	8.8	7.6
25C with 75R	6.8	4.2	10.6	8.7	6.0	5.8	10.0	8.1	5.1	5.0	8.3	7.3
75C with 25P	7.5	4.8	12.4	9.2	7.1	6.3	11.4	8.8	6.3	5.8	9.9	8.3
50C with 50P	6.8	4.3	11.2	8.5	6.2	5.5	10.4	8.3	5.6	5.1	8.8	7.4
25C with 75P	6.9	4.1	11.0	8.7	6.1	5.7	10.2	7.8	5.2	5.0	8.6	7.2
Significance	**	**	**	**	**	**	**	**	**	**	**	**
S _x	0.28	0.12	0.29	0.15	0.27	0.27	0.34	0.12	0.16	0.18	0.30	0.24

(*High T^o = High temperature; Low T^o = Low temperature)

TABLE 3.20 Mean leaf area per plant (cm²) of the 3 grass species at every harvest for the two temperature regimes

Species mixture	H ₁		H ₂		H ₃	
	High T ^o	Low T ^o	High T ^o	Low T ^o	High T ^o	Low T ^o
(A) RYEGRASS						
Monoculture	120.6	113.9	124.9	111.4	111.3	99.3
75R with 25P	133.0	126.1	129.2	120.3	116.9	103.0
50R with 50P	124.5	106.5	122.0	109.8	109.8	96.2
25R with 75P	119.6	99.0	118.6	102.1	107.3	91.1
75R with 25C	130.7	122.9	127.6	117.8	117.6	105.5
50R with 50C	130.3	119.1	125.5	115.1	113.8	101.7
25R with 75C	122.3	105.4	119.3	106.4	106.1	93.2
Significance	**	**	**	**	*	**
\bar{Sx}	3.27	5.38	2.04	2.91	3.91	2.15
(B) PRAIRIE GRASS						
Monoculture	217.9	160.0	207.5	176.2	205.1	125.3
75P with 25R	223.9	176.6	217.4	188.0	213.2	133.6
50P with 50R	216.9	168.3	210.4	179.2	208.3	128.2
25P with 75R	206.6	143.5	195.5	162.7	197.2	119.9
75P with 25C	224.9	171.7	213.9	186.9	210.4	135.2
50P with 50C	218.2	168.3	210.4	179.1	209.8	133.9
25P with 75C	209.8	160.2	201.0	172.7	193.9	120.5
Significance	**	**	*	**	**	**
\bar{Sx}	2.89	6.02	5.94	3.00	3.87	3.33
(C) COCKSFOOT						
Monoculture	124.0	105.8	120.8	104.3	109.6	82.9
75C with 25R	128.3	110.1	124.9	106.5	114.4	88.6
50C with 50R	118.2	99.6	119.9	98.9	106.5	81.1
25C with 75R	118.6	97.5	117.8	90.5	101.3	76.7
75C with 25P	128.3	107.8	128.6	108.1	113.9	84.9
50C with 50P	119.6	99.8	117.3	103.2	108.0	76.3
25C with 75P	117.5	97.7	115.7	89.7	103.2	75.4
Significance	*	**	*	**	**	**
\bar{Sx}	3.74	3.62	1.80	2.74	3.10	1.72

TABLE 3.21 Mean shoot weight (g plant⁻¹D.M.) of the grass species at every harvest for the two temperature regimes.

Species mixture	Harvest 1		Harvest 2		Harvest 3	
	High T ^o	Low T ^o	High T ^o	Low T ^o	High T ^o	Low T ^o
(A) RYEGRASS						
Monoculture	0.583	0.509	0.565	0.510	0.557	0.479
75R with 25P	0.607	0.519	0.572	0.516	0.564	0.493
50R with 50P	0.570	0.505	0.553	0.508	0.551	0.475
25R with 75P	0.547	0.495	0.538	0.501	0.545	0.474
75R with 25C	0.608	0.517	0.580	0.520	0.571	0.492
50R with 50C	0.594	0.514	0.571	0.513	0.561	0.484
25R with 75C	0.560	0.495	0.552	0.502	0.547	0.471
Significance	**	*	**	**	**	**
\bar{Sx} ($\times 10$)	0.067	0.047	0.032	0.027	0.027	0.018
(B) PRAIRIE GRASS						
Monoculture	1.238	0.974	1.033	0.981	0.982	0.833
75P with 25R	1.316	0.984	1.094	0.989	0.992	0.842
50P with 50R	1.255	0.977	1.054	0.984	0.985	0.836
25P with 75R	1.188	0.963	1.008	0.971	0.959	0.821
75P with 25C	1.314	0.981	1.057	0.990	1.003	0.849
50P with 50C	1.275	0.978	1.041	0.987	0.987	0.840
25P with 75C	1.192	0.973	1.015	0.978	0.972	0.832
Significance	**	**	**	**	**	**
\bar{Sx} ($\times 10$)	0.023	0.019	0.062	0.015	0.033	0.028
(C) COCKSFOOT						
Monoculture	0.553	0.487	0.522	0.497	0.533	0.414
75C with 25R	0.575	0.493	0.531	0.504	0.543	0.422
50C with 50R	0.535	0.481	0.515	0.490	0.524	0.404
25C with 75R	0.527	0.479	0.511	0.487	0.510	0.396
75C with 25P	0.566	0.488	0.530	0.497	0.537	0.418
50C with 50P	0.530	0.480	0.513	0.489	0.522	0.402
25C with 75P	0.510	0.478	0.505	0.485	0.509	0.396
Significance	**	**	**	**	**	**
\bar{Sx} ($\times 10$)	0.042	0.023	0.030	0.027	0.040	0.036

The growth and development of prairie grass and to a greater extent ryegrass was significantly reduced when grown with 75% cocksfoot, in comparison with their respective monocultures. This suppressive effect of cocksfoot is greater than that observed in earlier trials.

The effect of ryegrass on prairie grass in the 75R 25P mixtures is also greater than that observed earlier.

Although prairie grass plants produced the highest dry matter and cocksfoot the least, the differences between the species, especially between ryegrass and cocksfoot were less in this trial (Table 3.21). compared with the previous trials (Tables 3.5 and 3.13).

3.4.2.2 Dry Matter Production

Table 3.22 presents the dry matter accumulation (g per pot) at each harvest.

These results follow the same trends of the previous trials. Prairie grass yielded the highest dry matter per pot and the mixtures with prairie grass outyielded ryegrass-cocksfoot mixtures. Prairie grass contributed more dry matter than its seed proportions in all mixtures (Figure 3.8). Ryegrass outyielded cocksfoot, although the differences were less marked than earlier trials. The yields of all mixtures lay between the respective monocultures, and a decrease in sward productivity is seen with successive harvests.

3.4.3.3 Competitive Effects

Analysis of relative yield totals based on tiller numbers and shoot weights (Table 3.23), yield components (Table 3.24) and the products of the relative crowding coefficients (Figure 3.8) do not indicate a significant departure from unity.

TABLE 3.22 Dry matter yields (g pot^{-1})* of the micro swards for the two temperature regimes.

Sward type	Harvest 1		Harvest 2		Harvest 3	
	High Temp	Low Temp	High Temp	Low Temp	High Temp	Low Temp
100 R	7.160	6.721	6.401	5.973	6.455	6.047
75R 25P	9.025	7.982	7.973	7.267	7.600	7.034
50R 50P	10.885	9.456	9.601	8.747	8.825	8.038
25R 75P	12.814	10.818	11.238	10.208	10.039	9.090
100 P	14.271	11.840	12.530	11.353	11.042	9.889
75P 25C	12.568	10.504	11.168	10.224	9.917	8.799
50P 50C	10.373	9.039	9.344	8.611	8.551	7.487
25P 75C	8.180	7.351	7.431	7.199	6.940	6.237
100 C	6.072	5.833	5.685	5.680	5.604	5.002
75C 25R	6.374	6.113	5.987	5.808	5.850	5.260
50C 50R	6.649	6.319	6.146	5.831	6.055	5.544
25C 75R	6.983	6.577	6.279	5.985	6.304	5.853
Significance	**	**	**	**	**	**
\bar{Sx}	0.240	0.064	0.153	0.112	0.116	0.098

* Conversion factor to $\text{gm/m}^2 = \text{g/pot} \times 30.86$

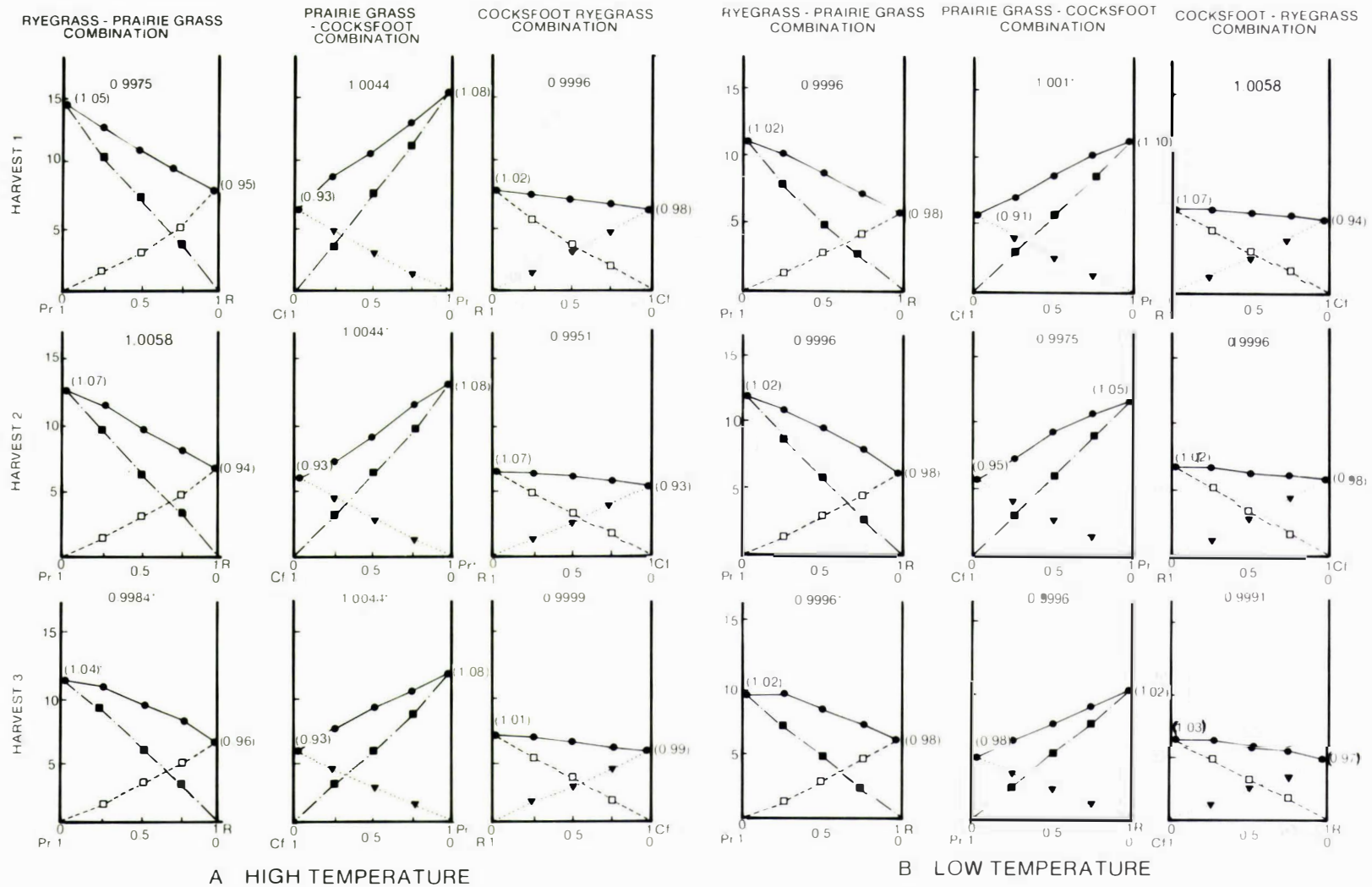


Figure 3.8 Replacement diagrams based on dry matter yields (g pot^{-1}) of species components in grass mixtures and the monocultures and total yields at each harvest for the high temperature (A) and low temperature (B) regimes. Symbols and conventions as for Figure 3.4.

TABLE 3.23 Relative yield totals based on vegetative characters of the 3 grass species at the two temperature regimes

(A) <u>Tiller numbers</u>	50% LI		95% LI (H ₁)		50% LI		95% LI (H ₂)		50% LI		95% LI (H ₃)	
	High T ^o	Low T ^o	High T ^o	Low T ^o	High T ^o	Low T ^o	High T ^o	Low T ^o	High T ^o	Low T ^o	High T ^o	Low T ^o
Ryegrass-Prairie-grass	0.993 ₊ .017	0.993 ₊ .008	0.997 ₊ .008	0.997 ₊ .015	1.001 ₊ .006	0.998 ₊ .008	1.001 ₊ .011	0.999 ₊ .014	0.995 ₊ .009	0.992 ₊ .007	0.996 ₊ .006	0.997 ₊ .007
Prairie grass-Cocksfoot	1.001 ₊ .013	0.999 ₊ .013	1.000 ₊ .007	0.996 ₊ .009	1.001 ₊ .010	0.993 ₊ .013	0.994 ₊ .010	0.990 ₊ .012	0.991 ₊ .014	0.993 ₊ .012	0.997 ₊ .006	0.998 ₊ .010
Ryegrass-Cocksfoot	0.999 ₊ .007	0.995 ₊ .011	0.995 ₊ .007	0.993 ₊ .011	0.996 ₊ .010	0.994 ₊ .008	0.997 ₊ .004	0.990 ₊ .010	0.994 ₊ .010	0.994 ₊ .008	0.998 ₊ .014	0.996 ₊ .009

(B) <u>Shoot weight</u>	Harvest 1		Harvest 2		Harvest 3	
	High T ^o	Low T ^o	High T ^o	Low T ^o	High T ^o	Low T ^o
Ryegrass-Prairie grass	0.998 ₊ .007	0.997 ₊ .004	0.999 ₊ .006	0.998 ₊ .005	0.994 ₊ .006	1.001 ₊ .002
Prairie grass-Cocksfoot	0.993 ₊ .011	0.996 ₊ .003	0.996 ₊ .005	0.996 ₊ .004	0.996 ₊ .004	0.993 ₊ .005
Ryegrass-Cocksfoot	0.994 ₊ .006	0.997 ₊ .004	0.999 ₊ .007	0.993 ₊ .005	0.999 ₊ .004	0.994 ₊ .006

TABLE 3.24 Relative yield totals based on yield components at every harvest for the two temperature regimes

Species combinations	Harvest 1		Harvest 2		Harvest 3	
	High T ^o	Low T ^o	High T ^o	Low T ^o	High T ^o	Low T ^o
Ryegrass-Prairie grass	1.009±.006	1.001±.003	1.005±.007	1.003±.009	1.002±.004	1.007±.005
Prairie grass-Cocksfoot	1.005±.011	1.008±.006	1.004±.010	1.008±.009	1.005±.003	1.006±.006
Cocksfoot-Ryegrass	1.006±.006	1.007±.010	1.006±.011	1.003±.009	1.005±.011	1.005±.007

Thus it can be concluded that under these experimental conditions the species were competing for the same environmental resources ('biological space') (de Wit and van den Bergh, 1965). This trend did not change with time.

The replacement diagrams were drawn and relative crowding coefficients calculated according to the 3-parameter model of Thomas (1970) (Appendix 1), as the between species variance tests were non significant. These diagrams and the relative crowding coefficients (Figure 3.8) illustrate the overall superior competitive ability of prairie grass over the other species and of ryegrass over cocksfoot. However, the relative crowding coefficients of both ryegrass and cocksfoot in their combinations with prairie grass are increased when compared with those of the earlier trials (Figures 3.4; 3.5 and 3.7). This illustrates an increase in their respective competitive abilities in this trial. The relative crowding coefficients of prairie grass are reduced when compared with those of the earlier trials, although still greater than those of the other species. Similar trends occur in the ryegrass-cocksfoot combinations.

The aggressivity indices based on tiller numbers and shoot weights (Table 3.25) also show the more aggressive nature of prairie grass over the other species and of ryegrass over cocksfoot. However, cocksfoot is more aggressive than both prairie grass and ryegrass in its 75% mixtures with these species (indicated by the negative aggressivity indices of prairie grass and ryegrass). Ryegrass is more aggressive than prairie grass in the 75R:25P mixture, and the increase in aggressivity of the weaker species are greater than that observed in earlier trials (Tables 3.11 and 3.18).

TABLE 3.25 Aggressivity indices of the more aggressive species based on the vegetative characters of the grass species at the two temperature regimes.

Species combinations	Aggressivity of Prairie grass in combination with Ryegrass					Aggressivity of Prairie grass in combination with Cocksfoot					Aggressivity of Ryegrass in combination with Cocksfoot				
	75R 25P	50R 50P	25R 75P	Signif	±SE	75P 25C	50P 50C	25P 75C	Signif	±SE	75C 25R	50C 50R	25C 75R	Signif	±SE
TILLER NUMBERS															
(A) High Temperature															
50% LI	-0.088	0.047	0.092	**	0.014	0.064	0.078	-0.061	NS	0.031	-0.062	0.034	0.064	**	0.015
95% LI (Harvest 1)	-0.056	0.018	0.055	**	0.011	0.067	0.047	-0.057	*	0.020	-0.066	0.026	0.084	**	0.010
50% LI	-0.104	0.012	0.086	**	0.015	0.081	0.074	-0.073	*	0.022	-0.084	0.005	0.040	**	0.014
95% LI (Harvest 2)	-0.069	0.011	0.048	**	0.013	0.072	0.040	-0.047	*	0.018	-0.063	0.029	0.077	**	0.012
50% LI	-0.113	0.020	0.116	**	0.032	0.117	0.061	-0.056	**	0.012	-0.115	0.027	0.147	**	0.023
95% LI (Harvest 3)	-0.073	0.029	0.052	**	0.014	0.069	0.036	-0.076	**	0.018	-0.047	0.037	0.093	**	0.017
(B) Low Temperature															
50% LI	-0.086	0.025	0.091	**	0.031	0.110	0.069	-0.025	**	0.019	-0.021	0.031	0.075	*	0.023
95% LI (Harvest 1)	-0.043	0.013	0.017	*	0.019	0.044	0.031	-0.042	**	0.014	-0.025	0.019	0.026	*	0.004
50% LI	-0.063	0.013	0.036	NS	0.041	0.068	0.036	-0.017	NS	0.036	-0.036	0.011	0.013	NS	0.029
95% LI (Harvest 2)	-0.034	0.024	0.038	**	0.007	0.072	0.044	-0.010	**	0.012	-0.038	0.043	0.059	**	0.005
50% LI	-0.091	0.034	0.075	**	0.013	0.077	0.053	-0.057	*	0.022	-0.076	0.029	0.074	*	0.026
95% LI (Harvest 3)	-0.062	0.025	0.045	*	0.027	0.076	0.037	-0.075	*	0.025	-0.029	0.002	0.006	NS	0.027
SHOOT WEIGHT															
(A) High Temperature															
Harvest 1	-0.079	0.036	0.126	*	0.024	0.069	0.051	-0.028	*	0.015	-0.048	0.024	0.042	**	0.005
Harvest 2	-0.018	0.021	0.053	**	0.008	0.027	0.011	-0.016	*	0.010	-0.020	0.011	0.024	**	0.007
Harvest 3	-0.018	0.006	0.015	**	0.005	0.029	0.008	-0.014	**	0.008	-0.022	0.008	0.031	**	0.011
(B) Low Temperature															
Harvest 1	-0.022	0.006	0.019	*	0.010	0.013	0.007	-0.007	*	0.004	-0.021	0.010	0.016	NS	0.014
Harvest 2	-0.011	0.004	0.013	*	0.006	0.015	0.012	0.003	NS	0.006	-0.015	0.009	0.019	*	0.008
Harvest 3	-0.021	0.007	0.011	**	0.006	0.032	0.019	-0.005	*	0.008	-0.017	0.017	0.035	*	0.011

The aggressivity indices again illustrate the significant changes in competitive abilities of species with a 25% change in species proportions. Competitive abilities of species do not change with time. However, the aggressivity indices in the higher temperature regime generally tend to be greater than those of the lower temperature, suggesting greater competitive interactions between plants under warmer conditions, where more rapid growth is observed.

3.4.4 DISCUSSION

This experiment again illustrates that competitive interactions between the selected grasses occur for the same 'biological space', as the relative yield totals do not deviate significantly from unity. The products of the relative crowding coefficients also highlight this relationship which is in close agreement with the previous experiments (Sections 3.2, 3.3), and many published reports on other grass mixtures reviewed by Trenbath (1974a). Van den Bergh and de Wit (1960) also illustrated similar relationships between grasses growing under uniform conditions in controlled environment rooms.

The main objective of this experiment was to evaluate the competitive relationship between the three species, when the initial advantages of early emergence was removed and larger initial seedling size of early emerging species reduced. The results highlight that under these conditions the competitive ability of the weaker species is enhanced, which leads to a reduction in the differences between the relative competitive abilities of the species. This effect is most prominent in the ryegrass-cocksfoot combinations, and in the 75% combinations of ryegrass and cocksfoot with 25% prairie grass, which was identified as the most aggressive species in earlier experiments.

Published reports (e.g. Blaser *et al.*, 1956; Harris, 1967; Rhodes, 1968a) and the results of earlier experiments highlight the importance of early emergence and to a greater extent the initial seedling size in determining competitive hierarchies in grass associations. Thus, the increased competitive ability of the weaker species in this experiment can be attributed to the absence of or reduction in the initial advantages normally possessed by the more competitive species, when seeds of both species are sown together.

Although the initial advantage of earlier emergence and/or the advantage of a larger seedling is minimized, the results confirm the earlier observed overall performance and competitive relationships and abilities of the three species, which lie in the order of prairie grass > ryegrass > cocksfoot. The more competitive species show greater dry matter accumulation and extensive growth of the shoot systems in mixtures and monocultures. Due to the close relationship between shoot and root growth of grasses (Troughton, 1956, 1960; Brouwer, 1963), the more competitive species can be expected to have a larger root system. Thus, although the initial advantages of early emergence and larger seedling sizes are absent or minimized, the overall greater competitive ability of prairie grass over the other species and ryegrass over cocksfoot can be attributed to more extensive growth, resulting in a larger plant in the seedling stage, which is related to competitive ability (Plummer, 1943; McKell, 1972). Thus, in mixtures, the more extensive and rapid growth of the more competitive species enables it to exploit a greater proportion of the environment, thereby affecting the growth of the associated weaker and smaller species by limiting the resources and space available for its growth. This effect will be magnified in these mixtures as the species occupy the same niche and compete for the same growth resources (as RYT = 1), and the poor growth of the weaker species in mixtures can be identified in this study.

In terms of dry matter production, the yields of the mixtures show "non-transgressive yielding", and this is in general agreement with most similar studies (Trenbath, 1974a).

The effects of temperature on competitive relationships have been reported by many scientists (e.g. van den Bergh and de Wit, 1960; McWilliam, 1978). More recently Harris *et al.* (1981 a,b) showed the effects of changes in temperature on competition between grass species with different temperature requirements. However, this study does not illustrate changes in overall competitive relationships between the species at the temperature regimes selected. This lack of change in competitive relationships may be related to the adequate moisture and uniform conditions at each temperature regime, as temperature generally affects water availability for plant growth (McWilliam, 1978). Thus while cocksfoot is considered a

species adapted to warm dry conditions (Langer, 1973; Vartha, 1975; Sheath and Greenwood, 1982), suppression of this species by prairie grass and ryegrass shows that water may be an important factor in determining competitive relationships between these species.

McWilliam (1978) reports that the optimum temperature for both dry matter accumulation and growth lies in the range of 20-30°C, for most temperate grasses. Thus the difference in growth of the species in the two climate rooms can be attributed to differences in the selected temperatures.

3.4.5 CONCLUSION

Extensive and rapid growth of seedlings during early growth resulting in a larger plant has a deterministic effect on the overall competitive abilities and competitive relationships between the selected grass species. However, the removal or reduction in initial advantages of the more competitive species allows better growth of the weaker species and enhances its competitive ability.

The temperature effects compared in this study do not affect the competitive relationships between the selected grass species.

3.5 CONCLUDING REMARKS

Three experiments were conducted to examine the competitive relationships between "Grasslands Nui" perennial ryegrass, "Grasslands Matua" prairie grass and "Grasslands Apanui" cocksfoot during the establishment period. The experimental conditions were developed to determine the competitive relationships when the mixtures were established from seed, seedlings of the same age and seedlings at the same stage of growth. In addition, the effect of competition between species during early growth on subsequent performance and the effect of temperature on competitive relationships were evaluated. The salient features that emerged from these experiments were -

- Competition between the selected species occurs for the same "biological space". Thus the species occupy the same ecological niche during the establishment phase.
- Prairie grass was the superior species in terms of growth, yielding ability and plant aggressivity under all experimental conditions. Cocksfoot was affected by other species when grown in mixtures and yielded the lowest dry matter. Ryegrass was affected by prairie grass but was more aggressive and higher yielding than cocksfoot.
- Initial seedling size and more importantly extensive and rapid seedling growth resulting in a larger plant has a deterministic effect on the competitive abilities of the selected grass species, which may be assisted by earlier emergence of the more competitive species (e.g. ryegrass and prairie grass over cocksfoot).
- Competitive relationships that develop in the establishment phase are continued on to later stages of growth, especially under uniform management. Species also compete for the same environmental resources at later stages of growth. However, long term studies may show departures from this trend.
- Yields of the mixtures of these species fall between those of the respective monocultures, which shows that if the highest yielding species is known for given conditions, there is no advantage in growing mixtures.

- Temperature alone had little effect on the competitive relationships between the selected grasses, when other environmental conditions were kept similar and at optimum levels.

These experiments were conducted under uniform conditions and when providing apparently adequate resources for optimum growth, in order to identify the inherent competitive ability of the species and the competitive relationships between the species. However, changes in environmental conditions such as water or nutrient limitations and management conditions such as delaying the addition of the more aggressive species to the mixtures or different cutting or grazing treatments may produce variations from the results obtained in these studies.

CHAPTER 4 AN EVALUATION OF THE COMPETITIVE EFFECTS ON THE DEVELOPMENT AND EARLY GROWTH OF INDIVIDUAL GRASS PLANTS GROWING IN BINARY MIXTURES.

4.1 INTRODUCTION

As each individual in a community of grass plants germinates, it gains access to resources necessary for further growth and development. The more competitive species which generally exhibits more extensive and rapid seedling growth and in certain instances, earlier emergence, obtains a greater share of the environmental resources, thus modifying the environment within the plant community (Black, 1966). These modifications of the environment restrict the normal growth of the later emerging or less aggressive species, which is manifested as competitive relationships between species in the mixture. Thus, the phenomenon of competition operates essentially at the plant level (Black, 1966), affecting individual plant performance, thereby having an effect on the performance of the entire plant population.

As the outcome of competition between plant species is best illustrated at the single plant level, detailed evaluations of competitive relationships need to be conducted with individual plants (Rhodes, 1970). Donald (1963) stated that the growth and behaviour of individual plants in isolation may differ considerably from that in a community. Subsequently, Harper (1964) and Black (1966) stressed the necessity of studies on individuals within an association. Thus a natural development from experiments observing competitive relationships between species is to consider the effects of different numbers of neighbouring plants of another species on the growth and development of a single plant (Mead, 1979). The plant under evaluation can be either the weak or the more aggressive species. In addition, in order to obtain adequate assessment of the response of a plant to competitive stress in mixtures, it is essential to observe the performance of the species in monocultures at similar densities and compare the growth patterns of the plants under the different situations (de Wit and van den Bergh, 1965).

Competition between grass plants results in reduced growth of the weaker species (Donald, 1963), which is generally exhibited as reduced dry matter accumulation. The economic yield of the grass

plant is associated with shoot dry matter production. Leaf and tiller development are important components of growth during the early vegetative phase, and have been identified as good indicators of plant response to stress and environmental changes (e.g. Langer, 1963; Higgins *et al.* 1964; Anslow, 1966; Friend, 1966). Thus an evaluation of leaf and tiller appearance and tillering patterns of grass seedlings growing in mixtures will highlight the effects of competition on the growth and development of a given species.

The specific objective of the experiment described in this section was therefore:

- To study the performance of individual plants of the three species growing in mixtures during the early growth phase, and relate that performance to the competitive relationships that develop between the species.

Sequential destructive sampling was carried out to monitor growth from seeding up to 95% light interception, in order to observe the development pattern of competitive relationships between the species, along with their growth patterns.

4.2 EXPERIMENTAL PROCEDURE

4.2.1 CULTURAL

Perennial ryegrass ('Grasslands Nui'), prairie grass ('Grasslands Matua') and cocksfoot ('Grasslands Apanui') seeds were graded for uniform weight and sown into plastic containers (approximately 18 x 18 x 18 cm) containing approximately four litres of sand, which was selected to facilitate easy root measurements. Sixteen seeds were sown in each container at a depth of approximately 1 cm, with one seed at each of the 16 locations on a 5 x 5 cm equally spaced matrix (i.e. - 400 plants m⁻²). Plant vacancies were replanted at the one leaf stage with seedlings grown under similar conditions.

The plants in the containers were arranged as a replacement series with the mixtures used in earlier experiments (Chapter 3). The species were distributed to ensure maximum interspecific separation. The pots containing the seeds were placed on trolleys and transferred to the



Plate 4. Experiment 4 - The general layout within the climate laboratory.

controlled environment rooms soon after planting.

During the experimental period, the plants were watered with 50 ml of $\frac{1}{2}$ strength "modified Hoaglands" mineral solution and 50 ml water per application, through an automated microtube system, twice daily.

4.2.2 ENVIRONMENTAL

This experiment was carried out in two controlled environment rooms of the Plant Physiology Division, D.S.I.R., during the period March-May, 1981. The temperature was controlled at 16°C day/ 8°C night $\pm 0.5^{\circ}\text{C}$ in both rooms. These temperature regimes were selected on the basis of results of the previous experiment (Section 3.4). As no difference in the competitive relationships between the selected species was observed at the high and low temperature regimes used in that study, an intermediate temperature regime was selected.

The water vapour pressure deficit in both rooms was 9.1 mb (day)/1.6 mb (night) representing relative humidities of 50% RH (day)/85% RH (night) $\pm 5\%$ RH.

The diurnal temperature and humidity changeovers occurred over 2 hours, the 12 hour photoperiod beginning and ending half way through the changeover. The mean photosynthetic irradiance at pot height in both rooms was 153 Wm^{-2} , provided by a combination of 4 x 1 kw 'metalarc' discharge lamps and a 4 x 1 Kw halogen lamp, filtered through a 3-cm water thermal barrier.

4.2.3 EXPERIMENTAL LAYOUT

Since no significant variation between replicates was observed in the previous trial in the controlled environment rooms (Section 3.4), two replicates, with one in each room, were used for this study. Nine pots containing 16 plants each placed together made up a micro-sward, and the 12 microswards of the species combinations were placed in each room. (Plate 4). The empty trolleys were progressively removed with reductions in pot numbers due to sequential harvesting.

4.2.4 MEASUREMENTS

All mixtures were examined from sowing to observe differences in emergence rates of species in different combinations.

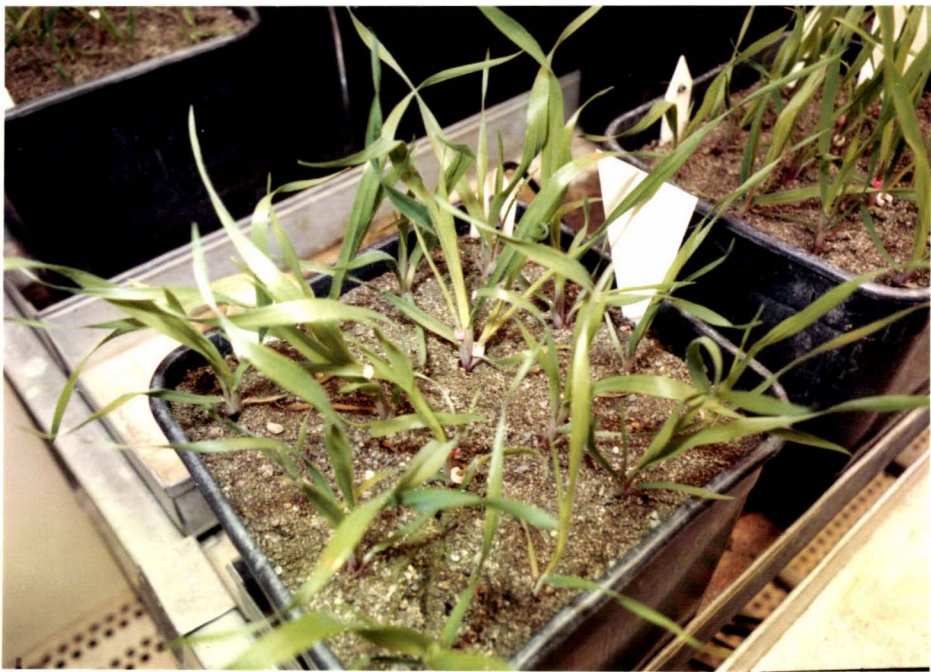


Plate 5. Tagging of tillers

The rate of leaf appearance on the main stem of the growing seedlings was determined by regular inspection at 3 day intervals. To avoid excessive handling of plants, every emerged leaf on the main stem was marked with a spot of oil paint.

The plants were also observed regularly at 4 and 5 day intervals to determine the rate of appearance of primary, secondary and tertiary tillers. The tillers were classified according to the method of Langer (1972) (Appendix 8). To facilitate ease of observation, the emerging primary, secondary and tertiary tillers were marked at each observation with red, white and blue plastic rings respectively. (Plate 5). The plastic rings were cut diagonally to allow expansion of tillers. All these measurements were carried out until the final harvest.

One randomly selected pot per treatment of each replicate was removed each week and the roots washed carefully on wire grids to obtain seedlings with intact root systems. The height of each species (from base of plant to tip of youngest leaf) and root length (from base to tip of longest root) was measured prior to separation into root and shoot components. Leaf area of each species was also determined and the shoots and roots were dried at 40°C for 24 hours in a vacuum oven to obtain dry matter production per plant. Seven harvests were carried out at weekly intervals. The final harvest was taken approximately 4 days after each sward reached 95% light interception. The swards containing major proportions of ryegrass and prairie grass reached this stage within 9-10 days after the seventh harvest, cocksfoot and swards with 75% cocksfoot reached this stage 12-14 days after the seventh harvest.

4.2.5 STATISTICAL ANALYSIS

The data was analysed according to the methods used in earlier experiments (Chapter 3). As dry matter production of swards was not measured replacement diagrams were not drawn and relative crowding coefficients not calculated.

The leaf and tiller appearance rates and dry matter accumulation rates of each species in mixtures and monocultures were compared by linear regression analysis, based on the formula $\log_e y = 1 + \beta x$ where y and x were plant characteristics and time in days respectively. The slope (β) obtained from each treatment as compared with that of its

monoculture by 't' tests, as described by Gomez and Gomez (1976) and Steel and Torrie (1981). The slopes indicated overall differences in growth rates of species in mixtures when compared with their respective monocultures. The times at which competitive interactions between species resulted in significant growth differences between plants growing in mixtures and monocultures of a species were identified by analysis of variance.

4.3 RESULTS

4.3.1 EMERGENCE

There was no significant difference ($P \leq 0.05$) in the time of emergence of each species in monocultures or in mixtures. The mean time taken for 75% emergence by ryegrass seedlings was 7.2 ± 0.2 days, while prairie grass and cocksfoot took 9.6 ± 0.1 and 13.9 ± 0.4 days respectively.

TABLE 4.1 Mean plant height (cm) of species in mixtures and monocultures

	H1*	H2	H3	H4	H5	H6	H7	H8
<u>(A) RYEGRASS</u>								
Monoculture	2.25	5.5	7.6	10.4	15.7	23.0	25.0	27.1
75R with 25P	2.40	5.7	7.6	10.8	15.9	23.8	25.2	27.8
50R with 50P	2.35	5.9	7.5	10.5	15.5	22.7	24.7	25.6
25R with 75P	2.40	5.5	7.6	10.2	15.2	22.4	23.2	26.5
75R with 25C	2.45	5.7	7.5	10.5	15.8	23.7	25.5	28.1
50R with 50C	2.30	5.4	7.3	10.1	15.5	23.4	24.9	27.9
25R with 75C	2.45	5.5	7.2	10.5	15.3	22.9	24.8	27.4
Significance	NS	NS	NS	NS	*	**	*	*
Sx	0.16	0.12	0.15	0.14	0.12	0.14	0.58	0.62
<u>(B) PRAIRIE GRASS</u>								
Monoculture		6.6	8.2	12.4	17.9	25.0	27.2	30.0
75P with 25R		6.8	8.4	12.8	18.5	25.1	27.9	32.6
50P with 50R		6.7	8.6	12.8	18.7	25.6	27.4	30.1
25P with 75R		6.7	8.8	12.4	18.1	25.0	26.9	29.2
75P with 25C		6.7	8.7	12.5	18.2	25.5	28.1	31.2
50P with 50C		6.6	8.3	12.5	18.2	25.1	27.8	30.7
25P with 75C		6.3	8.2	12.2	18.1	24.9	27.4	30.2
Significance		NS	NS	NS	NS	*	*	*
Sx		0.14	0.08	0.14	0.28	0.19	0.18	0.59
<u>(C) COCKSFOOT</u>								
Monoculture		1.9	3.8	4.8	7.6	12.2	15.2	17.8
75C with 25R		1.8	3.8	4.9	7.5	12.3	15.4	18.0
50C with 50R		1.6	3.6	4.7	7.2	11.8	14.9	17.5
25C with 75R		1.4	3.6	4.4	6.8	10.4	14.5	17.1
75C with 25P		1.7	3.6	4.5	7.6	11.9	14.9	17.5
50C with 50P		1.7	3.7	4.7	6.6	10.5	13.9	16.5
25C with 75P		1.9	3.8	4.5	5.2	9.3	14.1	17.0
Significance		NS	NS	NS	**	**	*	*
Sx		0.13	0.17	0.23	0.20	0.54	0.36	0.26

*Shoots of prairie grass and cocksfoot had not emerged at the first harvest.

TABLE 4.2 Mean root length (cm) of species in mixtures and monocultures

Treatment	H1	H2	H3	H4	H5	H6	H7	H8
(A) RYEGRASS								
Monoculture	3.55	5.3	8.0	9.0	15.5	19.9	24.7	27.8
75R with 25P	3.65	5.4	8.2	9.1	15.5	20.3	24.5	28.7
50R with 50P	3.65	5.3	8.0	9.0	15.3	18.6	23.6	26.9
25R with 75P	3.75	5.4	8.0	9.0	15.1	17.4	22.5	25.9
75R with 25C	3.70	5.4	8.1	9.2	15.6	21.1	25.3	28.4
50R with 50C	3.75	5.5	8.1	9.1	15.5	20.3	24.5	27.9
25R with 75C	3.80	5.4	8.0	9.0	15.3	19.7	22.9	26.7
Significance	NS	NS	NS	NS	NS	**	**	**
Sx	0.034	0.04	0.08	0.09	0.22	0.24	0.32	0.90
(B) PRAIRIE GRASS								
Monoculture	2.45	8.9	12.4	14.6	19.7	23.6	28.9	31.5
75P with 25R	2.50	9.2	12.5	14.7	20.3	24.1	29.6	32.7
50P with 50R	2.50	9.0	12.4	14.9	19.8	23.7	29.1	31.5
25P with 75R	2.60	9.0	12.3	14.7	19.5	21.6	27.3	28.7
75P with 25C	2.50	9.1	12.5	14.9	19.8	24.9	30.0	32.9
50P with 50C	2.55	9.0	12.5	14.8	20.2	24.4	29.2	32.3
25P with 75C	2.60	9.1	12.5	14.7	20.1	23.8	28.6	31.5
Significance	NS	NS	NS	NS	*	*	**	**
Sx	0.055	0.08	0.05	0.12	0.16	0.98	0.28	0.57
(C) COCKSFOOT								
Monoculture	0.39	3.2	4.9	6.4	12.3	18.7	21.8	27.4
75C with 25R	0.43	3.4	5.0	6.4	12.3	18.1	22.0	26.3
50C with 50R	0.42	3.3	5.1	6.3	12.2	17.2	20.7	25.1
25C with 75R	0.42	3.4	4.9	6.3	12.1	16.6	15.1	24.9
75C with 25P	0.40	3.3	4.9	6.4	12.5	18.8	22.4	27.4
50C with 50P	0.41	3.3	5.0	6.0	11.4	17.9	21.2	24.5
25C with 75P	0.42	3.3	5.0	6.2	10.6	16.6	19.3	23.9
Significance	NS	NS	NS	NS	*	*	**	*
Sx	0.023	0.08	0.16	0.11	0.22	1.04	0.51	0.75

TABLE 4.3 Mean leaf area (cm²) of species in mixtures and monocultures

Treatment	H4	H5	H6	H7	H8
<u>(A) RYEGRASS</u>					
Monoculture	6.18	10.82	33.99	71.94	122.5
75R with 25P	7.00	11.20	36.70	79.35	130.1
50R with 50P	6.53	11.23	32.79	70.88	121.2
25R with 75P	6.48	9.95	32.70	68.50	128.5
75R with 25C	6.56	11.69	35.43	79.20	128.9
50R with 50C	6.55	11.35	34.42	75.51	125.2
25R with 75C	6.40	10.41	34.31	72.81	116.8
Significance	NS	**	**	**	*
\bar{Sx}	0.27	0.26	0.67	1.91	5.24
<u>(B) PRAIRIE GRASS</u>					
Monoculture	9.09	14.96	49.11	105.5	179.6
75P with 25R	9.16	15.77	52.43	115.3	184.6
50P with 50R	8.85	15.43	50.43	110.9	178.8
25P with 75R	8.76	15.03	47.63	95.9	164.9
75P with 25C	9.45	16.43	52.92	122.9	188.0
50P with 50C	8.86	16.09	53.11	119.7	183.3
25P with 75C	9.01	15.45	50.07	115.5	179.6
Significance	NS	**	**	**	**
\bar{Sx}	0.19	0.15	0.77	4.43	2.77
<u>(C) COCKSFOOT</u>					
Monoculture	2.03	5.34	16.28	30.88	64.2
75C with 25R	2.19	5.88	17.27	36.55	67.5
50C with 50R	2.13	5.70	16.72	32.82	58.1
25C with 75R	2.34	5.13	15.96	29.45	51.3
75C with 25P	2.06	5.39	17.17	29.65	61.2
50C with 50P	2.23	5.78	15.63	27.10	52.0
25C with 75P	2.27	4.45	14.55	25.78	41.0
Significance	NS	NS	**	**	*
\bar{Sx}	0.18	0.50	0.43	1.28	4.70

TABLE 4.4 Mean shoot weight (g) of species in mixtures and monocultures

Treatment	H1*	H2	H3	H4	H5	H6	H7	H8
<u>(A) RYEGRASS</u>								
Monoculture	0.0016	0.0042	0.0147	0.067	0.148	0.512	0.832	0.993
75R with 25P	0.0017	0.0045	0.0153	0.068	0.152	0.539	0.852	0.981
50R with 50P	0.0021	0.0044	0.0149	0.067	0.156	0.516	0.830	0.911
25R with 75P	0.0018	0.0043	0.0150	0.067	0.149	0.489	0.768	0.858
75R with 25C	0.0019	0.0044	0.0149	0.069	0.160	0.549	0.874	0.998
50R with 50C	0.0019	0.0044	0.0157	0.070	0.154	0.517	0.854	0.971
25R with 75C	0.0016	0.0042	0.0150	0.063	0.147	0.498	0.829	0.927
Significance	NS	NS	NS	NS	*	*	**	**
Sx	0.0002	0.0001	0.0003	0.002	0.003	0.014	0.021	0.012
<u>(B) PRAIRIE GRASS</u>								
Monoculture		0.0056	0.0278	0.095	0.234	0.908	0.996	1.225
75P with 25R		0.0058	0.0280	0.100	0.239	0.935	1.087	1.373
50P with 50R		0.0057	0.0282	0.099	0.233	0.915	1.001	1.286
25P with 75R		0.0057	0.0280	0.096	0.239	0.860	0.972	1.154
75P with 25C		0.0059	0.0284	0.101	0.266	0.992	1.082	1.383
50P with 50C		0.0058	0.0282	0.097	0.255	0.955	1.040	1.367
25P with 75C		0.0056	0.0281	0.098	0.242	0.913	0.996	1.253
Significance		NS	NS	NS	*	**	**	**
Sx		0.0002	0.0003	0.002	0.008	0.060	0.018	0.049
<u>(C) COCKSFOOT</u>								
Monoculture		0.0011	0.0030	0.0093	0.051	0.201	0.428	0.617
75C with 25R		0.0013	0.0031	0.0095	0.052	0.206	0.431	0.633
50C with 50R		0.0012	0.0030	0.0095	0.049	0.199	0.415	0.578
25C with 75R		0.0011	0.0031	0.0094	0.046	0.189	0.398	0.580
75C with 25P		0.0011	0.0031	0.0094	0.050	0.200	0.425	0.636
50C with 50P		0.0012	0.0030	0.0094	0.045	0.187	0.418	0.553
25C with 75P		0.0011	0.0031	0.0093	0.043	0.178	0.392	0.535
Significance		NS	NS	NS	*	*	**	**
Sx		0.0002	0.0001	0.0008	0.002	0.011	0.010	0.025

* Shoots of prairie grass and cocksfoot had not emerged at the first harvest.

TABLE 4.5 Mean root weight (g) per plant of species mixtures and monocultures

Treatment	H1*	H2	H3	H4	H5	H6	H7	H8
<u>(A) RYEGRASS</u>								
Monoculture	0.0043	0.0063	0.0107	0.0144	0.130	0.250	0.510	0.665
75R with 25P	0.0044	0.0066	0.0112	0.0150	0.136	0.260	0.522	0.678
50R with 50P	0.0043	0.0063	0.0112	0.0151	0.127	0.239	0.506	0.644
25R with 75P	0.0044	0.0065	0.0108	0.0141	0.122	0.230	0.489	0.641
75R with 25C	0.0045	0.0068	0.0111	0.0156	0.138	0.275	0.536	0.697
50R with 50C	0.0042	0.0065	0.0110	0.0151	0.135	0.269	0.523	0.679
25R with 75C	0.0044	0.0065	0.0109	0.0149	0.127	0.245	0.499	0.656
Significance	NS	NS	NS	*	*	**	**	*
Sx	0.0002	0.0003	0.0015	0.0005	0.003	0.007	0.004	0.011
<u>(B) PRAIRIE GRASS</u>								
Monoculture	0.0041	0.0055	0.0172	0.0238	0.181	0.396	0.587	0.768
75P with 25R	0.0043	0.0059	0.0177	0.0242	0.189	0.448	0.614	0.783
50P with 50R	0.0042	0.0060	0.0173	0.0246	0.182	0.407	0.592	0.777
25P with 75R	0.0043	0.0057	0.0173	0.0239	0.174	0.389	0.569	0.748
75P with 25C	0.0045	0.0062	0.0187	0.0272	0.194	0.445	0.634	0.806
50P with 50C	0.0044	0.0058	0.0182	0.0254	0.191	0.443	0.613	0.788
25P with 75C	0.0041	0.0058	0.0176	0.0247	0.182	0.400	0.587	0.768
Significance	NS	NS	*	*	*	*	**	*
Sx	0.0003	0.0002	0.0003	0.0006	0.005	0.015	0.008	0.008
<u>(C) COCKSFOOT</u>								
Monoculture		0.0012	0.0094	0.0116	0.017	0.091	0.201	0.317
75C with 25R		0.0014	0.0097	0.0118	0.018	0.095	0.213	0.326
50C with 50R		0.0013	0.0095	0.0111	0.017	0.085	0.197	0.303
25C with 75R		0.0014	0.0094	0.0107	0.016	0.083	0.189	0.300
75C with 25P		0.0014	0.0094	0.0117	0.018	0.090	0.201	0.316
50C with 50P		0.0013	0.0093	0.0113	0.016	0.082	0.191	0.302
25C with 75P		0.0011	0.0090	0.0101	0.016	0.080	0.187	0.299
Significance		NS	*	*	*	*	**	*
Sx		0.0001	0.0001	0.0004	0.001	0.004	0.007	0.009

* Root weight of cocksfoot was not measured at the first harvest due to the very small size of the developing root systems.

4.3.2 VEGETATIVE GROWTH

The general trend observed in earlier trials (Chapter 3) was again identified in this study.

The vegetative characters measured, namely plant height, root length, leaf area, shoot and root dry weights are presented in Tables 4.1, 4.2, 4.3, 4.4 and 4.5 respectively. Prairie grass was the tallest species with the longest root system, producing greater quantities of dry matter. Cocksfoot was again the smallest species, while the growth patterns of ryegrass lay between those of the other species, except in terms of tillering. Ryegrass had the highest number of tillers per plant.

The plant interactions also presented similar results to those observed earlier. In all aspects, the growth of species in their 75% mixtures was superior to that of their monocultures. This again highlighted greater intra-specific competitive effects within the monocultures at the selected planting density, than interspecific competition in the 75% mixtures.

In terms of species performance, cocksfoot was affected to a greater extent by prairie grass than by ryegrass. Ryegrass was also again affected in mixtures containing equal or greater proportions of prairie grass. The more competitive species in all mixtures showed superior growth when compared with the respective monoculture, which was significant in certain instances. This trend was observed in all vegetative characters.

More importantly the results show the occurrence of significant differences ($P \leq 0.05$) between treatments at the 4th harvest (i.e. 4 weeks after planting) (Tables 4.1 - 4.5). More specifically, plant height, shoot weights and leaf areas of ryegrass plants in different mixtures are significantly affected by other species in the 5th week, while similar effects are observed in the root weights and lengths at 4th and 6th harvests respectively.

In prairie grass, the differences in terms of root weight became apparent at the third harvest. A significant ($P \leq 0.05$) increase in the

root weight of prairie grass growing in mixtures (especially with cocksfoot) when compared with its monoculture is observed at this stage. This highlights the superior competitive ability of prairie grass at very early stages, which enables it to grow at the expense of associate species in mixtures. Significant differences between treatments of prairie grass in terms of other characters were observed at the 5th and 6th harvests.

The adverse effects of companion species on the growth of cocksfoot can be seen in the 5th and 6th harvests after planting in terms of all vegetative characters except root weight. The root growth (in terms of weight) of cocksfoot is suppressed significantly at the 3rd harvest. In all instances, prairie grass had a greater suppressive effect on cocksfoot than ryegrass.

Closer examination of the results of vegetative characters of all species shows that during the first two weeks after planting, the plants in mixtures tend to show greater growth than their respective monocultures, although this effect was not statistically significant ($P < 0.05$). Relative yield totals calculated on the basis of shoot and root weights according to the technique of McGilchrist and Trenbath (1971) showed significant departures from unity at this stage. However, this effect does not continue after the 3rd harvest, when interspecific competitive effects develop.

4.3.3 LEAF AND TILLER APPEARANCE

(i) Leaf appearance:- Analysis of leaf appearance rates shows that both prairie grass and cocksfoot have a higher leaf appearance rate than ryegrass (Table 4.6).

TABLE 4.6 Leaf and tiller appearance rates† of species growing in mixtures and monocultures during early growth #
(Mixture treatments were compared with the respective monocultures
* Indicates significant differences ($P \leq 0.05$) of treatments from monocultures)

Species	Treatment	Leaf appearance		Tiller appearance					
		(β)	r^2	Primary		Secondary		Tertiary	
		(β)	r^2	(β)	r^2	(β)	r^2	(β)	r^2
Ryegrass	Monoculture	0.1497	95.5	0.2274	96.8	0.3342	92.2	0.3070	87.7
	75R with 25P	0.1576*	96.7	0.2426*	97.1	0.3481	92.1	0.3162	87.0
	50R with 50P	0.1440	94.2	0.2182	96.1	0.3120	92.3	0.2757*	83.0
	25R with 75P	0.1337*	93.7	0.2068*	94.7	0.2766*	94.9	0.2435*	71.5
	75R with 25C	0.1578*	96.3	0.2563*	96.9	0.3579*	95.4	0.3210*	88.1
	50R with 50C	0.1496	95.8	0.2364	96.8	0.3456	92.9	0.3101	87.4
	25R with 75C	0.1452	95.6	0.2269	96.6	0.3244	92.6	0.2922	88.2
Prairie grass	Monoculture	0.1554	96.8	0.2402	96.0	0.2677	80.5	0.2571	74.0
	75P with 25R	0.1590*	96.7	0.2462	96.1	0.2766	80.3	0.2660	73.8
	50P with 50R	0.1563	96.3	0.2403	95.5	0.2628	80.5	0.2416	68.7
	25P with 75R	0.1473*	95.4	0.2209	95.9	0.2258*	74.8	0.1920*	67.3
	75P with 25C	0.1635*	96.8	0.2648*	96.2	0.2851*	80.0	0.2690	68.5
	50P with 50C	0.1612*	96.6	0.2532*	96.2	0.2814	80.6	0.2558	68.4
	25P with 75C	0.1518	96.0	0.2406	96.0	0.2721	80.3	0.2417	68.7
Cocksfoot	Monoculture	0.1596	96.2	0.2175	87.7	0.2476	74.4	0.1986	66.1
	75C with 25R	0.1599	95.8	0.2197	87.7	0.2470	74.2	0.2046	65.7
	50C with 50R	0.1533	96.0	0.1973	85.4	0.2111	72.6	0.1677*	64.9
	25C with 75R	0.1490*	96.0	0.1835*	87.2	0.1762*	73.9	0.1045*	66.1
	75C with 25P	0.1605	94.7	0.2080	87.9	0.2295	72.2	0.1986	66.1
	50C with 50P	0.1456*	95.3	0.1843	81.9	0.1737*	57.9	0.1391*	66.7
	25C with 75P	0.1411*	92.0	0.1706*	80.6	0.1295*	57.4	0.0635*	66.6

† Calculated by linear regression analysis based on $\log_e y = a + \beta x$, where y = growth parameter and x = time in days

From seeding up to approximately 4 days after 95% light interception.

Within species, the leaf appearance rate of ryegrass is significantly ($P \leq 0.05$) increased when grown with 25% prairie grass and cocksfoot. However, when associated with 75% prairie grass, the leaf appearance rate of ryegrass is significantly reduced.

In prairie grass, leaf appearance rates are significantly increased when grown with 25% of ryegrass and 25% and 50% of cocksfoot. In turn, the leaf appearance rate of prairie grass is significantly reduced when grown with 75% ryegrass.

Cocksfoot does not show a significant increase in leaf appearance rates when associated with either of the other species. However, the leaf appearance rate of cocksfoot is significantly reduced when grown with 50% prairie grass and 75% of both ryegrass and prairie grass.

(ii) Tiller appearance:- Generally the tiller appearance rates of all species increased (some significantly) when associated with 25% of another species and decreased (some significantly) when grown with 75% of another species. The overall tiller appearance rate of ryegrass was greater than the other species.

More specifically, the primary, secondary and tertiary tiller appearance rates of ryegrass were significantly ($P \leq 0.05$) decreased when associated with 75% of prairie grass. In addition tertiary tiller appearance of ryegrass was reduced significantly when grown with 50% prairie grass. However, ryegrass exhibited a significant increase in the appearance rate of all types of tillers when associated with 25% cocksfoot, and of primary tillers when grown with 25% prairie grass.

Detrimental effects of another species on tiller appearance rates of prairie grass were minimal, and the only significant decrease was observed in secondary and tertiary tillers when grown with 75% ryegrass. However, the primary tiller appearance rate of prairie grass was increased significantly when grown with 25% and 50% cocksfoot, and the secondary tiller appearance rate was also significantly increased when grown with 25% cocksfoot.

While cocksfoot did not show a significant increase in tiller appearance rates when associated with either of the other species, primary,

secondary and tertiary tiller appearance rates were significantly reduced when grown with 75% ryegrass and 75% and 50% prairie grass. In addition, tertiary tiller appearance rate of cocksfoot was significantly reduced in mixtures with 50% ryegrass.

These results suggest that leaf appearance rate on the main stem is a more sensitive indicator of competitive effects than tiller appearance rate in these species.

4.3.4 DRY MATTER ACCUMULATION

Dry matter accumulation patterns of the three species from sowing up to approximately 8 weeks of growth are presented in Table 4.7. The dry matter accumulation rate of both shoots and roots of prairie grass was greater than the other species. Again, all species indicated an increased dry matter accumulation (although not significant in some instances) when grown with 25% of another species and a decrease when grown with 75% of another species.

In terms of species performance, the shoot and root growth rates of ryegrass is significantly increased when grown with 25% cocksfoot and is significantly reduced when grown with 25% prairie grass. The root growth rate is also significantly reduced when grown with 50% prairie grass.

TABLE 4.7 Dry matter accumulation rates[†] of shoots and roots of species grown in mixtures and monocultures during early growth.[#]
(Mixture treatments were compared with the respective monocultures.

* Indicates significant differences ($P \leq 0.05$) of treatments from monocultures.

Species	Treatment	Dry matter accumulation			
		<u>Shoots</u>		<u>Roots</u>	
		(β)	r^2	(β)	r^2
Ryegrass	Monoculture	0.1057	85.5	0.0752	82.0
	75R with 25P	0.1090	85.4	0.0765	83.2
	50R with 50P	0.1048	85.0	0.0736*	82.3
	25R with 75P	0.0997*	86.3	0.0724*	82.4
	75R with 25C	0.1107*	85.4	0.0784*	83.0
	50R with 50C	0.1081	85.8	0.0769	83.9
	25R with 75C	0.1053	84.7	0.0741	82.8
Prairie grass	Monoculture	0.1309	86.8	0.0873	87.2
	75P with 25R	0.1394*	86.6	0.0903	87.0
	50P with 50R	0.1333	86.5	0.0881	87.3
	25P with 75R	0.1266	87.0	0.0854*	86.4
	75P with 25C	0.1409*	87.2	0.0920*	87.8
	50P with 50C	0.1384*	86.3	0.0902	87.6
	25P with 75C	0.1321	86.9	0.0875	86.7
Cocksfoot	Monoculture	0.0681	77.1	0.0367	73.1
	75C with 25R	0.0692	77.3	0.0379	73.5
	50C with 50R	0.0654	77.1	0.0353	73.6
	25C with 75R	0.0645	77.8	0.0347*	73.4
	75C with 25P	0.0689	76.5	0.0365	74.2
	50C with 50P	0.0638*	77.7	0.0348*	72.3
	25C with 75P	0.0615*	77.8	0.0344*	72.0

[†] Calculated by linear regression analyses based on $\text{Log}_e x = a + \beta x$ where y = growth parameter and x = time in days.

[#] From seeding up to approximately 95% light interception.

While mixtures with 75% ryegrass has a significant detrimental effect on the root growth of prairie grass, the shoot and root growth is significantly enhanced when associated with 25% cocksfoot. The shoot growth rate is also significantly increased when prairie grass is associated with 25% ryegrass and 50% cocksfoot.

Again, while cocksfoot does not show significant increase in dry matter production, when grown with either species, the shoot and root growth rates are greatly depressed when grown with 75% ryegrass and 75% and 50% prairie grass.

4.3.5 COMPETITIVE EFFECTS

The competitive relationships between the species were determined by relative yield totals and aggressivity indices based on shoot and root weights. (Table 4.8, Table 4.9). The relative yield totals indicate that the species compete for the same environmental resources at later stages of growth, as the values do not deviate significantly from one. However, during the very early stages, the relative yield totals are significantly greater than one, thus implying that the species do not compete for similar environmental resources at this stage (de Wit, 1960; Trenbath, 1974a).

TABLE 4.8 Relative yield totals of species combinations based on shoot and root weights at every harvest

Species combination	H1	H2	H3	H4	H5	H6	H7	H8
<u>(A) Shoot weight</u>								
		*	*	*	*			
Ryegrass-Prairie grass		1.034±.0008	1.015±.0010	1.022±.0008	1.019±.002	0.999±.014	1.004±.025	1.003±.002
		*	*	*				
Prairie grass-Cocksfoot		1.053±.0014	1.024±.0015	1.021±.0010	1.002±.004	0.992±.012	1.010±.009	0.997±.011
		*	*	*				
Cocksfoot-Ryegrass		1.069±.0011	1.032±.0020	1.021±.0014	1.003±.009	0.998±.010	1.001±.014	0.999±.007
<u>(B) Root weight</u>								
	*	*	*	*				
Ryegrass-Prairie grass	1.053±.014	1.032±.011	1.018±.002	1.022±.001	1.008±.003	1.002±.010	0.998±.005	0.999±.011
		*						
Prairie grass-Cocksfoot		1.068±.008	1.011±.007	0.010±.009	0.997±.006	1.993±.009	1.002±.004	0.997±.016
		*	*					
Cocksfoot-Ryegrass		1.083±.012	1.002±.003	1.008±.015	1.003±.008	1.003±.012	0.998±.006	0.999±.007

* Indicates values significantly greater ($P \leq 0.05$) than one.

TABLE 4.9 Aggressivity based on shoot weight and root weight per plant of the more aggressive species growing in mixtures and monocultures

	Prairie grass-Ryegrass combination					Prairie grass-Cocksfoot combination					Ryegrass-Cocksfoot combination				
	75R25P	50R50P	25R75P	Sig.	± S.E	75P25C	50P50C	25P75C	Sig.	±S.E	75R25C	50R50C	25R75C	Sig.	±S.E.
(A) Shoot weight															
H2	-0.016	-0.014	0.006	NS	0.008	0.027	-0.048	-0.042	NS	0.032	0.024	-0.049	-0.018	NS	0.027
H3	-0.017	0.003	-0.004	NS	0.004	-0.005	-0.002	-0.048	NS	0.012	0.010	0.024	-0.016	NS	0.036
H4	0.001	0.017	0.017	NS	0.018	0.031	0.011	0.008	NS	0.019	0.002	0.014	-0.006	NS	0.023
H5	0.001	-0.029	0.008	NS	0.015	0.137	0.097	0.026	NS	0.031	0.080	0.036	-0.021	NS	0.016
H6	-0.052	0.001	0.037	NS	0.020	0.102	0.060	0.007	NS	0.025	0.067	0.011	-0.024	NS	0.019
H7	-0.025	0.029	0.090	*	0.019	0.084	0.934	0.003	*	0.016	0.059	0.028	-0.005	*	0.008
H8	-0.023	0.005	0.084	**	0.012	0.135	0.105	0.012	**	0.009	0.068	0.052	-0.016	*	0.009
(B) Root weight															
H1	-0.001	0.001	0.007	NS	0.013										
H2	-0.002	0.048	0.023	NS	0.014	0.080	-0.016	-0.054	NS	0.061	-0.049	-0.031	-0.093	NS	0.044
H3	-0.018	-0.019	0.011	NS	0.017	0.064	0.038	0.013	NS	0.031	0.023	0.013	-0.001	NS	0.013
H4	-0.019	-0.006	0.019	NS	0.008	0.138	0.049	0.016	NS	0.034	0.027	0.046	0.008	NS	0.029
H5	-0.044	0.014	0.054	NS	0.021	0.072	0.040	0.010	NS	0.059	0.054	0.028	-0.039	NS	0.025
H6	-0.028	0.036	0.107	NS	0.032	0.122	0.096	0.013	*	0.036	0.091	0.074	-0.033	NS	0.032
H7	-0.026	0.009	0.044	*	0.011	0.077	0.049	0.002	*	0.025	0.054	0.022	-0.040	*	0.024
H8	-0.025	0.021	0.027	*	0.009	0.050	0.034	-0.005	*	0.019	0.047	0.030	-0.023	*	0.025

The reduction in the relative yield totals towards unity occurs at different stages of growth in the different species combinations and measurements. In terms of root weight per plant, the values in the ryegrass-prairie grass combinations equal unity in the 5th week, while those of prairie grass-cocksfoot combinations reach unity in the 3rd and 4th week respectively. Similar effects are observed in terms of shoot weights, where the relative yield total values in the prairie grass-cocksfoot and ryegrass-cocksfoot combinations reach unity at the 5th harvest while those of the prairie grass-ryegrass combinations reach unity at the 6th harvest. Thus, competition for similar resources seems to occur between roots before shoots. In addition, such effects are seen to develop between the most aggressive species and the weakest species before similar effects are observed in other combinations.

In terms of species aggressivity, the results agree with those of earlier trials (Chapter 3). Generally, prairie grass is the most aggressive species, although ryegrass is more aggressive than prairie grass in the 75R 25P mixture. Ryegrass is also more aggressive than cocksfoot except in combinations with 75% cocksfoot.

The aggressivity effects of the species are generally highlighted at later harvests, with significant changes in the indices with changes in species proportions. Thus these indices also show that stabilization of competitive relationships occurs approximately four weeks after planting, corresponding to the time when relative yield totals tend to equal unity.

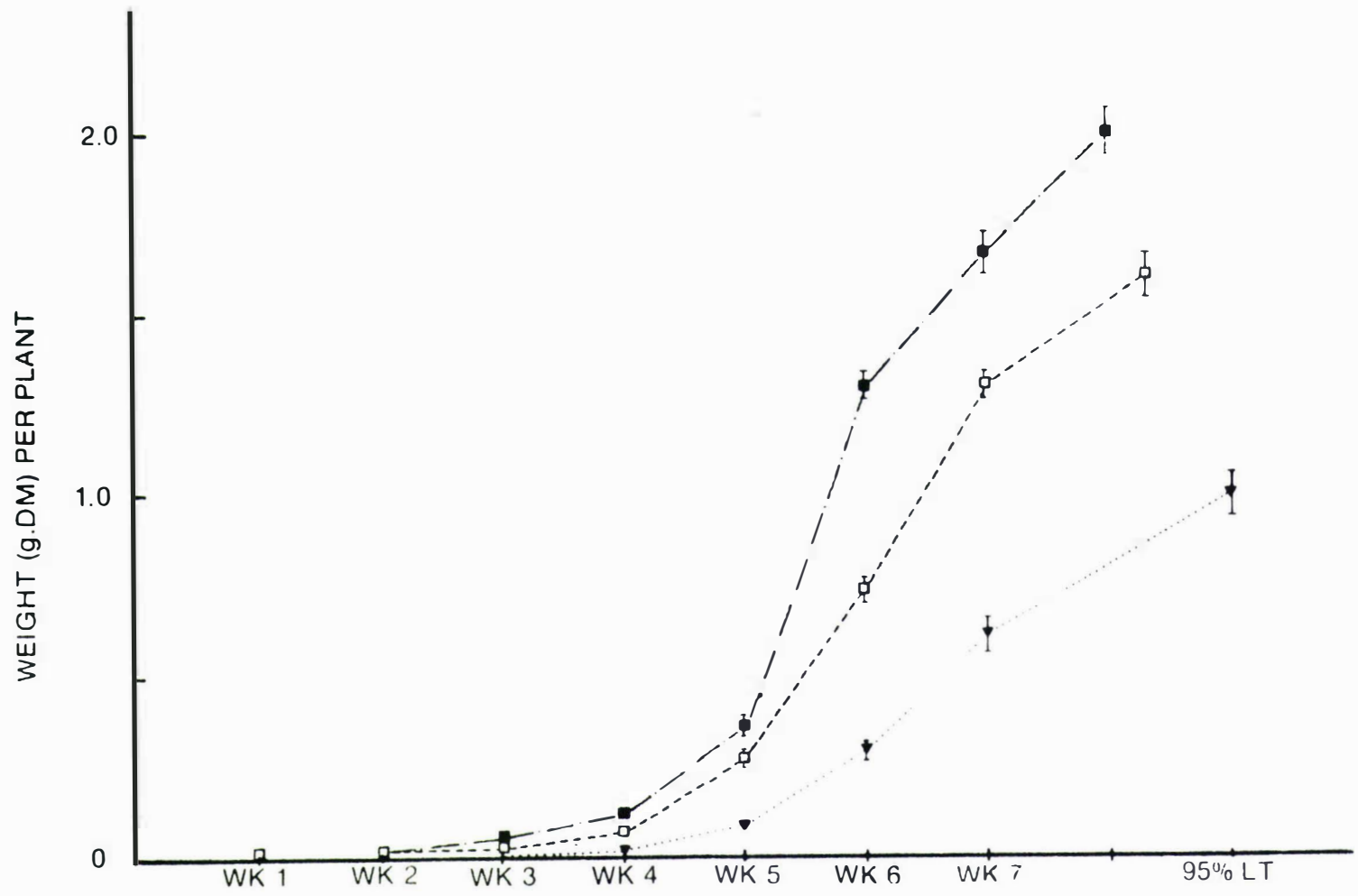


Figure 4.1 The rate of total dry matter accumulation, per plant, of Ryegrass (\square - - - \square): Prairie Grass (\blacksquare - - - \blacksquare), and Cocksfoot (\blacktriangledown - - - \blacktriangledown); measured at weekly intervals and at 95% light interception

4.4 DISCUSSION

Studies on individual growth parameters of the three species highlight the superior growth of prairie grass over the other species and of ryegrass over cocksfoot. The more rapid overall growth rate of prairie grass in terms of dry matter production per plant is illustrated in Figure 4.1, and this characteristic can be again considered a major determinant of its superior competitive ability over the other species.

Ryle (1964) working with monocultures, reported the more rapid leaf appearance rate of cocksfoot when compared with ryegrass, a phenomenon again seen in this trial (Table 4.6). The leaf appearance rate of prairie grass was also greater than ryegrass. These leaf appearance rates can be considered species characteristics. Similar species differences were also observed in terms of tiller appearance rates in the monoculture plants of the three species.

The results of both leaf and tiller appearance rates of the species in mixtures illustrate that these parameters of growth are affected by interspecific competition, which is in agreement with Rhodes (1968a, 1970). However, unlike the results reported by Rhodes (1968a, 1970) leaf appearance rate of these three species is more sensitive to competitive effects than tiller appearance rate, under the adopted experimental conditions.

Both light and temperature have a direct influence on leaf and tiller initiation and appearance rates in grasses (Langer, 1963; Anslow, 1966; Ludlow, 1978; McWilliam, 1978). As temperature regimes were uniform in this trial, reductions in leaf and tiller appearance rates of the weaker species in mixtures can be mainly attributed to light relationships within the microswards. Differences in plant height were observed in all species (Table 4.1), which has a direct bearing upon the light distribution patterns within the canopy, and on competitive effects for light (Donald and Black, 1958; Rhodes and Stern, 1978). Thus the taller species will intercept more light due to its stature and structure, thereby reducing the incident light energy available to the associated shorter species. This affects the leaf and tiller initiation process of the shorter species, along with reductions in the photosynthetic capacity, which finally results in slower or non emergence

of the initiated leaf and tiller buds due to lack of photosynthates. This is most evident in mixtures with equal or greater proportions of the taller and more aggressive species (e.g. prairie grass-cocksfoot combination). The relative difference in height tends to have a significant effect on leaf and tiller appearance rates of the weaker species. The effect of ryegrass on leaf and tiller appearance of cocksfoot is less than that of prairie grass in prairie grass-cocksfoot combinations. This could be due to the smaller difference in height of ryegrass and cocksfoot, when compared with prairie grass and cocksfoot.

The reduction in leaf and tiller appearance rates of the weaker species is finally reflected as reduced dry matter production of that species in the mixture. The increased production of the more aggressive species in mixtures can also be attributed to increased leaf and tiller appearance rates and increased photosynthetic activity, due to reductions in competitive effects for light.

Competitive relationships seen in pasture grasses are the resultant effect of many competitive interactions (Donald, 1963). Thus in addition to competition for light, competition between root systems can enhance these effects resulting in the overall suppression of the weaker species and increased productivity of the more aggressive species.

Analysis of competitive relationships based on relative yield totals indicates that during very early stages, the species do not compete for the same 'biological space'. This is observed as enhanced growth in mixtures as opposed to monocultures during this period. Although these differences in growth between plants in mixtures and monocultures are not significant, the relative yield total values exceed unity, thus implying that the species perform better in mixtures than in monocultures (Trenbath, 1974a). These observed differences during the very early stages may have arisen due to experimental error, or due to autotoxic or self inhibitory processes occurring during germination which affect growth. The existence of such autotoxic effects cannot be precluded (Harris, pers. comm); as similar effects have been reported in grasses (Rice, 1974; 1980); especially in ryegrasses (Newman and Rovira, 1975; Harries and Norrington Davies, 1977).

A separate study conducted to determine the significance of such autotoxic effects during germination and very early growth under laboratory conditions (Appendix 9) also suggested greater root growth of these species in mixtures than in monocultures. However, the differences were again not significant. Thus, further research is warranted to explore the possible existence of such autotoxic allelopathic effects by using seed and plant extracts, under carefully controlled conditions.

The relative yield totals become close to unity 4-5 weeks after planting, implying that the species compete for the same 'biological space' (de Wit and van den Bergh, 1965). This is in agreement with earlier experiments (Chapter 3) and published reports on grasses (Trenbath, 1974a). The relative yield totals based on root characters equal unity earlier than those based on shoot characteristics, implying that root competition begin earlier. These results are similar to those of other reports on grass competition (e.g. Weaver, 1926; Troughton, 1957; Milthrope, 1961; Rhodes, 1970). This result can be expected as grasses have similar root systems (Langer, 1972) occupying similar rooting zones (Troughton, 1957). This leads to greater intermingling of roots leading to overlapping of nutrient depletion zones. Thus competitive relationships develop as such effects are greatly determined by the degree of overlapping of rooting zones (Cable, 1969; Trenbath, 1975). In grasses, this effect can be further emphasized, as the root systems of the *Graminae* (*Poaceae*) generally have a larger surface area than shoot systems (Dittmer, 1937).

Although this experiment was conducted under apparently adequate nutrient levels, competition may have developed between roots for nutrients. This could have occurred as sand with a very low nutrient retentive capacity (i.e. - T.E.C. of 6.2 m. eq - Edge 1977) was used, which stored little nutrients for plant use. In addition, as all nutrients retained within a soil system are not available for plant growth (Hall, 1974a) competition can be expected to develop for the available nutrients from the limited supply retained in the sand. The earlier onset of competition can also be expected as seedlings take up nutrients even before the depletion of endogenous food reserves (McWilliams *et al.*, 1970). Among the range of nutrients utilized by plants, competition may have occurred for relatively mobile nutrients such as nitrogen, as the uptake of such nutrients is proportional to the length of actively growing and nutrient

absorbing roots of the competing species (Andrews and Newman, 1970). Further research with labelled nutrients is thus suggested to elucidate the process of competition between root systems.

Competitive effects between root systems observed in this study could have been further enhanced due to the size of the container used, which can act as a barrier to normal root growth. Due to the presence of a large number of plants within a pot, competition for space may have developed, in addition to competition for nutrients. Stevenson (1967) highlighted competitive effects between species for resources and space if the effective soil volume needed for plant growth is not available. Observations during root washing in this study indicated that within 5-6 weeks of planting, the root systems were greatly intermingled and completely filled the pots. Thus the rapidly growing root systems of the more competitive species can be expected to develop a crowding and thereby a restrictive effect on the slower growing species, as both species are dependent upon the same soil volume for space and nutrients. Thus in competition studies conducted in containers, where normal root growth of species is restricted by the size of the pot, competition for space between root systems may be a very important factor determining competitive relationships between the species.

The results illustrate that competitive interactions between prairie grass and cocksfoot develop before similar effects are observed in the other combinations (i.e. RYT = 1 earlier). This relationship can be attributed to the greater root mass of prairie grass (shown by greater root length and weight) having a suppressive effect on the growth of the smaller root system of cocksfoot, as both root systems occupy the same rooting zones. This effect occurs earlier with increasing densities of prairie grass. The delay in the development of similar relationships between the other species combinations may be related to their smaller differences in root sizes when compared with that seen in the prairie grass-cocksfoot combination. Detailed studies on the root distribution patterns of species within a soil system may further illuminate these effects.

The relative yield totals based on shoot weights approach unity later, indicating that competition between shoot systems occurs after the onset of root competition. The results follow a similar trend to

that of root competition effects, where the prairie grass-cocksfoot combinations illustrate competitive interactions before the other mixtures. This again can be attributed to the relatively large difference between the shoot systems of prairie grass and cocksfoot, when compared with the other mixture combinations.

The development of competition between shoot systems at later stages of growth can be associated with the availability of adequate space for development and the absence of overlapping of shoot systems until later stages of growth. However, the development of competitive relationships can be enhanced due to the early onset of root competition, as the overall competitive effects are caused by interactive processes of the whole plant (Donald, 1963).

4.5 CONCLUSIONS

Evaluation of competitive effects on individual plant components indicates that competition affects all parameters of growth. The reduction in shoot dry matter production per plant of the weaker species and corresponding increases in more aggressive species can be related to changes in leaf and tiller appearance rates, which determine the photosynthetic capacity of the plant.

Inherent characteristics such as larger root and shoot systems have a great effect on the competitive abilities of the selected species, under the conditions of this experiment.

Root competition begins 3-4 weeks after sowing due to greater and earlier intermingling of the root systems. Root competition begins earlier in mixtures with greater relative size differences between the root systems. However, the actual process of root competition is not clear, and as suggested earlier, further research using labelled nutrients is warranted.

Shoot competition begins at later growth stages (i.e. 5-6 weeks after sowing). Competitive interactions between shoot systems are observed earlier in mixtures with greater relative size differences between the shoot systems. Competition between shoot systems for light, although root interactions can have an influence on the growth of shoots and thus on the onset of competitive relationships between the shoot systems.

CHAPTER 5 A STUDY ON THE RELATIVE IMPORTANCE OF SHOOT AND ROOT COMPETITION IN DETERMINING THE OVERALL COMPETITIVE RELATIONSHIPS IN BINARY MIXTURES OF GRASS SPECIES

5.1 INTRODUCTION

Research workers have identified both root and shoot competition when plants are growing in mixtures. Donald (1958), using a simple model of competition between two plants provided a critical evaluation of both root and shoot competition, and noted the importance of root competition in plant mixtures. Subsequently, many researchers (e.g. Aspinall, 1960; Milthorpe, 1961; Idris and Milthorpe, 1966; Rhodes, 1968b; Cocks, 1969; King, 1971; Snaydon, 1971; Eagles, 1972; Remison and Snaydon, 1978, 1980; Snaydon and Harris, 1979; Scott and Lowther, 1980; Martin and Snaydon, 1982), have highlighted the importance of root competition in both crops and pasture species mixtures. Many of these scientists have also shown that root competition has a greater effect than shoot competition on the relative performance of species in mixtures.

Rhodes (1970), when reviewing plant competition, indicated that in an establishing population of plants, competition between root systems for nutrients and water commences in advance of shoot competition for light. Competition for light becomes important only at later stages. This effect was also observed in combinations of ryegrass, prairie grass and cocksfoot (Chapter 4). Significant competitive effects between root systems were identified before similar interactions were seen in the shoot systems. Thus, an experiment was designed to examine the relative importance of root and shoot competition in determining the overall competitive relationships between the selected grass species, during early growth.

Many techniques have been developed from the original method of Donald (1958) to evaluate shoot and root interactive effects between plants. These modifications include those of Aspinall (1960), Schreiber (1967) and Snaydon (1971). As these techniques had many deficiencies, Snaydon (1979) developed a technique to evaluate root and shoot competitive effects, by modifying that of Donald (1958) to incorporate the replacement series principle of de Wit (1960). This technique allowed for independent variation of the size of stand, the overall density, the

relative density of component species and the relative density of species in soil space and aerial space separately (Snaydon, 1979). Thus this technique, which has subsequently been used successfully (e.g. Remison and Snaydon, 1978, 1980; Scott and Lowther, 1980; Martin and Snaydon, 1982) was used for this study.

5.2 EXPERIMENTAL PROCEDURE

This experiment was conducted in two controlled environment rooms at the Plant Physiology Division, D.S.I.R., Palmerston North, during the period October 1981 - January 1982.

5.2.1 CULTURAL

Ryegrass "Grasslands Nui", prairie grass "Grasslands Matua" and cocksfoot "Grasslands Apanui" seeds were graded for uniformity of weight (see section 3.2) and sown into plastic containers (approximately 18 x 18 x 18 cm) containing approximately 4 litres of sand. Eight seeds of each species in a binary combination were sown into 4 rows at an approximate depth of 1 cm. (Figure 5.1).

The seeds were spaced 5 cm apart. Plant vacancies were filled at the single leaf stage of each species, with seedlings grown under similar conditions.

Prior to planting, the pots were divided into 4 equal compartments with vertical aluminized "sisalkraft" partitions, 18 cm high, which prevented the root systems of plants in one row intermingling with those of the adjacent row. Aerial partitions made of the same material and 20 cm tall were installed at 4 weeks after planting to separate shoot systems of the plant rows. Thus by planting the rows of component species either parallel or perpendicular to one another, and similarly arranging the above and below-ground partitions parallel or perpendicular to one another, 4 interactive situations of each species combination were obtained. These were - (a) no interspecific competition; (b) root competition only; (c) shoot competition only and (d) full competition between species (Figure 5.1). Thus 12 treatments were obtained with the binary combinations of the three species. However, unlike in previous experiments (Chapter 3, 4) root, shoot and full competition was evaluated only in 50:50 combinations.

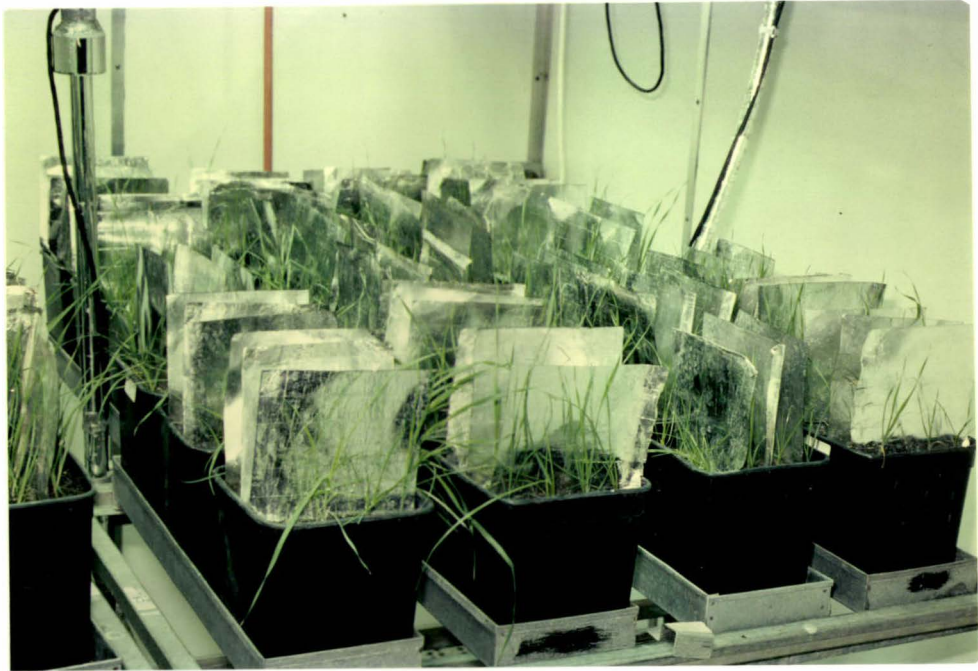


PLATE 6. Experiment 6. Partitioning of shoot and root competition.

The pots were placed in a heated glasshouse (25/15°C) for 2 weeks after planting, and then transferred to the controlled environment rooms. As the "sisalkraft" partitions prevented even distribution of nutrient solution within the pot if fed through the automatic microtube system, the pots were hand watered twice daily with 100 ml of ½ strength modified "Hoaglands" mineral solution.

5.2.2 ENVIRONMENTAL

The environmental conditions used in the controlled environment rooms were the same as those described in the previous experiment (Section 4.2.2).

5.2.3 EXPERIMENTAL LAYOUT

The experimental layout was also the same as that of the previous trial in the controlled environment rooms (Section 4.2.3) (Plate 6).

5.2.4 MEASUREMENTS

As competitive interactions were observed within 3-4 weeks after planting in mixtures of these grasses (Chapter 4), sampling was initiated 3 weeks after planting. At weekly intervals, plants in one pot per treatment per replicate were carefully removed and roots washed on a wire grid. The tiller numbers per plant were counted in these plants before drying the separated shoot and root systems at 40°C for 24 hours in a vacuum oven to obtain dry matter yields. The 6th harvest, corresponding to approximately 8 weeks of growth was carried out 4-5 days after the average light interception of all swards reached 95%. While one pot per treatment was destructively sampled at this stage, the plants in the remaining two pots were cut to a height level with the pot rim (i.e. 2.5 cm above the potting mixture surface). These plants were subsequently cut on two occasions, at approximately 4-5 week intervals, 4-5 days after the average light interception of the sward types reached 95%. These harvests were carried out to monitor the effects of different competitive interactions on the regrowth of the species.

5.2.5 STATISTICAL ANALYSIS

The analysis of data was carried out according to the methods used in earlier experiments (Chapter 3,4). The growth of plants under situations of full, root and shoot competition between species was compared with that of no competition, within each species. The nature of competition between the species was observed by calculating the relative yield totals

(RYT) de Wit and van den Bergh, 1965) and aggressivity indices (McGilchrist and Trenbath, 1971) based on shoot and root dry weights per plant.

5.3 RESULTS

Generally, full competitive situations, where both shoots and roots of the associated species interacted showed the greatest competitive effects between the species. Plants growing in conditions where root systems interacted were affected to a greater extent by competition than plants under conditions of shoot competition. This trend did not alter with any character measured or with time.

5.3.1 TILLER NUMBERS

Ryegrass plants had the highest tiller numbers per plant while cocksfoot had the lowest (Table 5.1). There was little difference between the tiller numbers of prairie grass and cocksfoot plants.

TABLE 5.1 Mean tiller numbers per plant of species grown in different interspecific competitive situations.

Species	Treatment	Harvest 1	Harvest 2	Harvest 3	Harvest 4	Harvest 5	Harvest 6	Harvest 7 (regrowth 1)	Harvest 8 (regrowth 2)
<u>(A) Ryegrass</u>									
	No competition	1.5	2.5	4.9	9.2	17.9	24.7	24.8	22.1
With Prairie grass	Full competition	1.6	2.4	4.6	8.4	15.4	20.9	19.6	18.4
	Root competition	1.6	2.3	4.8	8.7	15.7	22.2	20.9	19.9
	Shoot competition	1.5	2.5	4.9	9.0	16.5	22.4	23.1	20.2
	Full competition	1.5	2.5	5.2	9.5	21.5	29.4	28.6	27.0
With Cocksfoot	Root competition	1.7	2.5	5.0	9.3	19.9	28.5	28.0	26.6
	Shoot competition	1.7	2.5	5.0	9.4	19.5	27.4	26.1	24.4
	Significance	NS	NS	NS	*	**	**	**	**
	\bar{Sx}	0.17	0.35	0.09	0.09	0.31	0.54	0.29	0.56
<u>(B) Prairie grass</u>									
	No competition		1.2	2.7	6.2	11.3	14.7	14.0	12.2
With Ryegrass	Full competition		1.5	3.1	6.7	13.1	16.9	16.6	14.7
	Root competition		1.5	2.9	6.5	12.7	16.5	16.1	13.8
	Shoot competition		1.5	3.0	6.2	12.0	16.1	15.1	13.3
	Full competition		1.4	3.1	6.9	14.6	17.5	16.8	15.5
With Cocksfoot	Root competition		1.5	3.1	6.7	14.0	17.0	16.7	14.6
	Shoot competition		1.5	2.9	6.3	12.3	16.5	15.4	14.0
	Significance		NS	NS	*	**	**	*	*
	\bar{Sx}		0.15	0.18	0.12	0.35	0.38	0.43	0.48
<u>(C) Cocksfoot</u>									
	No competition			1.0	2.2	7.3	11.7	11.5	11.1
With Ryegrass	Full competition			1.0	2.0	5.1	9.1	9.5	8.6
	Root competition			1.0	2.2	5.7	9.6	9.9	8.9
	Shoot competition			1.0	2.1	6.5	10.7	10.5	10.1
	Full competition			0.9	2.1	5.9	8.4	9.1	8.1
With Prairie grass	Root competition			1.0	2.2	6.4	8.9	9.6	8.9
	Shoot competition			1.0	2.2	6.7	10.0	10.2	9.7
	Significance			NS	NS	**	*	**	**
	\bar{Sx}			0.06	0.05	0.25	0.27	0.19	0.25

TABLE 5.2 Mean shoot weight per plant (g.DM) of species grown in different interspecific competitive situations.

Species	Treatment	Harvest 1	Harvest 2	Harvest 3	Harvest 4	Harvest 5	Harvest 6	Harvest 7 (regrowth 1)	Harvest 8 (regrowth 2)
(A) Ryegrass									
	No competition	0.013	0.055	0.141	0.472	0.770	0.877	0.829	0.797
With Prairie grass	Full competition	0.014	0.054	0.138	0.460	0.751	0.858	0.815	0.774
	Root competition	0.014	0.055	0.138	0.466	0.760	0.861	0.820	0.788
	Shoot competition	0.014	0.055	0.142	0.472	0.766	0.865	0.827	0.791
	Full competition	0.015	0.056	0.138	0.488	0.830	0.898	0.886	0.858
With Cocksfoot	Root competition	0.014	0.057	0.148	0.487	0.819	0.887	0.885	0.817
	Shoot competition	0.014	0.057	0.144	0.484	0.792	0.886	0.866	0.815
	Significance	NS	NS	*	*	**	**	**	**
	\bar{S}_x	0.002	0.002	0.003	0.006	0.008	0.005	0.006	0.114
(B) Prairie grass									
	No competition	0.025	0.088	0.217	0.850	0.992	1.165	1.108	1.004
With Ryegrass	Full competition	0.026	0.094	0.224	0.875	1.034	1.195	1.156	1.064
	Root competition	0.027	0.092	0.225	0.880	1.013	1.194	1.135	1.015
	Shoot competition	0.026	0.092	0.219	0.865	1.009	1.186	1.117	1.010
	Full competition	0.026	0.095	0.241	0.880	1.148	1.197	1.287	1.112
With Cocksfoot	Root competition	0.027	0.092	0.229	0.877	1.121	1.195	1.231	1.060
	Shoot competition	0.026	0.092	0.224	0.864	1.148	1.190	1.184	1.049
	Significance	NS	NS	*	*	*	*	*	*
	\bar{S}_x	0.001	0.003	0.004	0.009	0.028	0.012	0.037	0.030
(C) Cocksfoot									
	No competition	0.002	0.007	0.048	0.187	0.403	0.572	0.516	0.508
With Ryegrass	Full competition	0.003	0.007	0.046	0.181	0.370	0.563	0.469	0.470
	Root competition	0.003	0.008	0.047	0.183	0.379	0.562	0.472	0.484
	Shoot competition	0.002	0.007	0.047	0.184	0.392	0.567	0.498	0.489
	Full competition	0.003	0.007	0.043	0.177	0.351	0.558	0.436	0.461
With Prairie grass	Root competition	0.003	0.007	0.046	0.181	0.360	0.560	0.459	0.470
	Shoot competition	0.002	0.008	0.047	0.185	0.389	0.564	0.436	0.478
	Significance	NS	NS	*	**	**	*	**	**
	\bar{S}_x	0.002	0.001	0.001	0.002	0.003	0.002	0.003	0.004

Within a given species, significant changes ($P \leq 0.05$) in the rate of tiller production due to different competitive interactions were observed at later stages of the experiment. The tiller numbers of both ryegrass and cocksfoot were affected by prairie grass and those of cocksfoot were also affected by ryegrass, but to a lesser extent. In all situations, where suppressive effects were observed in the weaker species, the more aggressive species showed a correspondingly superior performance when compared with the monoculture.

5.3.2 SHOOT WEIGHTS PER PLANT

Prairie grass yielded more dry matter per plant than the other species, during the experimental period. Cocksfoot again yielded the least dry matter (Table 5.2). Significant competitive effects ($P \leq 0.05$) were observed 5 weeks after sowing in all species. The interactive effects were similar to those observed for tiller numbers. Prairie grass had a suppressive effect on cocksfoot and to a lesser extent on ryegrass. The suppressive effect of ryegrass on cocksfoot was again less than that seen in prairie grass-cocksfoot combinations.

The growth of all species in different competitive situations indicated a slight increase in productivity at the very early stages of growth, when compared with plants growing in the absence of interspecific competition. This was similar to the observations of the previous experiment (Chapter 4) and again these differences were not significant.

5.3.3 ROOT WEIGHTS PER PLANT

The root weights of species growing in different competitive situations are presented in Table 5.3. The results follow the same trend seen in shoot weights per plant.

Significant interactions between treatments in both prairie grass and cocksfoot were apparent within 4 weeks of sowing. The root growth of prairie grass was significantly greater than its monoculture under conditions of full and root competition with cocksfoot. Significant reductions were observed in the root weight of cocksfoot in these combinations with prairie grass.

TABLE 5.3 Mean root weight per plant (g.DM) of species grown in different interspecific competitive situations

Species	Treatment	Harvest 1	Harvest 2	Harvest 3	Harvest 4	Harvest 5	Harvest 6
(A) Ryegrass							
With Prairie grass	Monoculture	0.0099	0.014	0.105	0.216	0.456	0.619
	Full competition	0.0108	0.014	0.097	0.206	0.449	0.608
	Root competition	0.0102	0.014	0.100	0.208	0.450	0.611
	Shoot competition	0.0097	0.015	0.105	0.213	0.454	0.613
With Cocksfoot	Full competition	0.0100	0.015	0.109	0.244	0.473	0.637
	Root competition	0.0106	0.014	0.107	0.240	0.466	0.633
	Shoot competition	0.0096	0.015	0.107	0.232	0.464	0.632
	Significance	NS	NS	*	**	**	**
	\bar{Sx}	0.0002	0.0003	0.002	0.005	0.004	0.004
(B) Prairie grass							
With Ryegrass	Monoculture	0.0151	0.022	0.181	0.358	0.567	0.781
	Full competition	0.0154	0.022	0.192	0.376	0.575	0.801
	Root competition	0.0163	0.022	0.190	0.372	0.574	0.796
	Shoot competition	0.0158	0.023	0.188	0.364	0.573	0.793
With Cocksfoot	Full competition	0.0160	0.025	0.204	0.414	0.589	0.804
	Root competition	0.0164	0.024	0.195	0.405	0.586	0.798
	Shoot competition	0.0160	0.023	0.193	0.380	0.589	0.796
	Significance	NS	*	*	*	*	*
	\bar{Sx}	0.0004	0.0008	0.010	0.009	0.006	0.009
(C) Cocksfoot							
With Ryegrass	Monoculture	0.0068	0.0095	0.015	0.096	0.173	0.306
	Full competition	0.0068	0.0095	0.015	0.084	0.167	0.295
	Root competition	0.0069	0.0094	0.015	0.088	0.169	0.299
	Shoot competition	0.0065	0.0098	0.015	0.092	0.171	0.302
With Prairie grass	Full competition	0.0070	0.0084	0.013	0.082	0.165	0.294
	Root competition	0.0068	0.0087	0.014	0.084	0.166	0.299
	Shoot competition	0.0073	0.0091	0.014	0.091	0.169	0.299
	Significance	NS	*	*	*	*	*
	\bar{Sx}	0.0003	0.0004	0.001	0.004	0.002	0.003

Similar effects in the ryegrass-prairie grass combinations were observed in the fifth week after planting, while the ryegrass-cocksfoot combinations illustrated these interactive effects at the sixth week after planting.

The root weights per plant of prairie grass were the highest indicating the large root system of this species. Cocksfoot plants had the smallest root system, as shown by root weights.

5.3.4 COMPETITIVE EFFECTS

The process of competition between species was evaluated on the basis of relative yield totals (RYT). There was no difference ($P \leq 0.05$) between the RYT values of different treatments (i.e. shoot competition, root competition and full competition) within a given species combination. Thus, the RYT values are presented as a mean value of all treatments for a given species combination at each harvest (Table 5.4).

In general, the RYT values did not deviate significantly from unity after the 3-4th weeks of growth. However, at the very early stages of growth RYT values were significantly ($P \leq 0.05$) greater than one, indicating that species do not compete for the same resources at this stage.

The relative yield totals based on root weights equalled unity prior to those based on shoot weights. In addition, RYT values based on prairie grass-cocksfoot combinations generally equalled unity before those of the other combinations.

The competitive ability of species growing under different interactive situations was determined by the aggressivity indices (McGilchrist and Trenbath, 1971), of species (Figures 5.2, 5.3). Prairie grass was the most aggressive species and cocksfoot the least aggressive species. While the aggressivity indices changed with time, the overall competitive abilities of species remained in the order of prairie grass > ryegrass > cocksfoot. There was a drop in the aggressivity indices under all competitive situations at the sixth harvest, which was based on 95% light interception. This effect was not observed at the subsequent two harvests, which were also based on 95% light interception (Figure 5.2).

TABLE 5.4 Relative yield totals based on shoot weights and root weights of species

Species combination	H1	H2	H3	H4	H5	H6	H7 (regrowth 1)	H8 (regrowth 2)
<u>(A) Shoot weight</u>								
	*	*	*					
Ryegrass-Prairie grass	1.034±.001	1.020±.002	1.027±.003	1.005±.007	1.005±.003	1.004±.003	1.005±.004	1.005±.007
	*	*						
Prairie grass-Cocksfoot	1.058±.001	1.026±.001	1.007±.014	0.996±.004	1.010±.004	1.001±.004	1.005±.002	1.003±.011
	*	*						
Cocksfoot-Ryegrass	1.039±.002	1.023±.002	1.009±.004	1.003±.012	0.999±.004	1.001±.003	0.995±.002	1.001±.006
<u>(B) Root weight</u>								
	H1	H2	H3	H4	H5	H6		
	*	*						
Ryegrass-Prairie grass	1.042±.001	1.030±.001	1.010±.006	0.998±.008	1.001±.002	1.003±.003		
	*							
Prairie grass-Cocksfoot	1.028±.002	1.014±.012	1.007±.003	1.006±.003	0.996±.006	0.997±.002		
	*	*						
Cocksfoot-Ryegrass	1.045±.002	1.018±.001	1.012±.007	1.007±.005	1.001±.005	0.999±.001		

(* indicates a significant departure from unity - $P \leq 0.05$)

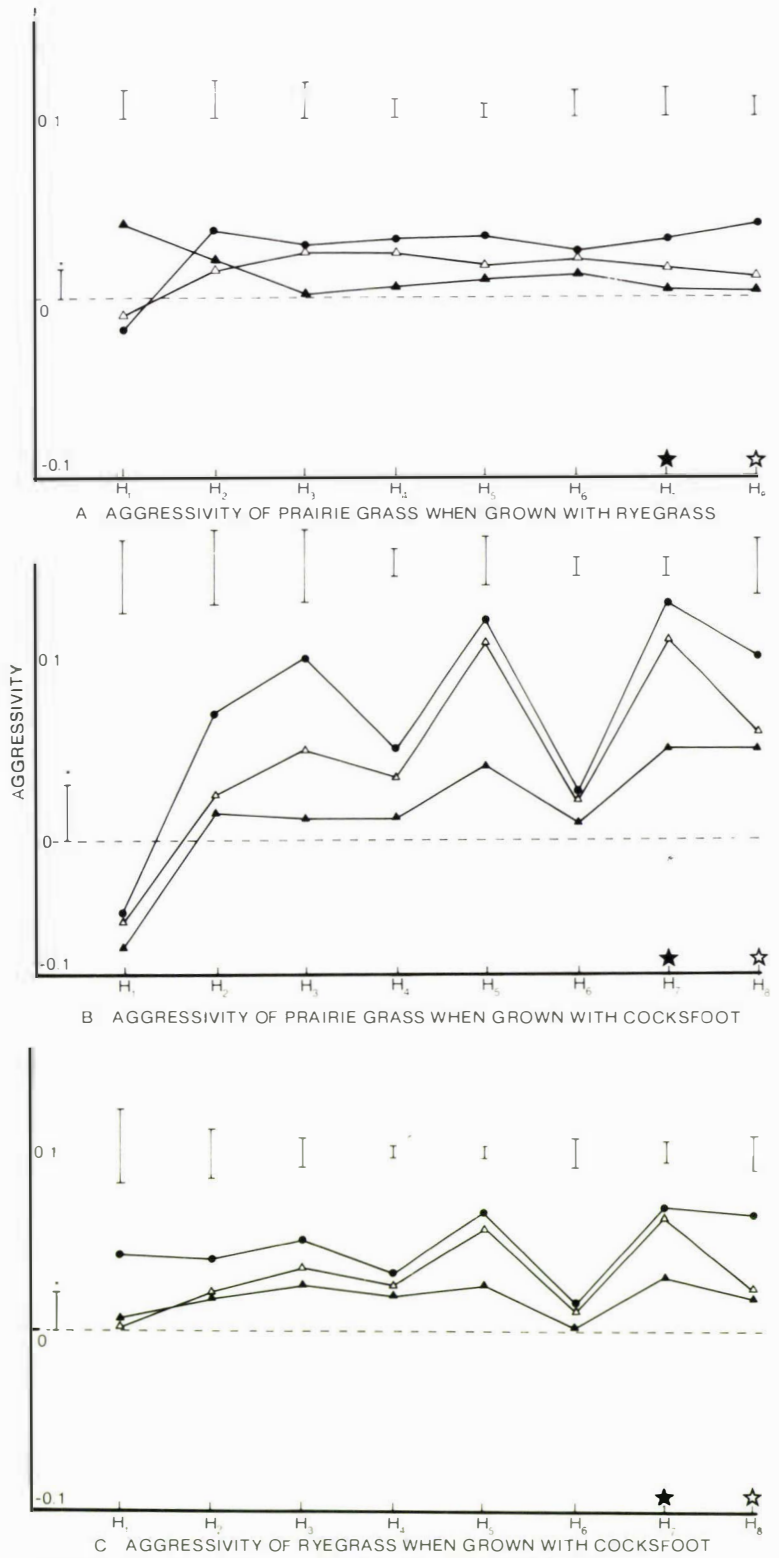


Figure 5.2: The competitive ability of species measured as aggressivity (McGilchrist and Trenbath 1971) based on shoot weights of plants of Ryegrass, Prairie Grass and Cocksfoot, when grown in binary mixtures under conditions of full competition (●—●); Root competition (△—△); and shoot competition (▲—▲).

| = LSD (P = 0.05) * indicates LSD (P = 0.05) starting at zero, to compare each value with zero.
 ★ (REGROWTH₁) ☆ (REGROWTH₂)

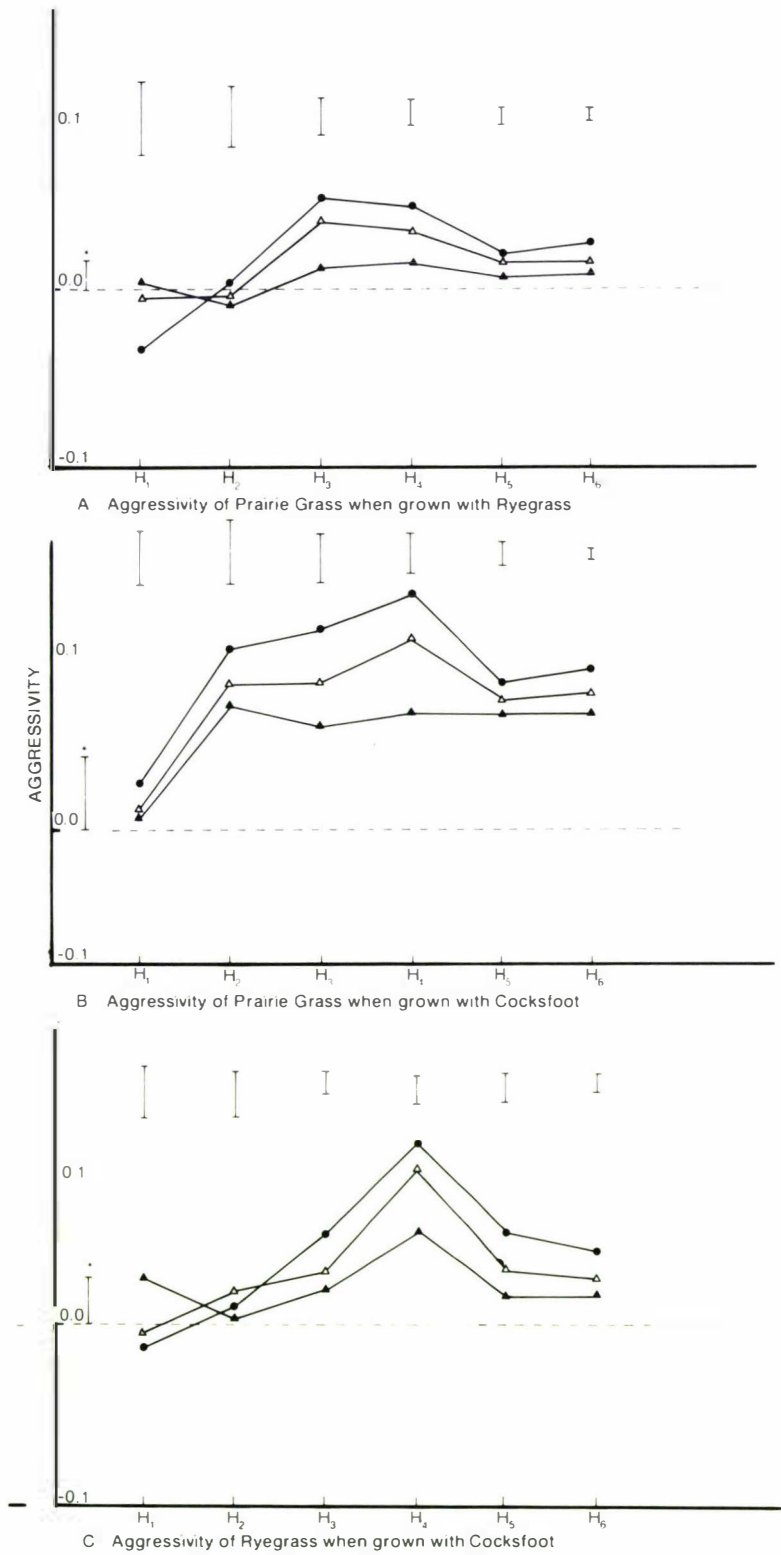


Figure 5.3 The competitive ability of species measured as aggressivity based on root weights of plants of Ryegrass, Prairie Grass and Cocksfoot when grown in binary mixtures under conditions of full competition (●—●); root competition (△—△); and shoot competition (▲—▲). *LSD (P = 0.05) * indicates LSD (P = 0.05) starting at zero. to compare each value with zero.

Full competitive interaction produced the highest aggressivity indices of the superior species, when calculated in terms of both shoot and root weights. The aggressivity of the more aggressive species was also higher under root competition than under shoot competition at all harvests. The results also indicated that aggressivity indices of species under conditions of full competition and root competition fluctuated to a greater extent than those under conditions of shoot competition.

5.4. DISCUSSION

The present study was conducted to investigate the relative effects of root and shoot interactions on the overall competitive relationships observed between the selected grass species, in earlier experiments. In all instances (i.e. tiller numbers and dry matter production of shoots and roots) plant mixtures growing under conditions of full competition exhibited the greatest competitive effects. This can be expected as both root and shoot interactions occurred in this situation.

Comparison of the aggressivity indices illustrate the greater competitive ability and effects of the more aggressive species under conditions of root competition. Vegetative characters also illustrate that the weaker species in a mixture is affected more under conditions of root competition than under shoot competition. Thus, it can be concluded that root competition is more intense and has a greater impact than shoot competition in mixtures between the selected grass species. This is in agreement with many published reports on grasses, other pasture species and crops (e.g. Donald, 1958; Aspinall, 1960; Rhodes, 1968b; Cocks, 1969; Snaydon, 1971; Snaydon and Harris, 1979; Scott and Lowther, 1980).

The greater stability of aggressivity indices under conditions of shoot competition can be attributed to the constancy of the light source within the climate laboratory. In contrast, nutrients were applied manually. Nutrient concentrations within the soil system therefore may have varied sufficiently to cause changes in competitive relationships and thus in the aggressivity indices under root competition. These changes could also have occurred under conditions of full competition, bringing about the observed greater fluctuation of the aggressivity indices under full competition (Figures 5.2, 5.3).

The earlier onset and the greater influence of root interactions than shoot interactions in determining the overall competitive relationships can be related to the growth patterns of the root systems of the seedlings. As discussed in Chapter 4, grass roots develop before shoots and also have a greater surface area, leading to a greater degree of overlapping. In addition, as grass roots occupy similar rooting zones (Troughton, 1957; Garwood, 1966) overlapping of root systems will be greater, thus developing greater competitive effects, as the degree of overlapping between roots determines competitive relationships (Cable, 1969; Trenbath, 1975). As a very low nutrient retentive rooting medium (i.e. sand) was again used in this experiment, competition may have developed between roots, as all roots of grass seedlings are active and capable of taking up nutrients (Langer, 1972) and as a positive relationship exists between the amount of active roots and nutrient uptake (Barley, 1970). The unavailability of all nutrients within a soil system for plant growth (Hall, 1974a) may have aggravated this competitive effect for nutrients in this experiment.

Constraint in pot size which can limit normal root growth may have developed a physical crowding effect on the slower growing species (e.g. cocksfoot), due to the presence of a large mass of actively growing root systems of the more competitive species (e.g. prairie grass). In this experiment, this effect could be further enhanced, due to the presence of partitions. Thus, while it is very difficult to demonstrate the mechanisms of competition below ground (Remison and Snaydon, 1980), further research on patterns of root distribution and total root lengths of these species during early growth may provide an insight into the occurrence of competition for space within pots, due to reduction in optimum effective soil volumes needed by roots for unrestricted growth. Evidence of competition for nutrients could also be obtained by the use of labelled nutrients.

In addition to competitive interactions for growth resources and space, the growth of one species (especially root growth) can be affected by allelopathic effects, which have been illustrated in many grass species (e.g.: Naqvi, 1972; Rice, 1974, 1980). The possibility of allelopathic interactions causing differences in root aggressivity and thus competitive ability has also been suggested by Remison and Snaydon (1978). Thus while no definite measurements were made, the presence of

allelopathic effects cannot be precluded in this experiment.

Many research workers have associated competitive ability with the rate and extent of root development (e.g. Pavlychenko, 1937; Donald, 1958; Lee, 1960; Rhodes, 1968b). Thus, the competitive ability of the roots of the selected grass species in terms of aggressivity indices can also be related to their root growth characters. Extensive and more rapid root growth will give the more competitive species a greater spread of roots and enable the species to exploit the rooting medium before the less aggressive species with smaller root systems, thus leading on to competitive effects. As mentioned earlier, in containers, this effect will increase due to the limited size of the rooting zone, which can develop crowding effects.

Competition between shoot systems occurs for light (Donald, 1958, 1963) and this is easily demonstrated by recording the effects of height and size of leaf canopies on light interception (Stern and Donald, 1962). Although not measured in this experiment, visual observations and earlier experiments indicated that prairie grass had the largest shoot system in terms of height and leaf area, while cocksfoot was the smallest species. As the competitive abilities of the three species lie in the order of prairie grass > ryegrass > cocksfoot, this phenomenon can be related to the growth patterns of the shoot systems, due to light interception capacities and the more extensive growth rates of the shoot systems of the larger and more competitive species.

The situation of full competition illustrated the greatest competitive effects between the species. This can be attributed to the influence of both root and shoot competition, as the final expression of competition is the outcome of interactive processes between shoot and root systems (Donald, 1958, 1963).

5.5 CONCLUSIONS

This study illustrates the greater influence of root competition than shoot competition in determining the overall competitive relationship between the selected grasses during early growth. This is in agreement with many published reports. As in the previous experiment (Chapter 4) the results again highlight the earlier onset of root

competition. The actual mechanisms and processes of root competition are not clear, although many possibilities such as competition for nutrients and space exist. However, a good relationship is shown between root size (in terms of weight and length from base of plant to tip of longest root) and competitive ability, which lie in the order of prairie grass > ryegrass > cocksfoot.

Shoot competitive ability can also be related to growth patterns of the shoot systems, which develop competitive relationships for light. However, shoot competition occurs at a later stage than root competition, and has a lesser impact on overall competitive relationships.

CHAPTER 6. SEED AND PLANT GROWTH CHARACTERISTICS OF GRASS SPECIES DURING THE SEEDLING PHASE.

6.1 INTRODUCTION

The importance of a large seed in securing a faster growth rate during the seedling phase was reported by Black (1957a). In grasses, the importance of seed size as a character associated with competitive ability was identified by Davies (1927) and Davies and Western (1937). More recently, similar studies on grasses have been reported by Rogler (1954); Kneebone and Cramer (1955); Thomas (1966); Arnott (1969) and Cocks and Donald (1973a) (See Chapter 2, Section 4).

Grime (1973) identified four features generally seen in the seedling of a more competitive species. These were

- (i) Tall stature
- (ii) A growth rate which allows extensive and intensive exploitation of the environment above and below ground
- (iii) A high maximum potential relative growth rate
- (iv) A tendency to deposit a dense layer of litter on the ground surface.

The influence of one or more of these characters on competitive ability has also been stressed by other researchers (see Section 2.4). In addition, the importance of the early non-photosynthetic stage of growth (i.e. rapidity of germination and coleorhiza development) in determining seedling vigour of grasses has also been reported by Whalley *et al.* (1966).

In the present series of experiments, competitive abilities of the selected grass species was in the order of prairie grass > ryegrass > cocksfoot, during the establishment phase, and this effect was seen even at later stages of growth (Chapter 3). Competitive ability of the more aggressive species was attributed to more rapid and extensive seedling growth which enabled these species to exploit and secure a greater share of the resources, to larger initial seedling size and to a lesser extent early emergence. The suppression of growth of the weaker and slower growing species was observed. It was also seen that root competition occurred before shoot competition and had a greater impact on the competitive relationships between



PLATE 7. The study of individual plants in a heated glasshouse.

the species (Chapters 4 and 5).

Due to the importance of seedling growth in determining competitive ability, this experiment was conducted to study the inherent seed characteristics and subsequent growth patterns of the selected species when grown in the absence of either inter or intraspecific competition. Emphasis was placed on root growth and distribution of roots within the soil profile as this aspect was difficult to evaluate in mixtures, and as a knowledge of the distribution and density of roots is important in evaluating the competitive ability of species in mixtures (Cable, 1969; Trenbath, 1975).

6.2 EXPERIMENTAL PROCEDURE

The experiment was conducted during the period March - May 1982, in a heated glasshouse (25^o/15^oC) of the Plant Physiology Division, D.S.I.R., Palmerston North.

6.2.1 CULTURAL

Seeds of "Grasslands Nui" ryegrass, "Grasslands Matua" prairie grass and "Grasslands Apanui" cocksfoot, which were previously graded for uniformity of weight (see Chapter 3) within a species, were planted to a depth of approximately 1 cm in plastic containers (dimensions 18 x 18 x 18 cm) filled with 4 litres of sand. Two seeds of one species were sown in each pot and thinned to one plant per pot soon after germination (Plate 7).

During the experimental period, 100 ml of $\frac{1}{4}$ strength modified "Hoagland" mineral solution was added twice daily to every pot.

6.2.2 EXPERIMENTAL LAYOUT

A randomized complete block design with 6 replicates was used. Each replicate contained 28 plants of each species.

6.2.3 MEASUREMENTS

(i) Seed Characteristics:-

10 samples, of 100 seeds of each species were taken randomly from the previously graded seeds of ryegrass, prairie grass and cocksfoot, and dried at 80^oC for 6 hours and weighed to obtain the 1000 seed weight.

Six samples, each containing 40 seeds of each species were randomly obtained from the graded seeds of the three grasses, and dried at 80°C for 6 hours and weighed. Their seed coats were removed and the de-husked seeds reweighed to determine the weight of the husks in relation to the total seed.

Another six samples containing 40 seeds of each species were imbibed in distilled water for 24 hours, and the embryo dissected out under a binocular dissecting microscope. The remaining seed fractions (endosperm and husk) were dried for 6 hours at 80°C and weighed to obtain the weight of the embryos and endosperms.

Approximately 20 g samples of each species were dried at 40°C for 24 hours in a vacuum oven and finely ground. The soluble carbohydrate content was determined by the rapid chemical analysis method described by Haslemore and Roughan (1976).

(ii) Plant Characteristics:-

Six plants of each species per replicate were harvested on each of 4 occasions, at two weekly intervals. At each harvest, the shoot system of each plant was carefully removed at the base of the plant. The plant height (from the base to tip of youngest leaf) was measured and tiller numbers per plant counted. The shoots were then separated into stems (stem and leaf sheath) and leaf blades. After obtaining the leaf area of each plant, the samples were dried at 40°C for 24 hours in a vacuum oven and weighed.

The sand containing the root systems in four of the six pots per species was removed and cut horizontally into 3 layers, each of 6 cm depth. The root system in each layer was carefully washed on a wire grid. The roots harvested from each layer were cut into approximately 4.5 cm lengths and the total root length in each layer was measured using a "Comair Root-Scanner", as described by Richards *et al.* (1979). These samples were dried at 40°C for 24 hours in a vacuum oven and weighed to obtain the dry matter of root material from each layer.

The entire root system of the remaining two pots of each species was washed and the length (from base of plant to tip of longest root) was measured.

6.2.4 STATISTICAL ANALYSIS

The plant characteristics of each species were compared in a manner similar to that described in the earlier experiments.

6.3 RESULTS

6.3.1 SEED CHARACTERISTICS

The 1000 seed weights of the 3 species are presented in Table 6.1. Prairie grass seeds were the heaviest and the cocksfoot seeds were the lightest. The differences in seed sizes and weights between ryegrass and cocksfoot was less than that between prairie grass and the other species.

TABLE 6.1 1000 seed weights (g) of Ryegrass, Prairie grass and Cocksfoot

Ryegrass	2.137±0.065
Prairie grass	9.873±0.104
Cocksfoot	0.925±0.924

The weights of individual seeds, the embryo and endosperm, along with the embryo: endosperm ratio, are presented in Table 6.2.

TABLE 6.2 The weights of seeds and seed components of Ryegrass, Prairie grass and Cocksfoot

Species	Individual Seed Weight	Embryo Wt	Endosperm Wt	Embryo: endosperm
Ryegrass	2.13 mg	0.06 mg	1.538 mg	1:25.6
Prairie grass	9.87 mg	0.24 mg	7.689 mg	1:32.0
Cocksfoot	0.92 mg	0.04 mg	0.567 mg	1:14.1

All weights and ratios of the embryos and endosperms of the three species follow the trend of individual seed weights which is prairie grass > ryegrass > cocksfoot.

The soluble carbohydrate content was 35.5% in ryegrass, 22.2% in prairie grass and 19.6% in cocksfoot.

6.3.2 PLANT CHARACTERISTICS

The plant heights and root lengths of the three species are presented in Figure 6.1. These were significantly different ($P < 0.05$).

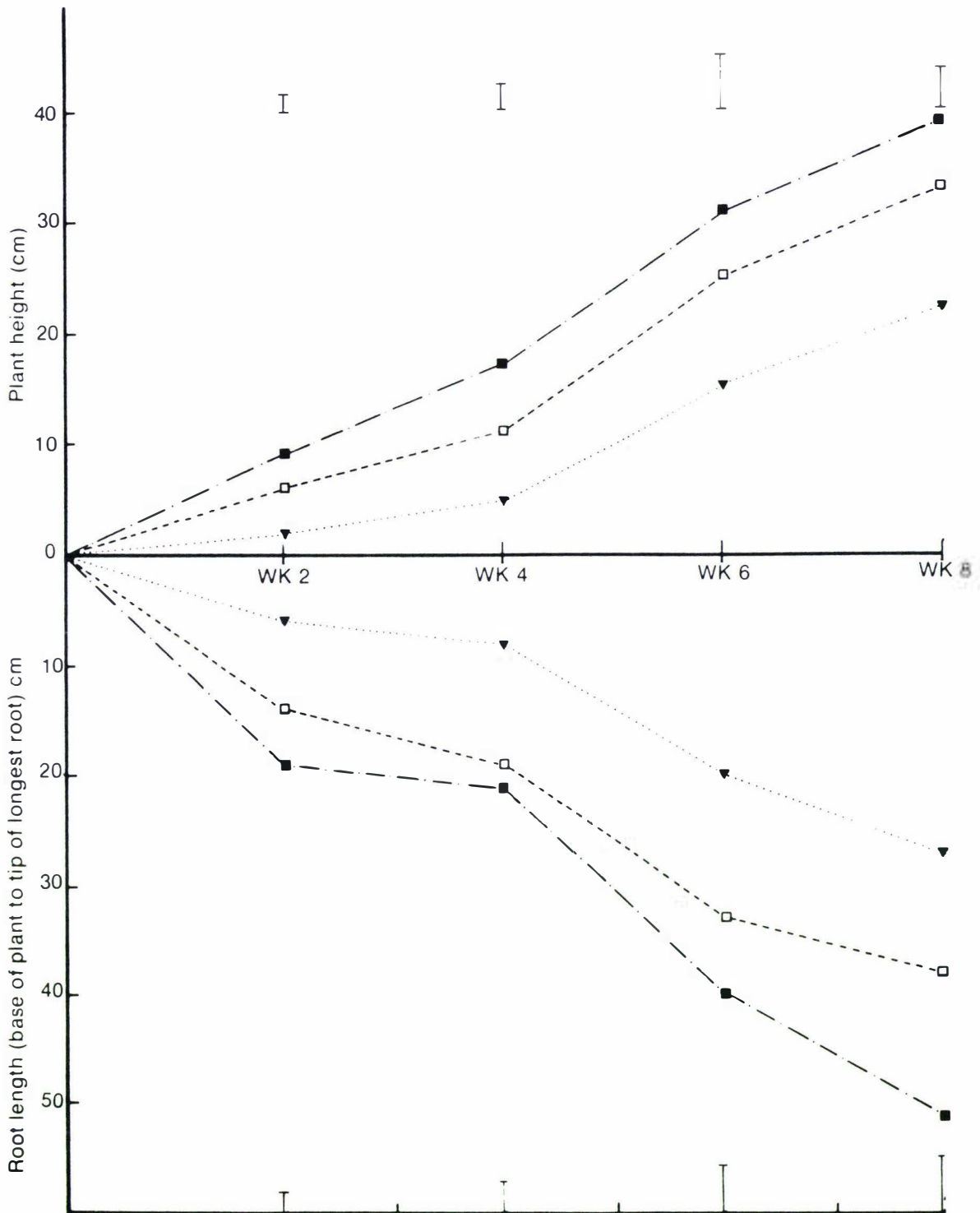


Figure 6.1 Plant height and root length (from base of plant to tip of youngest leaf and longest root) in Ryegrass (\square - - - - \square), Prairie Grass (\blacksquare - - - - \blacksquare), and Cocksfoot (\blacktriangledown - - - - \blacktriangledown) during early growth. (Bars indicate LSD ($P = 0.05$))

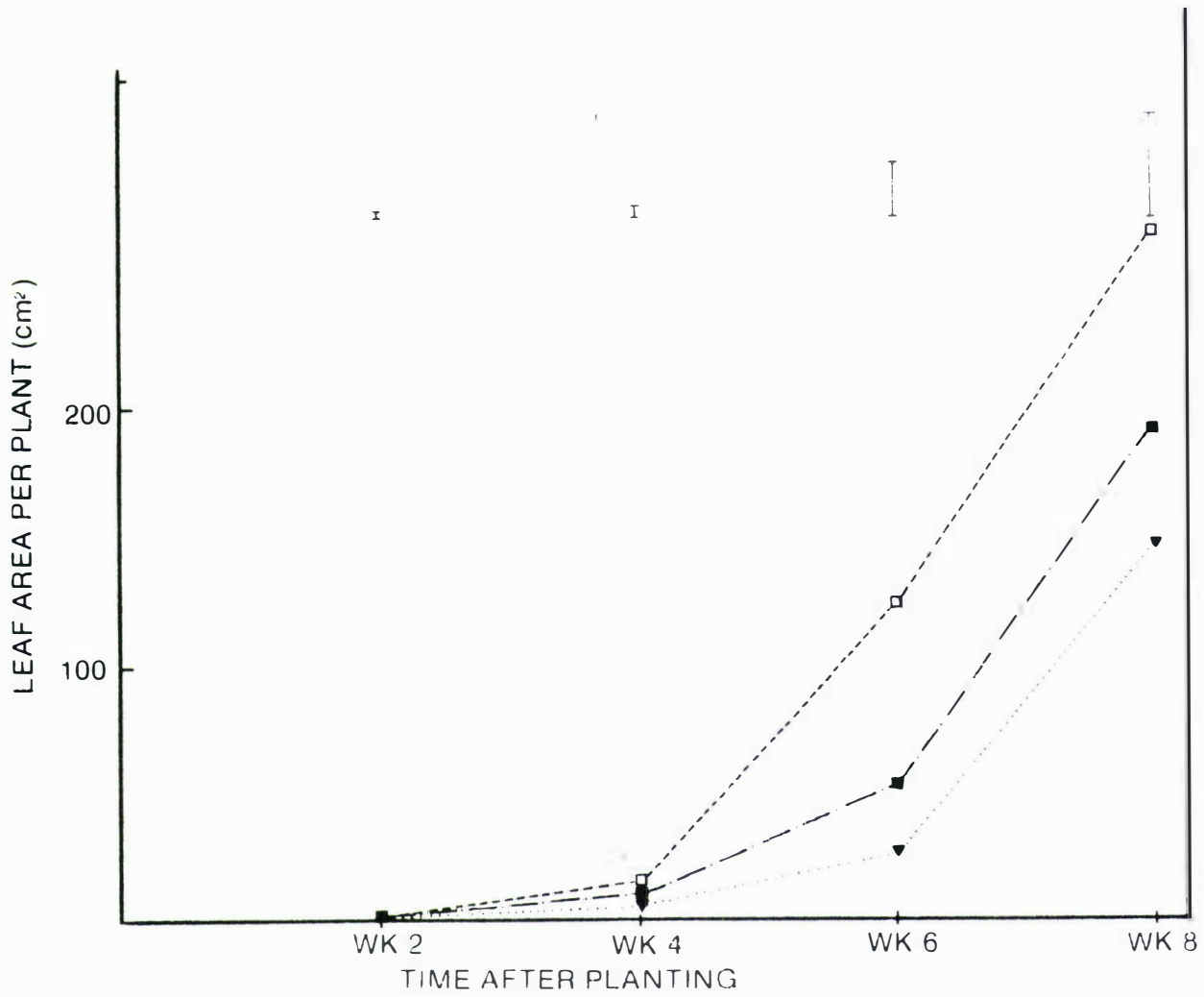


Figure 6.2: Leaf area per plant of Ryegrass (\square - - - - \square), Prairie Grass (\blacksquare - · - · \blacksquare), and Cocksfoot (\blacktriangledown · · · \blacktriangledown) during early growth. ($\bar{}$ LSD (P = 0.05))

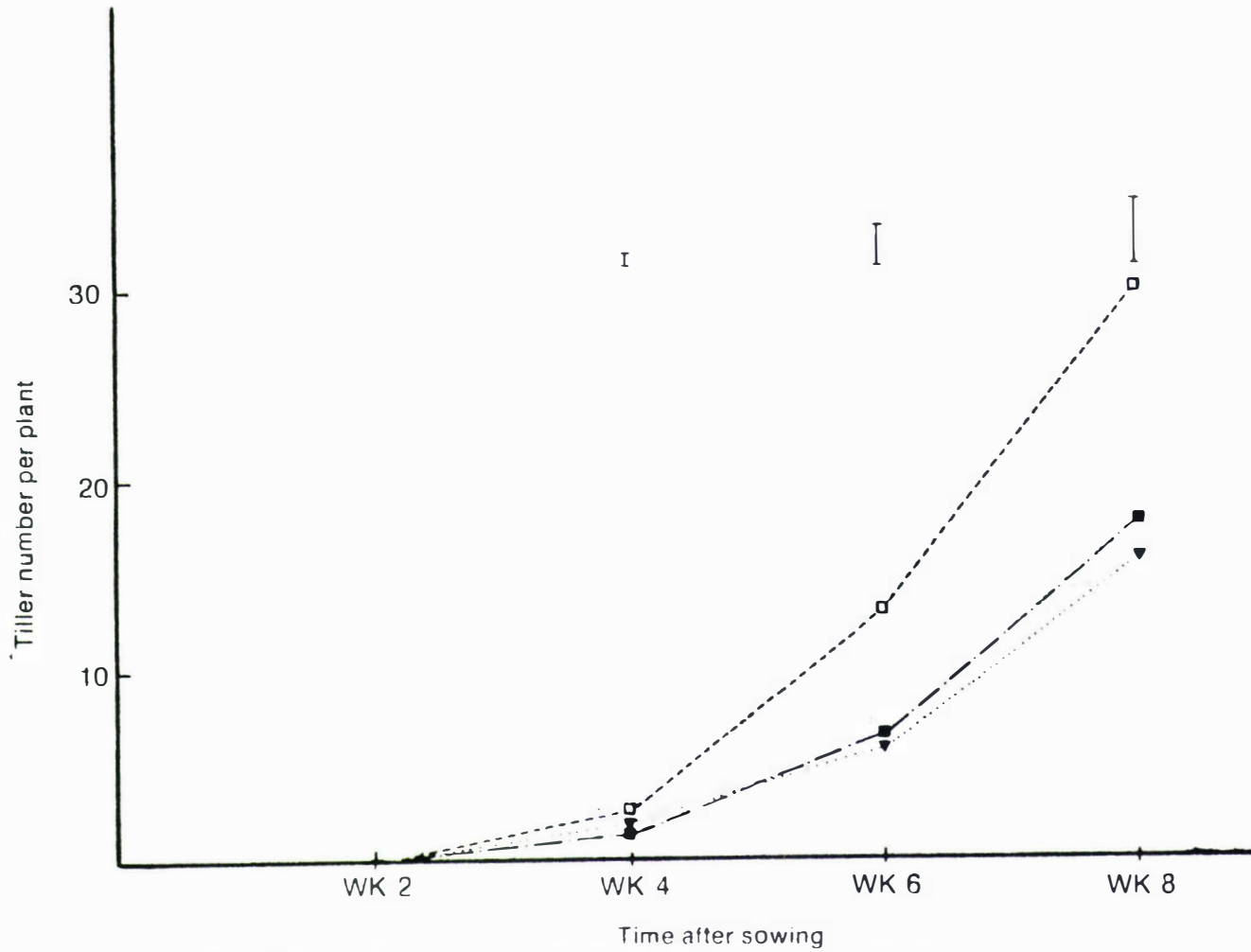


Figure 6.3 Tiller numbers per plant in Ryegrass (□-----□), Prairie Grass (■—■) and Cocksfoot (▼—▼), during early growth ([] = LSD (P = 0.05))

Prairie grass was the tallest plant with the longest root system, and the cocksfoot plants were the smallest. Evaluation of the leaf areas of the three species indicated a similar relationship (Figure 6.2).

Ryegrass had the most tillers, and the tiller numbers of prairie grass and cocksfoot plants were not significantly different ($P \leq 0.05$) (Figure 6.3).

The spatial distribution of roots (in terms of root lengths and weights in different parts of the profile) are presented in Tables 6.3 and 6.4. Prairie grass had the greatest weight and length of roots in all layers within the profile. The roots of all three species were most abundant in the top 6 cm of the soil, and a progressive decline in abundance was observed, with increasing depth. Cocksfoot had the smallest root system. There was no evidence of dead (brown and hardened) roots in any species over the experimental period.

TABLE 6.3 Total length of all roots (m) and pattern of root length distribution of ryegrass, prairie grass and cocksfoot within the rooting medium.

		Root length (m)			Signif	SE
		Ryegrass	Prairie grass	Cocksfoot		
Week 2	0-6 cm	1.44	3.49	1.24	**	0.136
	6-12 cm	0.67	1.33	0.24	**	0.088
	12-18 cm	0.34	1.06	0.00	**	0.043
	Total length	2.45	5.88	1.48	**	0.269
Week 4	0-6 cm	49.50	50.30	7.26	**	2.090
	6-12 cm	18.90	21.80	3.30	**	2.762
	12-18 cm	7.95	18.82	0.93	**	0.515
	Total length	76.35	90.92	11.43	**	3.316
Week 6	0-6 cm	177.0	302.2	109.0	**	7.56
	6-12 cm	112.8	196.7	54.6	**	4.80
	12-18 cm	56.2	76.3	29.5	**	2.49
	Total length	346.0	575.2	193.1	**	9.79
Week 8	0-6 cm	565.0	784.5	414.8	**	26.07
	6-12 cm	297.3	467.3	197.8	**	12.60
	12-18 cm	161.3	306.3	123.3	**	9.06
	Total length	1023.6	1558.8	735.9	**	45.25

TABLE 6.4 Dry weight (mg) of roots and pattern of root weight distribution of ryegrass, prairie grass and cocksfoot within the rooting medium.

		Root wt (mg)				
		Ryegrass	Prairie grass	Cocksfoot	Signif	SE
Week 2	0-6 cm	3.6	3.9	1.3	**	0.13
	6-12 cm	2.2	2.6	0.2	**	0.15
	12-18 cm	0.6	0.9	0.0	**	0.08
	Total wt	6.4	7.4	1.5	**	0.27
Week 4	0-6 cm	16.5	24.9	7.1	**	1.28
	6-12 cm	4.8	14.9	1.5	**	0.76
	12-18 cm	1.9	8.1	0.5	**	0.43
	Total wt	23.2	47.9	9.1	**	1.33
Week 6	0-6 cm	186.2	267.3	68.9	**	7.25
	6-12 cm	68.8	161.2	23.2	**	7.66
	12-18 cm	25.6	66.4	8.8	**	2.91
	Total wt	270.6	494.9	100.9	**	11.88
Week 8	0-6 cm	369.0	694.0	247.0	**	23.10
	6-12 cm	230.5	432.7	119.3	**	10.86
	12-18 cm	103.7	360.9	44.1	**	9.70
	Total wt	703.2	1487.6	410.4	**	50.17

The dry weights of shoots of the three species are presented in Table 6.5. The superior and extensive growth of prairie grass and the slow growth of cocksfoot is again seen in this data.

TABLE 6.5 Dry weight of shoots (mg per plant) of ryegrass, prairie grass and cocksfoot during early growth.

Species		Ryegrass	Prairie grass	Cocksfoot	Signif	SE
Wk 2	Leaf wt	3.5	6.8	9.8	**	0.22
	Stem wt	1.1	2.3	0.2	**	0.11
	Total shoot wt	4.6	9.1	1.0	**	0.29
Wk 4	Leaf wt	62.4	67.0	9.9	**	2.19
	Stem wt	8.6	24.9	3.4	**	0.51
	Total shoot wt	71.0	91.9	13.3	**	2.26
Wk 6	Leaf wt	354.4	782.7	145.5	**	17.60
	Stem wt	154.4	193.0	70.5	**	7.54
	Total shoot wt	508.8	975.7	216.0	**	22.10
Wk 8	Leaf wt	993.0	1623.0	707.0	**	41.96
	Stem wt	393.9	505.2	259.0	**	10.02
	Total shoot wt	1386.9	2128.2	966.0	**	41.91

All seed and plant characters of ryegrass were intermediate between those of prairie grass and cocksfoot.

An evaluation of the rate of dry matter accumulation of the three species grown as individual plants over the experimental period showed no significant difference ($P \leq 0.05$) between the species (Table 6.6).

TABLE 6.6 Dry matter accumulation rates* of ryegrass, prairie grass and cocksfoot during early growth

(A) <u>Shoots</u>	Rate of dry matter accumulation(β)	Reg. Coeff.(r^2)
Ryegrass	.136	.95
Prairie grass	.133	.96
Cocksfoot	.165	.98
(B) <u>Roots</u>		
Ryegrass	.117	.94
Prairie grass	.136	.81
Cocksfoot	.135	.98

(* Dry matter accumulation rates were calculated by the equation
 $\log_e Y = a + \beta x$
 where Y = dry matter of shoots and roots, and x = time)

6.4 DISCUSSION

In all three seed characters studied in this experiment, namely embryo and endosperm weight and embryo:endosperm ratio, the species again fall in the order of prairie grass > ryegrass > cocksfoot. Thus, it is likely that these seed characters have an influence on the growth patterns and rates and thereby on competitive abilities of these grass species during early growth. Although Wright (1971) states that there is little or no relationship between seed weight and seedling vigour among species, the results obtained from this study agree with earlier published work and demonstrate a positive relationship between seed size and seedling vigour and competitive ability (e.g.: Davies, 1927; Plummer, 1943; Bremner *et al.*, 1963; Cocks and Donald, 1973a).

Ryegrass seeds have a greater percentage of soluble carbohydrates than the other species. However, prairie grass has a larger seed, providing a greater total source of carbohydrates to the growing embryo. This larger reserve of carbohydrates can be expected to assist the growth of the larger prairie grass seedling when compared with ryegrass, although it germinates later than ryegrass.

The importance of early germination and extensive and rapid growth as characters associated with competitive ability has been presented (Section 2.4). These advantages can be enhanced by the early onset of autotrophic growth in young seedlings (McWilliam *et al.*, 1970). Similarly larger seedlings have potential competitive advantages over smaller seedlings (Black, 1958), and generally, competitive success lies with those plants having a greater size when competition begins.

The results of this study highlight the relatively large differences in the seedling growth characteristics of the three species. More importantly, the study illustrates the root distribution patterns of the species within a soil profile, which is a characteristic difficult to identify when plants are grown in mixtures. Prairie grass has a greater root mass in all layers of the profile, when compared with the other species, while cocksfoot has the smallest root mass in all layers. (Table 6.3, 6.4). This large root mass

will enable prairie grass to exploit the soil environment successfully in order to obtain nutrients and moisture required for growth, as all grass roots are active at the seedling stage (Langer, 1972) and as a good correlation exists between root abundance and nutrient uptake (Barley, 1970).

Although extrapolation of characteristics of plants grown in isolation to their likely performance in the presence of inter and intraspecific competition can be misleading (e.g. Salisbury, 1942; Harper and Clatworthy, 1963), the growth patterns of these species in isolation were consistent with those observed earlier (e.g. Chapter 4). Thus, when these species are grown in mixtures, the larger form of prairie grass plants will give this species a distinct advantage over the others, although in the absence of any form of competition, their rates of dry matter accumulation are not significantly different (Table 6.6). Similarly, ryegrass will have an advantage over cocksfoot. This competitive advantage can be attributed to the ability of the larger shoot and root systems to obtain light, nutrients and water more effectively than the smaller species. In addition to the competitive advantage for nutrients, which places the smaller species under stress, the possibility of the larger root mass developing an obstructing effect on the growth of roots the smaller species cannot be excluded. This obstructive effect may develop as grasses occupy similar rooting zones, and could be magnified when plant mixtures are grown in containers, due to restrictions on total root growth of all species.

6.5 CONCLUSIONS

The results of this study show that seed and seedling characteristics when plants are grown in the absence of intra and inter-specific competition lie in the order of prairie grass > ryegrass > cocksfoot. This is similar to their respective competitive abilities observed in earlier experiments. It can be considered therefore, that seed characters, seedling size and growth characteristics of ryegrass, prairie grass and cocksfoot have an important bearing on the competitive relationships that develop between them when

grown in binary mixtures, especially during early growth, which as reported by Charles (1961) is a highly competitive stage in sward establishment.

CHAPTER 7.* GRASS SPECIES USED AND PASTURE ESTABLISHMENT IN CENTRAL NEW ZEALAND

7.1 INTRODUCTION

Literature on grassland farming in New Zealand does not provide much quantitative data on the pasture species used by farmers when renovating old pastures or establishing new ones. Harris (1968) conducted a survey of pasture seed mixtures used in the lower regions of the North Island, and indicated that seed mixtures generally contained an average of 3.9 species. The composition of mixtures in the survey was predominantly two grasses and two legumes. A series of recommendations of pasture mixtures made by White (1973) contains 2-5 grass species and 1-2 legumes.

The series of experiments reported in this study evaluated competition between binary mixtures of three common pasture grasses in New Zealand, during the establishment phase. The results indicated a competitive hierarchy among the species during this phase of growth, and these effects were continued during later stages of growth. Thus, in order to relate these studies to practical grassland farming, a survey was conducted in the central regions of New Zealand during the period October-November 1981. The broad objectives of the survey were -

- To ascertain the types of mixtures used by farmers in establishing or developing pasture in the region.
- To determine the grass species used by farmers in the recent past and to be used in the near future, along with seeding rates.
- To assess differences between dairy and sheep farmers in the practice of pasture establishment.

These objectives were extended in an endeavour to take account of the many factors that surround the procedure of pasture establishment. Consequently, the survey questionnaire was designed to obtain a general overview of the process of pasture establishment and development.

* Published under the same title in *New Zealand Journal of Experimental Agriculture*, 1982. 10: 359-364.

7.2 METHODOLOGY

7.2.1 SURVEY METHOD

A mail survey was necessary because of the limited resources available and time restrictions.

To achieve a maximum response rate, emphasis was placed on the comprehensibility, yet simplicity of the questionnaire (Appendix 10B). A letter stating the objectives of the study (Appendix 10A) accompanied the questionnaire. Articles were also published in newspapers and farming weekly bulletins within a week of mailing the questionnaire, in order to bring the study to the attention of farmers. As a further aid in encouraging responses, a gift was used as a prize for a ballot conducted among the returned questionnaires.

7.2.2 THE SAMPLE

To relate the results of this survey to the farming community of New Zealand, the sample was drawn from predominantly sheep and dairy farms within the regions from South Auckland to Canterbury. This included 71 counties (of a national total of 106) in the statistical regions of South Auckland-Bay of Plenty, East Coast, Hawkes Bay, Taranaki, Wellington, Marlborough, Nelson, Westland and Canterbury. Resource limitations led to the exclusion of regions North of Auckland and South of Canterbury (Figure 7.1).

The selection of the population of sheep and dairy farms for this study was based on land area. The sheep farms selected were within the range of 250-350 hectares and dairy farms in the range of 65-76 hectares, reflecting the national average farm sizes of sheep and dairy farms respectively (N.Z. Statistics, 1981).

A total population of 2072 farms consisting of 1305 dairy units and 767 sheep units were identified in the study area. A random sample of 570 farms was drawn (307 dairy and 263 sheep farms) which represented 27.5% of the total population.

7.2.3 RESPONSE

Of the questionnaires mailed out, 48.2% were returned giving a total of 269 completed documents. The percentage returned by the

post office as "Gone - No Address" was 1.2. On this basis, the response rate for each statistical region is shown in Table 7.1.

TABLE 7.1 Response rates of questionnaires for each region.

Statistical region	Total no of farms	Number mailed	Respondents (Percentage of total mailed)
South Auckland-Bay of Plenty	1040	240	50.0
East Coast	45	13	15.4
Hawkes Bay	156	50	58.0
Taranaki	335	102	44.1
Wellington	270	86	41.8
Marlborough	27	8	25.0
Nelson	36	14	42.8
Westland	8	3	33.3
Canterbury	155	54	53.8
	2072	570	47.19

The 269 respondents consisted of 151 dairy farmers and 118 sheep farmers, representing a 49.2% and 44.8% response rate respectively.

If it is assumed that respondents to the survey are representative of the total population, the response rate achieved for this survey provides estimates, with the following precision at the 95% confidence level (Yamane, 1973).

Total sheep farms \pm 7.6%

Total dairy farms \pm 8.5%

All farms \pm 5.6%

These precision levels indicate the reliability of the responses.

7.3 RESULTS

The results have been aggregated into farm type (either dairy or sheep) or according to the statistical region, in order to maintain anonymity of the respondents.

7.3.1 GENERAL CHARACTERISTICS OF THE POPULATION SAMPLED

7.3.1.1 Size of holding

The average land area of the dairy and sheep farms surveyed was 79 and 320 ha respectively, the range was 37-431 ha and 200-820 ha.

Although the population selected was assumed to fall within land areas of 65-75 hectares and 250-350 hectares for dairy and sheep farms, the survey produced much wider ranges in farm sizes.

The land area used for grazing by the respective farm type was:-

Dairy farms 92.4%

Sheep farms 90.6%.

7.3.1.2 Land accessible by tractor

The percentage of land area accessible by tractor in each farm was assessed in order to identify the topography of the farm, as this has a direct bearing upon the pasture establishment practices. Farms with less than 25% land accessible by tractor are identified as hill country farms, while farm units easily accessible by tractor (i.e. over 75% of the land being accessible by tractor), are regarded as flat lands, ideally suited for dairy farming. The percentage of each type of farm from the total sample is presented in Table 7.2.

TABLE 7.2 The percentage of tractorable land in each type of farm.

Characteristic of Land	Percentage of Sample
Less than 25% of land accessible by tractor	17.8%
25-50% of land accessible by tractor	13.8%
50-75% of land accessible by tractor	17.1%
Over 75% of land accessible by tractor	51.3%

7.3.1.3 Type of pasture

Pastures on most farms (61%) consist of grasses and legumes. Mixtures of grasses only were seen in 30% of farms, of which most were dairy units.

7.3.2 ESTABLISHMENT OF PASTURES

7.3.2.1 Pattern of establishment

Some 79% or 213 farmers had established new pastures or renovated existing pastures within the last 5 years. The proportion of land developed over the last 12 months into either new or renovated pastures, compared with the total land area of the farms show that on an average, both types of farmers develop approximately 6% of their total holdings per year. A similar assessment of land developed over the last 5 years shows that both dairy and sheep farmers have developed approximately 20% of their total farm area within this period.

The number of farmers who stated their intention of establishing new pastures or renovating old pastures within the next two years was 162 (60%). Twenty one percent of the farmers indicated that they will not sow new pastures or renovate existing pastures over this period because their pastures were well developed and productive. Some respondents (10%) were not certain that they would establish new pastures or develop existing pastures within the next 2 years, and they were requested to assume that they would sow new pastures and answer the questionnaire.

7.3.2.2 Land used for pasture establishment

Information was requested on the types of land (whether existing pastures or previously uncultivated land) used by farmers to establish pastures. The results have shown that most farmers (both dairy and sheep) have renovated existing pastoral land with or without cultivation. Only 17% of the responding farmers indicated that new land had been sown into pastures. Similar trends are also seen in the future intentions of farmers for pasture development and renovations. Major differences between dairy and sheep farms with respect to the land developed into pastures or land to be developed into pastures were not demonstrated by this survey.

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7.3.2.3 Method of pasture establishment

The techniques used to establish new or renovate existing pastoral or cropping land by farmers, and the comparison between methods of establishment and topography of the farm is presented in Table 7.3. Farmers were requested to denote all methods used to establish pastures.

TABLE 7.3 Techniques used and to be used by farmers to establish pastures (% use of each method)

Techniques of seed establishment	< 25%		% Land accessible by tractor					
			25-30%		50-75%		> 75%	
	*A	B	A	B	A	B	A	B
A. <u>Dairy Farms</u>								
(i) Broadcasting	100%	37%	50%	62%	54%	76%	44%	45%
(ii) Broadcasting & Drilling	0%	13%	30%	13%	23%	0%	30%	13%
(iii) Drilling	9%	50%	20%	25%	23%	24%	26%	42%
B. <u>Sheep Farms</u>								
(i) Broadcasting	36%	45%	27%	53%	25%	33%	19%	14%
(ii) Broadcasting & Drilling	20%	21%	27%	16%	19%	7%	17%	14%
(iii) Drilling	44%	34%	46%	31%	56%	60%	64%	72%

* A Techniques used

B Techniques to be used.

The table shows interesting relationships between farm types, land topography and method of pasture establishment. Most dairy farmers in all classes of farms broadcast pasture seed. This is most prominent in the hill country dairy farms. This trend is not evident in sheep farms, where drilling has been used to a greater extent. Future trends of selecting a particular method of seed establishment is not clear among dairy farms. However, a greater future preference for broadcasting in hill country farms and drilling in flat lands has been indicated by sheep farmers.

Except for hill country dairy farmers and to a lesser extent hill country sheep farmers, all other categories have indicated a greater use of either broadcasting or drilling for future pasture establishment, rather than the use of both methods.

7.3.3 MIXTURES AND SPECIES OF GRASSES

7.3.3.1 Mixtures

Information obtained on the type of pasture mixtures that have been sown on farms in the recent past, and those to be sown in the near future are presented in Table 7.4.

TABLE 7.4. Pasture mixtures sown and to be sown (% of all farmers using each type of mix)

Type of mixture	Past use*	Future use*
One grass species	28%	9%
Mixture of grass species	28.2%	26.1%
One grass species and one legume	15.1%	14.7%
Mixture of grasses and legumes	60.3%	60.5%

(*Farmers were requested to note all types of mixtures that have been used and will be used for pasture establishment).

As one would expect, farmers generally use pasture mixtures containing both grasses and legumes for pasture establishment, and will continue to do so. However, it does appear that fewer farmers intend to sow one grass species alone, which may reflect an expected

decline in pasture renovation where the use of a single grass species for oversowing or direct drilling is commonly practiced. For example, the 9% of farmers who intend sowing a single species have indicated that it will be used in special circumstances such as oversowing or direct drilling for pasture renovations. Another possibility is, of course, a reduction in the number or area of sowings for seed production.

7.3.3.2 Grass species and cultivars

One or more cultivars of ryegrass have been incorporated in 98% of all seed mixtures sown by farmers, and 93% intend using the species for future sowings. It is clear that ryegrass is and will continue to be the most popular grass species sown in New Zealand.

7.3.3.3 Cultivars of ryegrass

'Grasslands Nui' perennial ryegrass is the most common cultivar used by farmers. It was used by 65% of all farmers and a similar number intend to continue using the cultivar. Ellet ryegrass is the next most commonly used cultivar and 39% of farmers have used it. The other cultivars of ryegrass, namely Ruanui, Ariki, Tama, Manawa and Paroa have been used only in a small number of mixtures (the number ranges from 5-25%). Future trends for pasture seed mixtures do not show an increase in the use of these cultivars. Pasture mixtures generally contain 2-3 cultivars of ryegrass and this pattern is likely to continue into the future.

7.3.3.4 Other grass species

All other grass species are not as frequently used as ryegrass.

(A) Cocksfoot:- Cocksfoot was used by 57% of the surveyed farmers and they intend using it in future pasture seed mixtures, indicating that cocksfoot is still widely used in pasture mixtures in most districts. It is not used as the main species in mixtures. Although White (1973) indicated a greater use of cocksfoot by dairy farmers, this survey did not demonstrate major differences between the farm types in the use of this species.

(B) Timothy:- This species was used by 27% of the surveyed farmers as a component of their pasture seed mixtures. The same number of

farmers intend using it for future sowings.

(C) Tall Fescue:- This species will be used only by two farmers from South Auckland and Taranaki. No farmer in the survey has incorporated this species in their recent sowings.

(D) Phalaris:- One farmer in South Auckland has used it and none intend using it in the future.

(E) Prairie grass:- Prairie grass has been incorporated into the seed mixtures by 17% of the farmers surveyed, of whom a major proportion own dairy units. Some 27% of the farmers surveyed intend using prairie grass in the future, and its popularity is projected to rise especially among dairy farmers. The survey indicated that prairie grass is most commonly used and will be used in South Auckland, Taranaki and Canterbury regions.

(F) Other Species:- A small percentage (4%) of the farmers surveyed have used other species of grasses, among which Brown-top plays a prominent role.

It is however possible that many farmers are unfamiliar with or even unaware of the most recent species and cultivars such as those of Tall fescue and Phalaris, and their place and potential in grassland farming. Significant changes in regional patterns of use may well emerge with time and experience.

7.3.3.5 Number of grass species and cultivars in mixtures

The number of grass species or cultivars that make up pasture mixtures range from 1 to 7. However, the major proportion of farmers have used either 3 or 4 grass species or cultivars in their pasture mixtures. This is an increase from that reported by Harris (1968) who showed that the majority of seed mixtures sampled had 2 grass species. The study also shows a difference between dairy farmers and sheep farmers, when comparing the number of grass species that make up the pasture seed mixtures. A large proportion of dairy farmers will still incorporate 4 grass species or cultivars into future seed mixtures. The number of grass species or cultivars that will be incorporated into mixtures by most sheep farmers is two, thereby

showing a simplification of the pasture mixtures not seen among dairy farmers.

7.3.3.6 Major species in mixtures

One of the ryegrass cultivars makes up the major component of all seed mixtures that contained this species. "Nui" ryegrass was the major component in 53% of all mixtures sown, and was predominant in pasture seed mixtures in all districts surveyed except Hawkes Bay and East Coast. "Ellet" ryegrass was the major component in 25% of the seed mixtures, and more particularly, in seed mixtures used by dairy farmers. It was the major cultivar in most mixtures used in Hawkes Bay and East Coast.

This highlights a major change from the results of the survey in 1968 (Harris, 1968), where Ruanui and/or Manawa made up the major component in 90% of the mixtures. Thus it is seen that most farmers have changed the perennial ryegrass cultivar in pasture seed mixtures to either "Nui" or "Ellet", which were released in the mid and late 1970's (Table 7.5).

TABLE 7.5 Percentage of farmers using a particular ryegrass cultivar as the major component in the seed mixture

Type of farm	Long lived cultivars			Short lived cultivars			No answer
	Nui	Ellet	Ruanui	Ariki	Tama	Manawa	
Dairy farms	54.5%	32.2%	3.3%	5.0%	1.7%	0.8%	2.5%
Sheep farms	51.6%	17.2%	16.1%	4.3%	0.0%	2.2%	8.6%
Total	53.3%	25.7%	8.9%	4.6%	0.9%	1.4%	5.1%

7.3.4 FACTORS ASSISTING SELECTION OF GRASS SPECIES

Previous experience was the most useful factor assisting farmers and their experience will play a greater role in future selections of grass species and mixtures. The advice of Ministry of Agriculture and Fisheries officers has been of most value to 16% of the farmers surveyed, in selecting seed for their pasture mixtures. The advice of stock and station agents has been useful to a similar number of farmers. While the advice of M.A.F. will play a similar role in future selection, the role of stock and station agents is projected to

decline in the future. Other factors that assist the farmers in selecting pasture seeds were stated as advice of graduate members of the family and species seen at demonstration farms (Table 7.6).

TABLE 7.6 Factors assisting farmers in selection of pasture species
(% of farmers surveyed)

Factors assisting selection	Past seed selections	Future seed selections
Previous experience	39.3%	62.6%
Discussion with other farmers	11.6%	3.8%
Advice of M.A.F.	16.4%	15.2%
Advice of stock and station agents	16.3%	8.5%
Read about it	7.5%	2.4%
Other	8.9%	5.2%
No answer		3.3%

7.3.5 SATISFACTION

Most farmers (83%) who had established new pastures or renovated existing pastures indicated satisfaction with the seeds used by them, while 8% showed dissatisfaction. The major reason for this dissatisfaction was stated as poor establishment.

7.3.6 SOURCES OF PASTURE SEED

Over 95% of the farmers surveyed purchase their seed from seed merchants, who also blend the seed mixtures for them. The survey also shows that the seed merchants will play a predominant role in providing quality seeds and making up the seed mixtures in the future. A smaller group of farmers make up their own seed mixtures.

7.3.7 SEED RATES

As expected, the seed rates used by farmers for pasture establishment change with the species and mixtures sown. Farmers sowing a single grass species use seed rates ranging from 5-10 kg per hectare. The seed rate used by farmers for sowing a single grass species is projected to rise to 10-15 kg per hectare in the future. As most farmers use mixtures of grasses and legumes, the seed rates used lie

within the range of 30-35 kg per hectare. This pattern is likely to continue into the future.

The survey does not show a significant variation in seed rates used by sheep and dairy farmers, in different regions. It does not indicate major differences in seeding rate used for different methods of sowing pasture seed.

7.3.8 TIME OF SOWING

Most farmers (83%) sow their pasture seeds in autumn, while 15% sow in spring. The time of sowing does not change with region or farmtype.

7.4 DISCUSSION AND CONCLUSIONS

The results of this survey need to be considered in a broad perspective, when ascertaining the pasture establishment practices adopted by farmers. This is due to the lack of sufficient responses in certain districts to warrant specific comments or enable the examination of features relevant to all the different districts. The main points arising from the analysis, which pertain to the objectives of this study were

- Sheep and dairy farmers in different regions do not differ significantly in their pastures establishment practices.
- Farmers use and intend using mixtures containing both grasses and legumes for pasture establishment. The mixtures will contain 2-4 grass species. A single grass species has been and will be used to renovate existing pastures and establish special purpose pastures by oversowing or overdrilling, or for seed production.
- Ryegrass is seen to be the most popular grass species being used. "Grasslands Nui" ryegrass is the most widely used cultivar. Cocksfoot is commonly incorporated in seed mixtures, although not as a major constituent.

Other interesting points that arose from the survey were -

- A large number of farmers sow pasture seed every year and a majority of them renovate existing pastures rather than develop new land into grasslands.
- Most farmers either broadcast or drill the pasture seed, while a small proportion use both methods for seed establishment.
- Future trends project a decline in the use of both methods concurrently by farmers, and there is a projected increase in the future use of drilling as a technique for pasture establishment, especially in flat lands.
- Previous experience has been and will be the major factor assisting farmers in pasture seed selections.
- Farmers tend to purchase their seed from seed merchants who generally make up the seed mixtures.
- Seed rates used by farmers lie in the range of 30-35 kg per hectare for mixtures. Farmers sowing single species have used seed rates between 5-10 kg per hectare and this is projected to rise in the future to 10-15 kg per hectare.
- Farmers in New Zealand generally sow their pastures in autumn irrespective of the region.

The results of this survey are similar to those of Harris (1968) in terms of farmers using simple seed mixtures to sow their pastures. However, changes are seen in terms of the ryegrass cultivars presently being used by farmers. There is a great shift towards the use of new ryegrass cultivars, namely "Grasslands Nui" and "Ellet" ryegrass from "Grasslands Ruanui" and "Grasslands Manawa", which were the predominant cultivars in the 1968 survey.

This study was conducted to ascertain the grass species used by farmers when establishing new pastures or renovating existing

pastures. As the pastoral scene of New Zealand involves both grasses and legumes, information on the types of legumes used will also be an important factor in determining the pasture establishment practices of farmers.

Although the scope of this study does not provide a detailed description of pasture establishment practices of farmers in all regions of New Zealand, the results do provide a quantitative estimate of information which has not been previously gathered. Farmers still use simple seed mixtures for establishment of general purpose pastures, and the selection of species and the entire operation of pasture establishment is guided to a large extent by past experience. It is also seen that farmers are aware of most of the species and cultivars available. Thus the need for good extension work using techniques such as demonstration farms and plots arises, to help the farmer observe and appreciate the merits of species and cultivars available for use, and the best methods of establishment. This will undoubtedly aid the farmer in obtaining a well established or renovated pasture with species best suited to the given situation on his farm.

CHAPTER 8. GENERAL OVERVIEW AND CONCLUSIONS

This thesis presents the results of a series of experiments conducted to evaluate the competitive relationships that exist between three grass species widely used in the pastoral industry of New Zealand. Emphasis was placed on the establishment phase as competitive hierarchies established in the early growth stages tend to persist at later stages (Rhodes, 1967; Harris, 1973).

Herriot (1958) defined "seedling establishment" as the establishment phase up to 4-6 weeks from sowing, while, "young plant establishment" was considered the establishment shown from seedling stage up to the end of the seeding year. The "establishment phase" considered in these studies was similar to the "seedling establishment" defined by Herriot (1958), which was the first 8-9 weeks from sowing, when, depending on the species, the swards reached approximately 95% light interception.

The de Wit (1960) replacement series model, being a widely accepted and successfully used technique for evaluating competitive relationships between plants (Trenbath, 1978; Spitters, 1979), was used in the present study. A uniform planting density of 400 plants per square meter, which was considered to be similar to normal pastoral conditions (Hill and Shimamoto, 1973) was used in all treatments. The adoption of this uniform density in all experiments enabled the comparison of species performance across different experiments.

The results of the individual experiments have been discussed in their respective chapters. Thus, this discussion will be concerned with the relationships between different experiments and the objectives of this study, presented in Chapter 1.

8.1 COMPETITION BETWEEN "GRASSLANDS NUI" PERENNIAL RYEGRASS, "GRASSLANDS MATUA" PRAIRIE GRASS AND "GRASSLANDS APANUI" COCKSFOOT.

8.1.1 COMPETITIVE RELATIONSHIPS IN THE ESTABLISHMENT PHASE

8.1.1.1 The nature of competition

The results of this series of experiments show that the selected grass species compete for similar growth resources during the establishment and early growth phase, when grown in binary mixtures. This is

illustrated by the products of the relative crowding coefficients (Figures 3.4; 3.7; 3.8) obtained in the first three experiments and the relative yield totals obtained in all experiments (e.g. Tables 3.9; 3.19; 3.23; 4.8; and 5.4), which did not depart significantly from unity. This is in agreement with most reports on grass mixtures (e.g. van den Bergh, 1968; Trenbath, 1974a, 1978). This was not surprising, as developing grass species have similar growth patterns, (Barnard, 1964; Jewiss, 1966; Langer, 1973), occupy similar areas of the environment and require similar resources for their growth and development.

The competitive hierarchy between the three species was in the order of prairie grass > ryegrass > cocksfoot. The low competitive ability of cocksfoot, which has been previously identified in mixtures under field and experimental conditions (e.g. Stapledon and Davies, 1927; Blaser *et al.*, 1956; O'Brien, 1960; Arens, 1962) was again illustrated by the relative crowding coefficients (Figures 3.4; 3.7; 3.8) and the aggressivity indices (Tables 3.11; 3.18; 3.25; 4.9; Figures 5.2; 5.3). The superior competitive ability of prairie grass over the other species and of ryegrass over cocksfoot were also illustrated by these coefficients and indices.

8.1.1.2 Growth of species in mixtures

All three species showed superior growth over their respective monocultures, when associated with 25% of another species. This is well illustrated by the shoot weights, especially of ryegrass and prairie grass (e.g. Tables 3.5; 3.13; 3.21 and 4.7). This, as reported earlier, can be attributed to greater intraspecific competition effects within monocultures of the more aggressive species at the density selected for this study. However, decreasing numbers of the more aggressive species does not lead to substantial increases in its per plant production. In contrast, interspecific competition by increasing numbers of the associated species replaces intraspecific competition, and affects the growth of the more aggressive species (e.g. Tables 3.5; 3.13; 3.21; 4.7). Thus even the weakest species (e.g. cocksfoot in mixtures with prairie grass) when dominant in plant numbers (e.g. 75%) has an effect on the more aggressive species. The increased growth of a species in its 75% combination is relatively small when mixtures are established from seed, as seen by the plant characteristics of the species in the field trial (Tables 3.4, 3.5).

The aggressivity indices also illustrate this effect (e.g. Tables 3.11; 3.18; 3.25 and 4.9), where a 25% change in a species proportion changes the relative aggressivity of the species in a mixture. Thus, the proportion of the selected species in a given mixture determines the expression of its relative competitive ability.

8.1.1.3 Characters associated with the competitive abilities of the selected species when grown in mixtures.

The field trial showed that prairie grass and ryegrass emerged before cocksfoot (Table 3.2), and the more extensive growth was also demonstrated in terms of dry matter accumulation of both shoots and roots (Table 3.5, Appendix 4). In addition, both species had larger seedlings at emergence, when compared with cocksfoot. Thus, the superior competitive ability of prairie grass and ryegrass over cocksfoot was attributed to their earlier emergence, larger initial seedling size and subsequent growth characteristics, based on the results of the field experiment.

Milthorpe (1961) and Trenbath *et al.* (1977) showed that more competitive species generally offset the disadvantage of later emergence by more rapid growth, thereby gaining competitive superiority over earlier emerging species. Thus, the superior competitive ability of the later emerging prairie grass over ryegrass can also be related to its larger initial seedling size and subsequent overall growth characteristics.

Attempts to evaluate the importance of the time of seedling emergence on the competitive abilities of the three species (Experiment 2), by using seedlings of the same age to construct the swards failed to change the competitive hierarchy between the three species (Figure 3.7). Thus it was concluded that larger initial seedling size and subsequent growth patterns of the three species have a greater impact on their competitive abilities than does the time of emergence. Nevertheless, earlier emergence can be considered a contributory factor to the attainment of competitive superiority by a grass species, as illustrated by other workers (e.g. Stapledon and Davies, 1928; Blaser *et al.*, 1956; Cocks, 1969 - see Chapter 2).

The competitive hierarchy of the three species lay in the order of prairie grass > ryegrass > cocksfoot, even when the swards were

made up of seedlings of similar growth stage (i.e. seedlings at the 2 leaf stage - Experiment 3). This was illustrated by the relative crowding coefficients (Figure 3.8) and aggressivity indices (Table 3.25). Thus, the growth patterns of the three species, resulting in a larger plant size of the most competitive species (prairie grass) can be considered the most important criterion determining the overall competitive abilities of these grasses, when grown in mixtures. The more extensively growing plant with its larger root and shoot system will obtain a greater share of the environmental resources, thereby limiting the availability of resources to the smaller species.

Although the overall competitive hierarchy between the species was similar to that observed in earlier experiments, the weaker species (e.g. cocksfoot grown with prairie grass) had a greater suppressive effect on the growth of the more aggressive species in this experiment (Experiment 3). This is illustrated by the lower relative crowding coefficients of the more aggressive species (ryegrass and prairie grass) when compared with those of the box experiment (Experiment 2) (Figures 3.7, 3.8). The lower aggressivity indices of prairie grass and ryegrass in Experiment 3, when associated with 75% cocksfoot (Table 3.25) also illustrate the increased competitive ability of cocksfoot in this experiment, especially when incorporated at higher proportions in mixtures.

Thus, a comparison of experiments 2 and 3 shows that a larger initial seedling size has a beneficial effect on the competitive ability of a species, especially if incorporated as a minor component of a grass mixture.

8.1.1.4 Environmental factors affecting competitive ability

Although changes in the environment have a deterministic effect on competition between pasture grasses (Chapter 2 - Section 5), this study evaluated only the effect of temperature on competitive relations, due to its importance in autumn and spring sowings. In addition, it was desired to evaluate the effects of the seasonal growth characteristics of these species (Chapter 1) on their competitive abilities. The selected temperatures however had no significant effect on the overall competitive ability of the species. Cocksfoot, which is identified as a summer producer (Langer, 1973), demonstrated superior growth under the warmer temperature regime (Table 3.21). This resulted in the reduced aggressivity of both ryegrass and prairie grass especially in the 75% cocksfoot mixtures in this temperature regime

(Table 3.35).

Temperature is generally associated with water availability to plants (McWilliam, 1978). Thus the regular application of water and nutrients in the growth room experiment (Section 3.4) may have masked any changes in the competitive ability due to temperature and water interactive effects. However, the field trial showed the superior growth of cocksfoot over summer in the second year. As cocksfoot is considered a good producer under warm dry conditions, during long periods of relatively warm temperatures and low rainfall as experienced in many parts of New Zealand, this species may become increasingly aggressive and thus dominant in mixtures such as those used in this study. Thus studies on the effect of temperature combined with water stress over long periods may highlight the existence of such changes in competitive ability.

8.1.1.5 Yields of mixtures and monocultures

The yields of mixtures in the first three experiments lay between those of their respective monocultures during the establishment phase (Tables 3.6; 3.15; 3.22). This agrees with most published reports (e.g. Donald, 1963; England, 1965; van den Bergh, 1969; Trenbath, 1974a; Norrington-Davies *et al.*, 1981). This is due to increased production of the more competitive species being offset by the reduced production of the weaker species, especially under uniform conditions such as those adopted in this series of experiments. Thus, as suggested by Harper (1977), the general conclusion is that there is no advantage to a farmer if his aim is to maximize production under uniform conditions. It is also stated that this conclusion is only valid if it is known in advance which pure stand will yield the most under the given conditions. However, if there is uncertainty or change in the environment and/or management as in practical farming situations, mixtures will tend to perform better than monocultures (Remison and Snaydon, 1980). This can be attributed to the complimentary growth characters of the species in mixtures being expressed under changing conditions.

Some research reports have shown the superior performance of mixtures over monocultures, especially at the later stages of growth (e.g. Whittington and O'Brien, 1968). However, the results of the

field trial did not show such effects in the second year (Table 3.7) under the conditions adopted; which provided regular fertilizers and was defoliated infrequently as in a 'hay' situation in normal farming conditions. As suggested in Chapter 3, the adoption of a frequent cutting regime which is more akin to grazing conditions may highlight changes from those observed in this study, due to differential response of species to regular defoliation.

8.1.2 COMPETITIVE RELATIONSHIPS BETWEEN THE SELECTED SPECIES IN THE SECOND YEAR AFTER SOWING.

Extension of the field experiment into the second year indicated that the species compete for similar resources during this period, under the adopted management conditions (i.e. infrequent cutting). This is illustrated by the relative yield totals (Table 3.10) and the products of the relative crowding coefficients (Figure 3.5). However, a major proportion of these indices were greater than one (although not significantly), and further evaluations of yields over another or several seasons may show variations from those observed in this study, as Whittington and O'Brien (1968) reported greater productivity of mixtures in the third year after planting, under an infrequent or 'hay' cutting regime. This may occur due to species occupying different rooting zones or developing different ecological niches and competition avoidance mechanisms.

The relative crowding coefficients of the three species varied with seasonal changes (Table 3.8), and the relative competitive ability of a species increased during seasons favourable to its growth. This can be expected as the outcome of competition is affected by the time of the year (Fowler, 1982), when conditions favour the growth of a species in a mixture. The expression of the seasonal growth characteristics especially of the weaker species however was prevented by the competitive relationships between the species. This is in agreement with studies of Wilson and Peake (1956).

Although seasonal variations were observed the competitive hierarchy between the species did not alter during the second year. These results thus demonstrate that competitive relationships established between these species during early growth persist at later stages, agreeing with reports on other grasses (e.g. Rhodes, 1967; Harris, 1973). In addition, the competitive relationship between

these species did not alter under conditions of uniform management, during the second year.

8.2 RESPONSE OF INDIVIDUAL PLANTS TO COMPETITIVE STRESS DURING ESTABLISHMENT AND EARLY GROWTH.

Donald (1963); Harper (1964) and Black (1966) highlighted the need for studies on individual plants growing in mixtures, as their growth patterns in isolation may be largely irrelevant to the understanding of their behaviour in competitive situations.

In experiment 4, (Chapter 4) detailed studies of the response of plants of the three species to competitive stress were carried out. Individual plant responses in terms of dry weights and tiller numbers were similar to those observed in the earlier experiments. A positive relationship between dry matter production and leaf and tiller appearance patterns was identified (Tables 4.6, 4.7), which is in agreement with earlier published results (e.g. Lazenby and Rogers, 1962; Crocker and Martin, 1964; Rhodes, 1968a). This was expected as both tiller and leaf production rates have been identified as major components of shoot dry matter production (e.g. Cooper, 1951; Langer, 1963; Anslow, 1966).

Tiller production and to a greater extent leaf appearance on the main stem of the three species showed a very plastic response to competitive stress during seedling growth (Table 4.6). These parameters showed the same directional response to competition as shoot dry matter production (Tables 4.6, 4.7).

Light has been identified as an important factor affecting leaf and tiller production in grasses (e.g. Mitchell, 1953a,b; Mitchell and Coles, 1955; Langer, 1963; Anslow, 1966). Thus the suppression of leaf and tiller appearance of these species can be associated with the light relationships within the swards. For example, the taller prairie grass plants can shade the shorter ryegrass or cocksfoot plants in mixtures, thus causing competitive effects for light and reducing the leaf and tiller production patterns. This is finally reflected as lower dry weights of the shaded species. The shading effect on the shorter species, which reduces its leaf and tiller appearance rates and thus its dry weight, increases with increasing density of the more aggressive species (Table 4.6; 4.7).

In addition to competition for light, the reduction in the rate of leaf appearance of the weaker species can bring about a decrease in the number of tillers, due to the reduction of sites for tiller development and the lack of expression of existing sites. Thus the decrease in tiller numbers of the weaker species due to competition can also be associated with this factor.

Although considered a major contributory factor, competition for light alone cannot be considered the only factor determining leaf and tiller appearance rates of species in mixtures, as competitive effects are a result of many interactive processes (Donald, 1963; Black, 1966). Thus the effects of competition between roots of these species on their leaf and tiller appearance cannot be precluded, as Rhodes (1968b) showed that competition for nutrients was the main cause of suppression of tillers of the weaker species growing in binary mixtures, especially, during early growth.

8.3 ROOT AND SHOOT COMPETITION BETWEEN THE SELECTED GRASS SPECIES

Both experiments 4 and 5 demonstrated the occurrence of competition between the root systems before similar effects were observed between the shoot systems of the selected species, which is in agreement with previous studies on grasses (e.g. Troughton, 1957; Donald, 1958; Rhodes, 1968b; Cocks, 1969). Root competition between the species was observed within 3-4 weeks of sowing and similar relationships (i.e. RYT = 1) between shoot systems were seen 5-6 weeks after planting (Tables 4.8; 5.4). In addition, the results highlighted the fact that root competition between the selected grass species had a greater effect than shoot competition in determining the overall competitive relationships in pastures (e.g. Donald, 1958; Rhodes, 1968b; Cocks, 1969; Snaydon, 1971; Remison and Snaydon, 1978, 1980).

It was not the aim of this study to determine all the factors leading to the responses observed in the experiments. However, it was postulated that competition between roots may have developed for nutrients, as competition for nutrients feature prominently in root competition studies (e.g. Snaydon, 1971; Martin and Snaydon, 1982). Growing seedlings have also been shown to absorb nutrients even before the depletion of endogenous food reserves (McWilliam *et al.*, 1970). In addition, all nutrients within a soil system are

not available to plant growth (Hall, 1974a). Luxury consumption by grasses during early growth has also been identified (Williams, 1955), which can have an effect on nutrient availability. Thus, although nutrients and water were added regularly, due to the low nutrient retentive potting medium used, the young seedlings with a greater actively growing root system may have taken up the available nutrients, thereby depriving the slower growing species of its nutrient requirements. The existence of this effect can be expected, as the species utilize the same 'biological space', and thus the slower growing species will always be occupying an environment already exploited by the larger and more extensively growing species.

In addition to competition for nutrients, the more extensively growing root system of the more aggressive species may have a restrictive effect on the normal root growth of the weaker species. This effect could be accentuated when plant mixtures are grown in containers, due to limited available rooting volume. Under field conditions, grasses occupy similar root zones (Garwood, 1966) and thus the possibility of such effects cannot be excluded, although not reported in the literature for grasses. Thus, these theories remain to be tested and detailed experiments to examine the mechanisms of root competition are warranted.

Shoot competition, which occurs at later stages, can be primarily attributed to competition for light (Donald, 1958). Its relatively smaller influence on the overall competitive relationships during establishment can be attributed to later onset of overlapping of shoot systems. However, shoot competition can be triggered by the earlier onset of root competition. At later stages, shoot competition may influence root growth and thus affect root competition (Donald, 1958).

During the first 2-3 weeks of planting, growth of species in mixtures were greater than in their respective monocultures (e.g. Table 4.5) at the adopted density, although these differences were not significant. A study under controlled conditions (Appendix 9) failed to show significant differences, although similar trends were identified. Possible causes for this phenomenon include autotoxic allelopathic effects, which have been identified in grasses (e.g. Rice, 1974, 1980; Newman and Rovira, 1975; Bokhari, 1978), and negative allelopathy (Tukey, 1969, 1970). These chemical effects

could give the more aggressive species an advantage in mixtures, in terms of better growth when compared to its monoculture, and thus have an important bearing on interspecific competition. Thus, further studies are needed to determine the influence of such effects on competition between grass species.

8.4 SPECIES CHARACTERISTICS AFFECTING COMPETITIVE ABILITY DURING ESTABLISHMENT AND EARLY GROWTH.

Many scientists state the need for caution in extrapolating plant performance in the absence of competition to their likely growth in mixtures (e.g. Salisbury, 1942; Harper and Clatworthy, 1963), due to variation in the performance of species under competitive stress. However as shown by O'Brien *et al.* (1967) on other grasses, plant characteristics of these species when grown in isolation were similar to those observed when grown in mixtures; thus these characteristics can be considered good indicators of their competitive ability. As discussed in Chapter 6, prairie grass had the largest seed, with the heaviest embryo and endosperm and greatest endosperm:embryo ratio. In addition, prairie grass had the largest shoot system (i.e. - at 8 weeks after seeding prairie grass shoots were 1.5 times heavier than ryegrass and 2.2 times heavier than cocksfoot), and the most extensive and heaviest root system (i.e. at 8 weeks, 2.1 times heavier than ryegrass and 3.6 times heavier than cocksfoot). This will enable it to successfully compete with the other species due to its ability to exploit the environment more effectively and extensively than smaller associated species, thereby depriving the latter of the necessary growth requirements.

Analysis of the rates of dry matter accumulation (i.e. relative growth rates) however did not highlight any significant differences between the three species when grown in isolation. Similar analysis based on shoot weights of the three species at corresponding time intervals in experiment 4 (Chapter 4) showed a similar relationship (Table 8.1).

TABLE 8.1 Dry matter accumulation rates based on shoot weights of ryegrass, prairie grass and cocksfoot at 2, 4, 6 and 8 weeks after planting (Adapted from Experiment 4).

Species	β	r^2
Ryegrass	.131	.92
Prairie grass	.131	.90
Cocksfoot	.158	.97

* Dry matter accumulation rate calculated on the basis of $\log_e y = a + \beta x$,

where y = dry weight of plants and x = time.

However dry matter accumulation rates calculated from the time of planting based on weekly harvests over the same period of time (i.e. from planting up to 56 days) (Table 4.7) shows that prairie grass had a greater dry matter accumulation rate than cocksfoot reflecting the differences between species in their speed of germination, seedling size and growth within the first two weeks. Calculation of absolute growth rates based on shoot and root dry weights in all experiments will also indicate the superior growth rate of prairie grass over the other species and of ryegrass over cocksfoot. Thus, although the three species have similar potential for dry matter accumulation, it is likely that the initial seed and seedling size of the grasses has a deterministic effect on their overall growth patterns in mixtures, which determines their respective competitive abilities. This advantage of size therefore can be considered to be a significant feature determining the competitive abilities during early growth of ryegrass, prairie grass and cocksfoot when grown in mixtures.

8.5 PRACTICAL IMPLICATIONS OF THE EXPERIMENTS TO PASTURE ESTABLISHMENT PRACTICES OF NEW ZEALAND FARMERS

The grasses selected for this study were recently released cultivars of grasses commonly used in the pastoral industry of New Zealand. In order to identify their role in the practical farming situation, a survey (Chapter 7) was carried out among dairy and sheep farmers in central New Zealand. Attempts were also made to identify the seed establishment practices of New Zealand farmers due to their relevance to this study.

The survey highlighted that most farmers (79%) have either established new pastures or renovated existing pastures in the

recent past; while 60% of the surveyed farmers intend doing so in the next two years. The survey also demonstrated that farmers incorporate many grass species into their seed mixtures. Among these, 'Nui' ryegrass was the most popular cultivar currently being used by farmers. Cocksfoot was used by most farmers as a minor component in mixtures and the future intention of many dairy farmers to use prairie grass in mixtures was highlighted. Thus as competition during early growth has a deterministic effect on subsequent performance of swards, these studies conducted on the competitive relationships between 'Nui' ryegrass, 'Matua' prairie grass and 'Apanui' cocksfoot can be considered as being relevant to the pastoral industry of New Zealand.

Farmers generally use 30-35 kg of seed per hectare, when sowing pastures. This seed rate is similar to that used in prairie grass monocultures in this experiment, but is in excess of seed rates for either the mixtures or the other monocultures (i.e. ryegrass and cocksfoot). Thus, as increased density tends to enhance competitive relationships (e.g. Holliday, 1960; Fowler, 1982), under farming situations competitive effects will have a major impact on the performance of species in newly sown pastures.

Farmers generally try to obtain optimum conditions for the sown pasture seeds to germinate and establish a good pasture with the desired species combinations. Thus attempts are made to ensure good soil conditions with adequate moisture and fertility. The experiment conducted under such conditions (e.g. Experiment 1) highlighted competitive relationships between sown species. Thus, the inherent competitive abilities of the species have a deterministic effect on the establishment and early growth of newly sown pastures, which affects the performance of species in mixtures.

The results of these experiments show that the competitive hierarchy between the species was in the order of prairie grass > ryegrass > cocksfoot, under the adopted conditions. This effect is most pronounced when seeds are sown together, as would be carried out by farmers. Thus competition during the early growth phase will affect plant performance when aggressive and weak species are sown together. The rapidly growing and more aggressive species while providing early feed will affect the growth of slow growing species such as cocksfoot, and thereby mask the expression of their potentially

valuable agronomic features in subsequent years (Jones and Charles, 1961; Arens, 1962). This suppressive effect on the slower growing species increases with increasing density of the more aggressive species. Thus, a farmer desiring cocksfoot in his pastures will not be able to obtain the full potential of the species by incorporating more aggressive species, especially at higher proportions in his seed mixtures, unless suitable management techniques can be adopted to reduce the competitive effects.

Many grassland researchers have suggested methods of overcoming initial dominance of a more competitive and aggressive species during establishment. Frame and Hunt's (1964) research suggests the incorporation of a higher proportion of the weaker species and/or a lower proportion of the more aggressive species in the mixture. A reduction in the total population may also be envisaged, which will delay the onset of competition, thereby giving the weaker and slower growing species a chance to establish before competitive interactions begin. However, these methods generally result in a lower yielding pasture in the establishment phase, which is also open to greater ingress by weeds, and therefore may not meet the requirements of the farmer.

Variations in the establishment procedure might also be considered and adopted to reduce these competitive effects. For example, the weaker species could be sown earlier, giving it an opportunity to establish, before the more aggressive species is overdrilled to meet the required species balance of the pasture sward. However, the practical and economic feasibility of establishing species twice need to be considered in such operations.

Pasture renovations by overdrilling can also be classified as a method of overcoming the suppression of the weaker species at establishment. In order to facilitate the growth of the later introduced species, the established weaker species could be grazed to reduce hinderances to the establishing species. However, adoption of such techniques need to be considered with caution, as the situation present in overdrilling is that of competition between an established pasture and establishing seedlings, which was not evaluated in this study. For example, regular defoliation of the established species in order to reduce its dominance may also hinder the growth of the seedlings of the later introduced species, especially if it is susceptible to continuous grazing, a characteristic identified with prairie

grass.

Grass species are generally sown together in pasture establishment. Thus management of the establishing sward has a great impact on the competitive effects that develop between pasture species (Jones, 1933; Donald, 1963), and the effects of defoliation and fertilization are well documented (e.g. Reith *et al.*, 1964; Rhodes, 1967; Harris, 1978). In such situations, the initial dominance of a species can again be reduced by light regular defoliations, thereby preventing shading and thus encouraging the growth of the weaker species.

The management of the experiments of this study was similar to infrequent defoliation, as in most instances, plants were defoliated at 95% light interception. Under such conditions, the weaker species (e.g. cocksfoot) is suppressed by the more aggressive species (e.g. prairie grass). However, if frequent defoliation was carried out to ensure the success of cocksfoot, a different outcome may have been observed during the establishment phase, as prairie grass is greatly affected by frequent defoliation (Langer, 1973; Pineiro and Harris, 1978a, b; Lancashire, 1982).

The survey also demonstrated that farmers generally sow pastures in autumn, and this could be related to climatic conditions and other farm practices such as cropping and pasture renewal sequences, feed demands of the herd or flock or weed ingress (Brougham, 1969). Although the importance of these factors was not identified in these experiments, attempts to study the effects of simulated spring and autumn temperatures did not show any differences in the relative competitive abilities of the species. The spring sown field trial also showed similar relationships between the selected species, due to rainfall ensuring adequate soil moisture (Appendix 2A, B) during establishment. Thus under normal climatic conditions, differences may arise in the establishment, performance and competitive relationships of these species in mixtures, due to temperature and moisture interactions.

The results show that under the experimental conditions used, there is no advantage in sowing grass mixtures to obtain the highest yield. Thus under farming situations, if the environmental and management conditions can be predicted in advance or the variability minimized, the farmer will obtain the highest yield by sowing the species that yields the most in that situation. However, under practical farming

conditions, there is great variability in soil, climate and management factors which play an important role in determining the success of a sown pasture. Thus, in order to allow sufficient flexibility for the variability of these factors and obtain feed for livestock under changing conditions, farmers sow mixtures of grasses, a feature identified in the survey. This suggests the need to evaluate the performance of pasture mixtures and monocultures under practical farming conditions, in order to identify constraints and benefits of using grass mixtures, and to investigate the possible use of monocultures for special purpose pastures.

When devising the composition of pasture seed mixtures, the purpose for which the pasture is to be used must be the deciding factor. Management factors and the environment must be defined first, and then the most suitable species selected. Data such as those presented in this study can be an important tool in this selection process, as competition between the species will have an important bearing on the performance of mixtures. For instance, prairie grass which has been identified as a fast growing and aggressive species, capable of providing early feed will suppress the other desirable but slower growing species such as cocksfoot. Thus in order to avoid the dominance of more aggressive species management and/or seeding rates needs to be adjusted to maintain the required balance between the species, thereby resulting in the desired composition of the sown pasture consisting of the more aggressive and weak species.

8.6 CONCLUSIONS

This series of experiments was carried out to evaluate the competitive relationships between "Grasslands Nui" perennial ryegrass "Grasslands Matua" prairie grass and "Grasslands Apanui" cocksfoot, during the early growth stages. The results highlight the following conclusions.

- The selected grass species compete for the same environmental resources (i.e. "biological space") during the early growth stages.
- The competitive hierarchy between the three species is in the order of prairie grass > ryegrass > cocksfoot.

- The proportion of the selected species in a given mixture determines the expression of their competitive abilities.
- The growth pattern of a given species determines its competitive ability in a mixture, although the species demonstrated similar dry matter accumulation rates when evaluated over a given period of time. Initial seedling size which gives rise to a larger plant, (and to a lesser extent early emergence) assists the competitive ability of the more aggressive species.
- The selected temperature regimes, the only environmental factor studied due to its relationship to planting times, did not have a significant effect on the overall competitive relationships between the selected grass species.
- Yields of mixtures lay between those of the respective monocultures during the early growth stages.
- Competitive hierarchies established during the early growth stages persist at later stages under similar management conditions. The yields of mixtures lay between those of the monocultures during later stages, under uniform management. Although seasonal growth characteristics of the species were observed, competitive relationships did not change under the adopted experimental conditions.
- Tiller production per plant and to a greater extent leaf appearance on the main stem showed a plastic response to competitive stress.
- Root competition occurs before shoot competition and has a greater impact on the overall competitive relationships between the species during early growth.
- The relationship between the seed characters of the three species is similar to their competitive relationships. Thus seed characters are likely to have a deterministic effect on the competitive relationships between the selected grasses.

- Growth patterns of these species in isolation are similar to their growth in monocultures, and thus are good indicators of their competitive abilities.

In terms of the practical value of this study, the survey identified among many features, the use of grass mixtures for pasture establishment by New Zealand farmers. The use of the species selected for this study was also highlighted. Thus as competition during early growth has a deterministic effect on the growth of species in mixtures, this study highlights some aspects of the competitive relationships between three grasses commonly used in New Zealand agriculture.

APPENDIX 1

The mathematical model to calculate the Relative Crowding Coefficients

(de Wit, 1960)

(Adapted from Harris and Thomas 1970, Harris et al., 1981b).

The model used is derived as follows -

2 species or varieties S_1 and S_2 are grown in seed or seedling populations Z_1 and Z_2 where $Z_1 + Z_2 = 1$.

These species are assumed to compete for hypothetical "space" which consists of the sum of various limited environmental factors, including actual ground area. It is assumed that one seed of species S_1 uses b_{11} units and one seed of species S_2 uses b_{12} units the space needed by species S_1 . Similarly a seed of species S_1 uses b_{21} and one of species S_2 uses b_{22} units of the space needed by species S_2 .

Thus, for given proportions Z_1 and Z_2 and total number of seeds N , the total "space" used by the two species is indicated as

$$N(b_{11}Z_1 + b_{12}Z_2)$$

$$N(b_{21}Z_1 + b_{22}Z_2)$$

The model hypothesizes that the yield of each species is proportional to the proportion of 'space' used by that species. These proportions are

$$b_{11}Z_1 / (b_{11}Z_1 + b_{12}Z_2)$$

$$b_{22}Z_2 / (b_{21}Z_1 + b_{22}Z_2)$$

These proportions do not depend on the actual values of b_{11} , b_{12} , b_{21} and b_{22} , but only on the ratios

$$k_{12} = b_{11}/b_{12}$$

$$k_{21} = b_{22}/b_{21}$$

Thus it can be written

$$O_1 = M_1 K_{12} Z_1 / (K_{12} Z_1 + Z_2)$$

$$O_2 = M_2 K_{21} Z_2 / (K_{21} Z_2 + Z_1)$$

Where O_1 and O_2 are the yields and M_1 and M_2 are the constants of proportionality. However, putting $Z_2 = 0$ in the first equation and $Z_1 = 0$ in the second equation, shows that M_1 and M_2 are the monoculture yields of species S_1 and S_2 . The parameter K_{12} is called the Relative Crowding Coefficient of Species S_1 with respect to Species S_2 .

If the hypothetical space is the same for the two species,

$$b_{11} = b_{21}$$

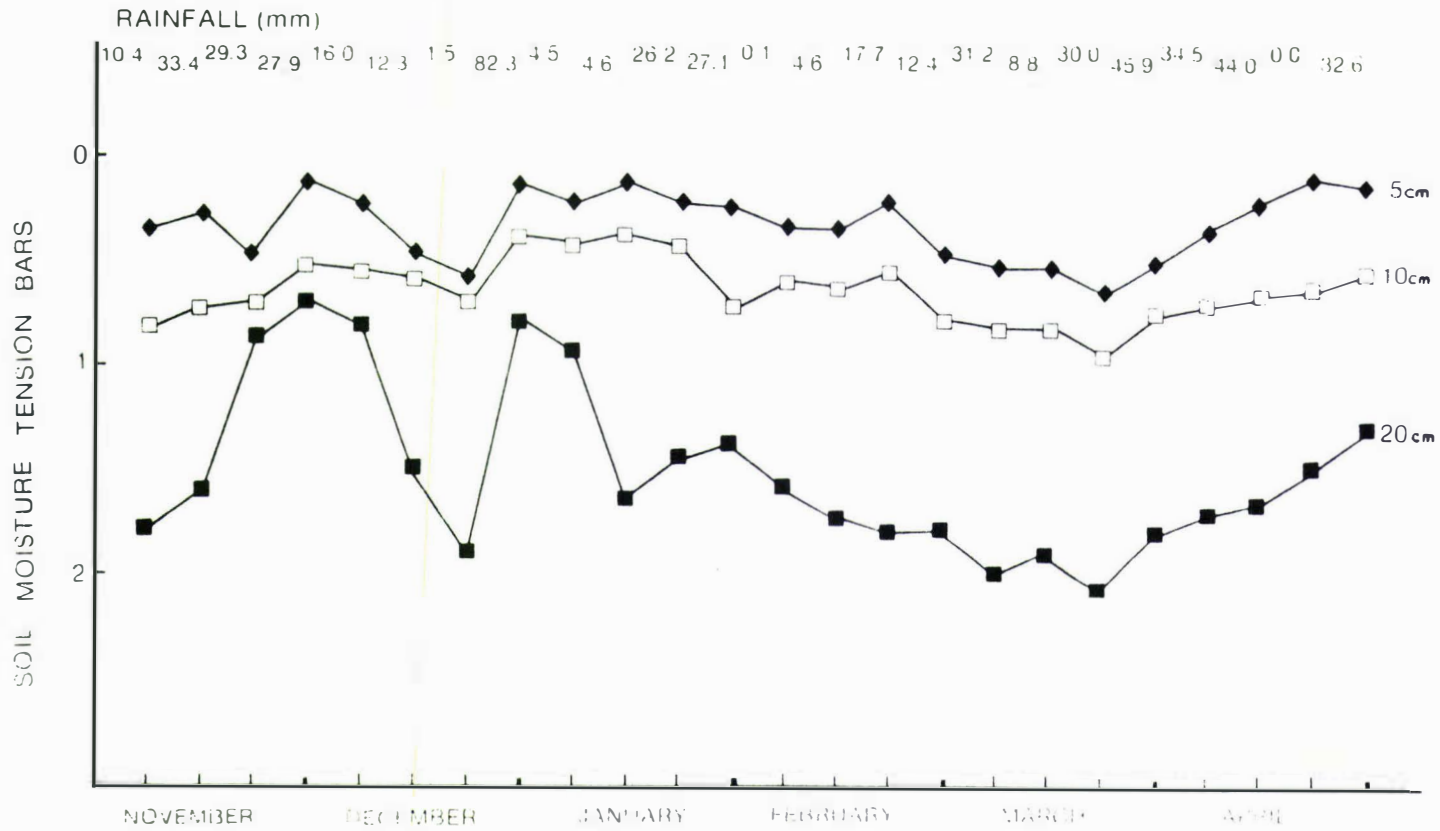
$$b_{12} = b_{22}$$

$$\text{and } k_{12} = 1/k_{21}$$

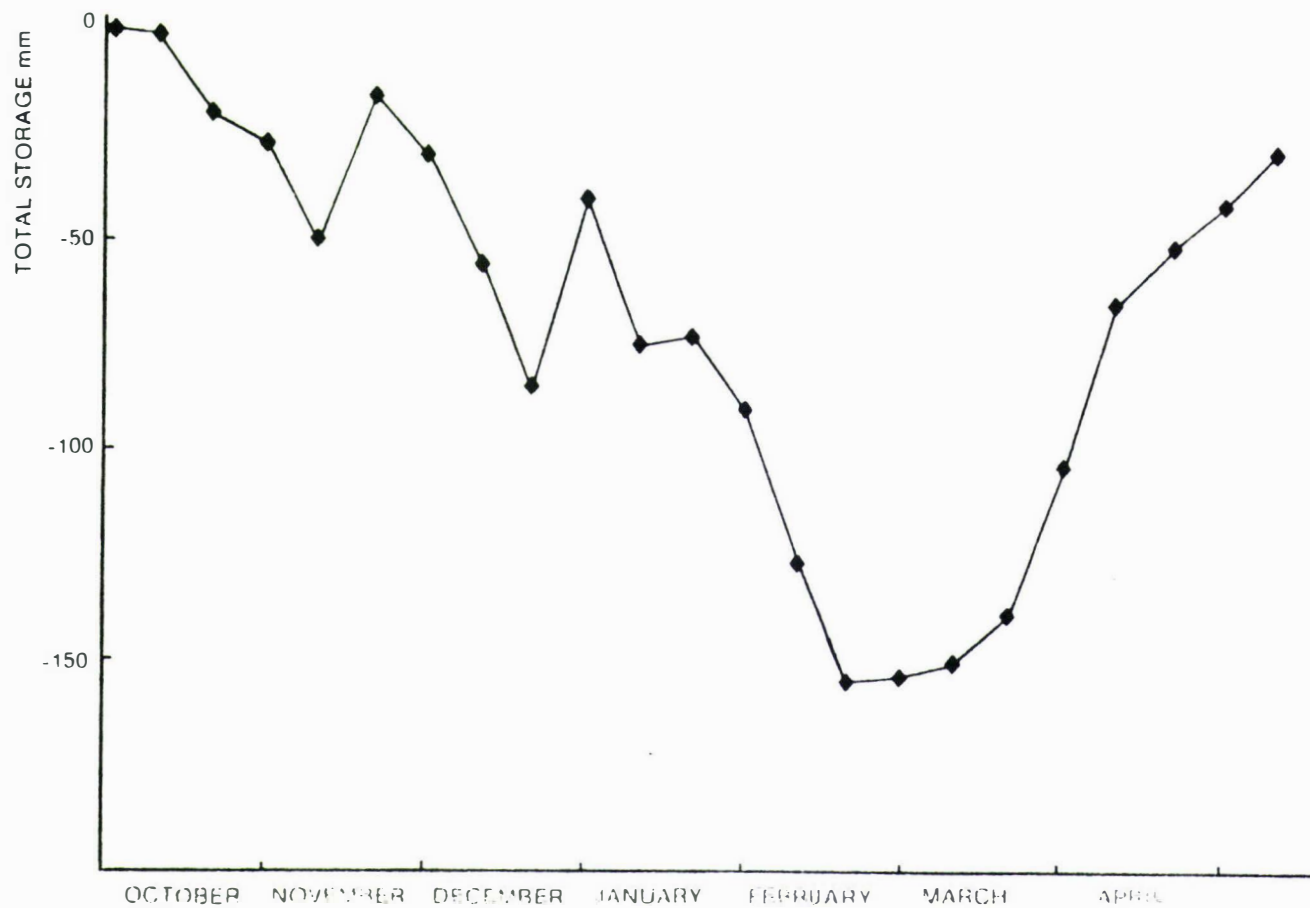
Thomas (1970) developed a procedure for estimating parameters M_1 , M_2 , k_{12} , and k_{21} , together with a test of whether $k_{12} = 1/k_{21}$ or equivalently, whether $k_{12} k_{21}$ differs significantly from 1.

In the computer model of Thomas (1970) two models are fitted, the four parameter model (4P) with separate values of k_{12} and k_{21} ; and the three parameter model (3P) which has the constraint that $k_{12} k_{21}$ equals 1. If the former provides a significant fit, it is considered that the species crowd for different 'spaces'. The biological significance of $k_{12} k_{21} = 1$ or greater or less than 1 is described by de Wit (1960), Bakhuis and Kleter (1965); van den Bergh (1968). To apply this, it is necessary to test whether the residual variances of the cultivars differ significantly. If they do differ, it is not valid to apply the test for competition for the same space, which distinguishes between competition for the same space or different spaces. Thus a significant result in the "between cultivar variance" (4 parameter model) indicates that the "between models" test (3 parameter) can not be applied.

APPENDIX 2A: Soil moisture tension (Bars) within the top 20cm layer of soil, and the weekly rainfall figures (monitored at the D.S.I.R. Palmerston North) over the experimental period.



Appendix 2B: Computed soil water storage of the experimental site over the experimental period using the method of Scotter et al (1979 a, b)



APPENDIX 3. Mean plant height (cm) of species grown in mixtures and in monocultures during early growth

Species mixture	Week 5	Week 6	Week 7	Week 8 (H ₁)	Week 13 (H ₂)	Week 17 (H ₃)
(1) RYEGRASS						
Monoculture	11.8	13.8	15.0	16.6	16.4	16.4
75R with 25P	12.0	13.9	15.1	16.7	16.6	16.6
50R with 50P	11.7	13.9	14.9	16.4	16.2	16.2
25R with 75P	11.8	13.8	15.0	16.5	15.8	16.1
75R with 25C	11.9	13.8	15.0	16.8	17.1	16.7
50R with 50C	11.9	13.8	15.0	16.5	16.5	16.5
25R with 75C	11.8	13.8	15.0	16.5	16.3	16.3
Significance	NS	NS	NS	NS	**	**
S _x	0.11	0.09	0.15	0.12	0.09	0.09
(2) PRAIRIE GRASS						
Monoculture	12.8	15.2	16.6	18.1	20.1	19.0
75P with 25R	12.9	15.1	16.6	18.3	20.8	19.1
50P with 50R	12.7	15.2	16.5	18.0	20.5	19.1
25P with 75R	12.7	15.1	16.5	18.0	19.9	18.6
75P with 25C	12.9	15.3	16.7	18.2	21.2	19.5
50P with 50C	12.9	15.1	16.7	18.1	20.4	19.2
25P with 75C	12.8	15.1	16.8	17.9	20.2	19.1
Significance	NS	NS	NS	NS	**	**
S _x	0.08	0.13	0.15	0.15	0.11	0.10
(3) COCKSFOOT						
Monoculture	7.1	10.5	12.5	15.1	15.1	14.8
75C with 25R	7.2	10.4	12.4	15.3	15.1	14.9
50C with 50R	7.2	10.4	12.4	15.0	14.7	14.7
25C with 75R	7.2	10.4	12.5	15.1	14.4	14.5
75C with 25P	7.1	10.4	12.5	15.2	15.0	14.8
50C with 50P	7.1	10.4	12.4	15.1	14.5	14.5
25C with 75P	7.1	10.4	12.4	15.0	14.2	14.3
Significance	NS	NS	NS	NS	**	**
S _x	0.11	0.15	0.14	0.15	0.09	0.10

APPENDIX 4 Mean depth of roots (cm) per plant grown in mixtures and in monocultures during early growth

Species mixtures	Week 5	Week 6	Week 7	Week 8
(1) RYEGRASS				
Monoculture	8.9	10.1	12.5	13.8
75R with 25P	9.1	10.2	12.8	14.1
50R with 50P	8.7	9.8	12.3	13.7
25R with 75P	8.6	9.6	12.1	13.4
75R with 25C	9.3	10.5	12.7	14.1
50R with 50C	9.0	10.2	12.7	14.0
25R with 75C	8.8	9.9	12.4	13.7
Significance	**	**	**	**
\bar{Sx}	0.06	0.05	0.10	0.10
(2) PRAIRIE GRASS				
Monoculture	11.3	13.3	14.4	15.2
75P with 25R	11.5	13.7	14.6	15.5
50P with 50R	11.5	13.3	14.4	15.3
25P with 75R	11.0	13.0	14.1	15.0
75P with 25C	11.7	13.7	14.9	15.6
50P with 50C	11.5	13.4	14.7	15.5
25P with 75C	11.2	13.2	14.4	15.3
Significance	**	**	**	**
\bar{Sx}	0.10	0.12	0.11	0.06
(3) COCKSFOOT				
Monoculture	6.8	8.2	10.2	12.8
75C with 25R	6.9	8.4	10.3	13.0
50C with 50R	6.7	8.1	10.1	12.7
25C with 75R	6.4	8.0	9.9	12.5
75C with 25P	6.7	8.2	10.1	12.8
50C with 50P	6.5	8.0	9.8	12.5
25C with 75P	6.4	7.8	9.5	12.4
Significance	**	**	**	**
\bar{Sx}	0.07	0.14	0.12	0.08

APPENDIX 5. Mean weight (g) of roots of species grown in mixtures and in monocultures during early growth

Species mixture	Week 5	Week 6	Week 7	Week 8
(1) RYEGRASS				
Monoculture	0.096	0.171	0.356	0.578
75R with 25P	0.096	0.172	0.359	0.583
50R with 50P	0.092	0.165	0.349	0.575
25R with 75P	0.087	0.161	0.343	0.570
75R with 25C	0.100	0.182	0.362	0.589
50R with 50C	0.100	0.176	0.357	0.584
25R with 75C	0.092	0.170	0.354	0.578
Significance	**	**	**	*
\bar{Sx}	0.001	0.003	0.003	0.002
(2) PRAIRIE GRASS				
Monoculture	0.102	0.267	0.451	0.667
75P with 25R	0.109	0.275	0.458	0.687
50P with 50R	0.103	0.272	0.457	0.676
25P with 75R	0.100	0.266	0.450	0.664
75P with 25C	0.109	0.277	0.459	0.682
50P with 50C	0.108	0.270	0.458	0.673
25P with 75C	0.101	0.268	0.450	0.665
Significance	**	**	**	*
\bar{Sx}	0.002	0.009	0.002	0.002
(3) COCKSFOOT				
Monoculture	0.052	0.088	0.176	0.299
75C with 25R	0.054	0.088	0.178	0.301
50C with 50R	0.049	0.083	0.170	0.293
25C with 75R	0.048	0.081	0.165	0.288
75C with 25P	0.053	0.088	0.176	0.299
50C with 50P	0.049	0.081	0.170	0.290
25C with 75P	0.047	0.078	0.165	0.285
Significance	**	**	**	*
\bar{Sx}	0.002	0.002	0.003	0.002

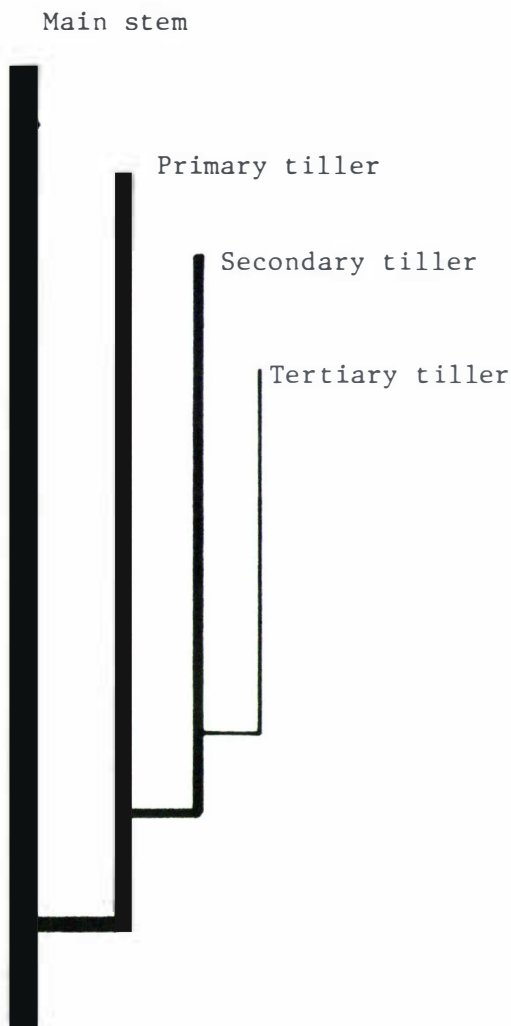
APPENDIX 6 Mean plant height (cm) of the grass species during early growth and prior to every harvest, when grown in mixtures and in monocultures.

Species Mixture	Mean plant height (cm)						
	Time of measurement (wks) after transplanting						
	4	5	6	7(H ₁)	12(H ₂)	16(H ₃)	20(H ₄)
<u>(A) RYEGRASS</u>							
Monoculture	14.8	19.7	24.2	27.8	18.8	17.1	15.7
75R with 25P	15.8	20.2	24.7	28.1	19.5	17.6	16.0
50R with 50P	14.5	19.5	24.1	27.7	18.9	16.9	15.7
25R with 75P	13.8	19.2	23.8	27.4	18.2	16.5	15.3
75R with 25C	15.6	20.4	25.1	27.9	19.2	17.3	15.9
50R with 50C	15.2	20.1	24.7	27.7	18.9	16.3	15.9
25R with 75C	14.7	19.6	24.2	27.1	18.4	16.1	15.1
Significance	**	**	**	NS	**	**	*
\bar{S}_x	0.12	0.10	0.07	0.12	0.06	0.08	0.09
<u>(B) PRAIRIE GRASS</u>							
Monoculture	19.8	24.5	29.1	32.5	25.2	22.5	20.3
75P with 25R	20.6	24.8	29.5	32.9	25.9	23.0	21.0
50P with 50R	20.0	24.5	29.3	32.6	25.4	22.8	20.8
25P with 75R	19.7	24.2	28.9	32.4	24.7	21.9	19.7
75P with 25C	20.0	25.4	29.7	33.3	25.8	22.9	20.7
50P with 50C	20.1	25.0	29.6	32.8	25.6	22.6	20.6
25P with 75C	20.0	25.2	29.6	32.8	24.5	22.1	19.8
Significance	*	**	NS	*	**	**	**
\bar{S}_x	0.08	0.10	0.14	0.09	0.05	0.08	0.05
<u>(C) COCKSFOOT</u>							
Monoculture	12.6	15.7	19.2	23.9	17.0	14.7	14.9
75C with 25R	12.8	15.9	19.6	24.0	17.3	14.8	15.1
50C with 50R	12.4	15.0	19.0	23.9	17.1	14.5	14.6
25C with 75R	12.0	14.3	18.2	23.5	16.8	14.5	14.4
75C with 25P	12.7	15.9	19.5	24.1	17.1	14.8	15.0
50C with 50P	11.9	15.5	18.6	23.6	17.1	14.6	14.7
25C with 75P	11.5	15.1	18.0	23.1	16.8	14.5	14.8
Significance	**	**	**	**	NS	*	**
\bar{S}_x	0.09	0.12	0.15	0.08	0.02	0.05	0.04

APPENDIX 7 Mean plant height (cm) of the grass species at high and low temperatures, measured at an average light interception of 50% and 95% across all treatments

Species Mixture (A) Ryegrass	50% LI		95% LI(H ₁)		50% LI		95% LI(H ₂)		50% LI		95% LI(H ₃)	
	High T ⁰	Low T ⁰	High T ⁰	Low T ⁰	High T ⁰	Low T ⁰	High T ⁰	Low T ⁰	High T ⁰	Low T ⁰	High T ⁰	Low T ⁰
Monoculture	20.1	15.4	25.9	22.8	17.4	16.5	24.5	21.2	17.6	15.4	22.1	20.1
75R with 25P	20.5	15.6	26.6	23.3	18.0	16.8	24.8	21.4	17.8	15.6	22.8	20.3
50R with 50P	19.7	15.2	25.5	22.3	17.0	16.2	24.2	20.8	17.1	15.2	21.7	19.9
25R with 75P	17.3	15.1	25.5	22.2	16.6	16.2	24.2	20.7	17.0	15.1	21.3	19.8
75R with 25C	20.5	15.7	26.5	22.9	17.9	16.9	24.9	21.6	17.8	15.7	23.1	20.5
50R with 50C	20.2	15.5	26.2	23.0	17.7	16.6	24.6	21.4	17.5	15.6	22.7	20.3
25R with 75C	19.6	15.2	25.4	22.4	17.1	16.1	24.0	20.6	17.1	15.1	21.5	19.9
Significance	**	**	**	**	**	**	**	**	**	**	**	**
S _x	0.39	0.07	0.14	0.28	0.14	0.08	0.09	0.16	0.09	0.08	0.15	0.11
(B) Prairie grass												
Monoculture	32.8	23.7	38.3	32.6	29.1	25.5	38.3	30.9	24.5	23.4	35.6	28.3
75P with 25R	33.3	23.8	39.1	33.3	29.7	25.9	38.8	31.3	24.8	23.5	36.0	28.8
50P with 50R	33.2	23.7	38.8	32.9	29.6	25.7	38.5	31.0	24.6	23.4	35.8	28.5
25P with 75R	32.3	23.3	37.7	32.3	28.3	25.2	37.6	30.6	24.0	23.1	34.8	27.9
75P with 25C	33.0	24.0	38.5	32.9	29.9	25.8	38.8	31.2	24.9	23.8	36.0	28.0
50P with 50C	32.8	23.8	38.1	32.8	29.5	25.6	38.6	31.1	24.7	23.6	35.8	28.5
25P with 75C	31.5	23.5	37.9	32.2	28.9	25.2	37.6	30.5	24.0	23.2	35.0	27.9
Significance	**	**	**	**	**	**	**	**	**	**	**	**
S _x	0.27	0.10	0.14	0.20	0.12	0.14	0.09	0.15	0.06	0.10	0.08	0.20
(C) Cocksfoot												
Monoculture	18.5	14.3	22.1	19.8	14.9	13.8	20.1	18.9	13.2	14.3	17.8	18.2
75C with 25R	19.1	14.6	22.5	20.3	15.2	14.1	20.9	19.3	13.5	13.9	18.4	18.5
50C with 50R	18.3	14.0	21.6	19.5	14.6	13.7	19.8	18.7	13.0	13.3	17.4	18.0
25C with 75R	18.1	13.6	21.5	19.1	14.6	13.6	19.8	18.7	12.9	13.1	17.3	17.8
75C with 25P	18.7	14.5	22.3	20.1	15.1	13.9	20.5	19.3	13.7	13.8	18.2	18.2
50C with 50P	18.1	14.1	21.5	19.6	14.5	13.5	20.0	18.7	13.0	13.4	17.4	17.9
25C with 75C	17.9	13.9	22.1	19.4	14.5	13.4	19.6	18.7	12.8	13.1	17.4	17.9
Significance	*	**	*	**	**	**	**	**	**	NS	**	*
S _x	0.34	0.13	0.23	0.13	0.06	0.09	0.11	0.19	0.09	0.50	0.12	0.21

Appendix 8: Classification of Tillers (Langer: 1972).



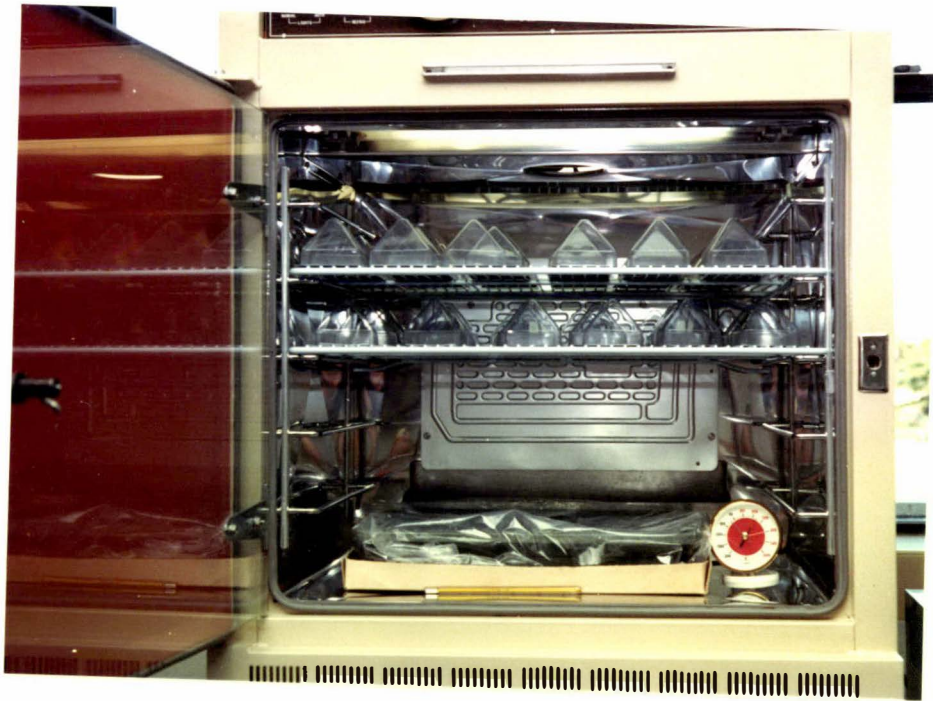


PLATE 8. Layout within the germination cabinet.

APPENDIX 9 SHOOT EMERGENCE AND ROOT DEVELOPMENT OF RYEGRASS,
PRAIRIE GRASS AND COCKSFOOT WHEN GERMINATED IN BINARY
COMBINATIONS.

A9.1 INTRODUCTION

Some of the depressive effects of a plant upon neighbouring plants cannot be well explained on a basis of monopolization of resources by one species (Harper, 1977). Thus, an alternative is that certain species release toxic materials that affect the growth of neighbouring plants. These biochemical interactions have been termed allelopathy by Molisch (1937 - cit Rice, 1980), and have been reported in pasture grasses (Rice, 1974; 1980).

An increase in the growth of prairie grass, ryegrass and cocksfoot seedlings when compared with their respective monocultures was observed during very early growth stages (Section 4.2). This caused the relative yield total values to be significantly greater than unity during this early period (Table 4.8). While these growth effects were not significant between treatments within any species, the presence of autotoxic effects during germination and early growth cannot be precluded (Harris, pers. comm), as autotoxic effects have been observed in other grasses (e.g. Newman and Rovira, 1975). Thus, a small experiment was conducted under controlled conditions in an attempt to quantify these effects during germination and early growth.

A9.2 EXPERIMENTAL PROCEDURE

A.9.2.1 Cultural

The experiment was conducted at the Seed Technology Centre, Massey University, during September, 1981. Seeds of "Grasslands Nui" perennial ryegrass, "Grasslands Matua" prairie grass and "Grasslands Apanui" cocksfoot were graded for uniform weight and placed on sterile germinating paper according to the replacement series adopted in earlier experiments (e.g. Section 3.2). A single seed was placed at each of 16 locations on a 4 x 4 cm equally spaced matrix, on germination paper of dimensions 15 x 15 cm. A closer spacing to that of the pot trial (experiment 4) was used to increase the magnitude of any effects or interactions.

The germination papers with the seeds in place were covered with disinfected plastic caps and placed in a sterile germinating chamber, (Plate 8) and dampened with distilled water to initiate the process of

germination. The temperature of the germinating chamber was set at 30°C day/20°C night \pm 0.5°C as this temperature was considered to be ideal for the germination of these species (ISTA Handbook 1979). A 12 hour photoperiod was imposed within the chamber. Care was taken to avoid any possible contamination which may have affected the results.

A9.2.2 Experimental Design

A randomized block design with 6 replications was used for the study.

A9.2.3 Measurements

The development of the first seminal root of each seed was measured with vernier calipers 4 days after placing the seed mixtures in the germinating chamber, and thereafter at regular 2 day intervals for a period of 16 days. The number of days taken for the emergence of the first leaf from the coleoptile in 75% of the seedlings of each species in the different treatments was also recorded.

A9.2.4 Statistical analysis

Differences between treatments within each species were analysed using techniques described earlier (Section 3.2.2).

A 9.3 RESULTS

The time taken for the first green leaf to emerge in 75% of the seeds in each species is presented in Table A9.1. There was no significant difference between any treatments, nor was there any definite trends which suggested autotoxic effects, affecting shoot emergence.

In contrast to leaf appearance, the root length measurements (Table A9.2) indicated an increase in the seedlings growing in mixtures when compared with those in the monocultures. This effect decreased at later stages. The results were similar to those observed in the earlier experiment (Section 4.2.3). However, these differences in root lengths were again not significant, but a distinct trend was observed during the very early stages of growth, in all species.

Ryegrass developed the first seminal root earlier than other species. However, at the completion of the experiment, prairie grass had the most developed coleorhiza and the greatest mass of roots.

TABLE A9.1 Shoot emergence*of ryegrass, prairie grass and cocksfoot when germinated in binary combinations

Species	Treatment	No of days
(A) Ryegrass	Monoculture	7.0
	75R with 25P	6.9
	50R with 50P	7.0
	25R with 75P	7.0
	75R with 25C	6.9
	50R with 50C	6.9
	25R with 75C	6.9
	Significance	NS
	\bar{Sx}	0.05
(B) Prairie grass	Monoculture	9.6
	75P with 25R	9.6
	50P with 50R	9.6
	25P with 75R	9.7
	75P with 25C	9.7
	50P with 50C	9.7
	25P with 75C	9.7
	Significance	NS
	\bar{Sx}	0.06
(C) Cocksfoot	Monoculture	15.1
	75C with 25R	15.0
	50C with 50R	14.9
	25C with 75R	14.9
	75C with 25P	14.9
	50C with 50P	15.0
	25C with 75P	15.0
	Significance	NS
	\bar{Sx}	0.09

* Shoot emergence was noted when 75% of seeds were seen to develop the first greenleaf from the coleoptile.

TABLE A9.2 Root length (cm) of species growing in mixtures and monocultures

Species	Treatment	Days after soaking						
		4	6	8	10	12	14	16
(A) <u>Ryegrass</u>	Monoculture	0.31	0.81	1.60	2.30	2.91	3.50	4.80
	75R with 25P	0.35	0.83	1.63	2.36	2.95	3.53	4.80
	50R with 50P	0.35	0.85	1.66	2.31	2.98	3.51	4.78
	25R with 75P	0.38	0.83	1.61	2.36	2.93	3.48	4.76
	75R with 25C	0.35	0.83	1.63	2.25	2.96	3.63	4.88
	50R with 50C	0.38	0.85	1.65	2.31	2.98	3.60	4.80
	25R with 75C	0.36	0.90	1.66	2.30	2.92	3.58	4.85
	Significance	NS	NS	NS	NS	NS	NS	NS
	Sx	0.025	0.026	0.028	0.051	0.049	0.053	0.026
(B) <u>Prairie grass</u>	Monoculture		0.45	1.28	2.21	3.53	4.45	5.83
	75P with 25R		0.48	1.50	2.26	3.55	4.45	5.93
	50P with 50R		0.48	1.33	2.31	3.46	4.55	5.88
	25P with 75R		0.50	1.32	2.23	3.56	4.50	5.93
	75P with 25C		0.46	1.33	2.25	3.50	4.48	5.98
	50P with 50C		0.50	1.35	2.23	3.60	4.48	5.93
	25P with 75C		0.46	1.31	2.36	3.55	4.41	5.88
	Significance		NS	NS	NS	NS	NS	NS
	Sx		0.029	0.064	0.056	0.063	0.061	0.041
(C) <u>Cocksfoot</u>	Monoculture			0.23	0.86	1.30	2.20	3.03
	75C with 25R			0.25	0.86	1.40	2.23	3.00
	50C with 50R			0.28	0.93	1.35	2.20	3.11
	25C with 75R			0.26	1.03	1.31	2.25	3.01
	75C with 25P			0.26	0.93	1.35	2.28	3.05
	50C with 50P			0.26	0.96	1.35	2.23	3.01
	25C with 75P			0.30	0.93	1.31	2.23	2.98
	Significance			NS	NS	NS	NS	NS
	Sx			0.028	0.049	0.043	0.034	0.055

A9.4 DISCUSSION AND CONCLUSIONS

Autotoxic allelopathic effects in grasses have been postulated by many researchers. Grant and Sallans (1964) identified these effects in many grasses including brome grass and cocksfoot, and Newman and Rovira (1975) identified similar effects in *Lolium perenne* (L). Other reports on such effects in grasses include those of Harries and Norrington-Davies (1977) on diploid and tetraploid ryegrasses and on *Bouteloa gracilis* and *Agropyron smithii* by Bokhari (1978).

Autotoxic effects are caused by the release of toxins which affect the growth of the species releasing it. Hence, in mixtures, the toxin producer would experience a lower overall contact, thus exhibiting a greater degree of growth than in the monoculture. As results of this study exhibit such a relationship, autotoxic effects may have existed within the three species during very early stages of growth. However, this effect is seen only in terms of root growth and not in leaf emergence or overall germination of the species.

In contrast to autotoxic effects, negative allelopathy could also occur, by the release of growth stimulating hormones (Tukey, 1969, 1970). This could lead to the stimulation of one species by the release of such hormones by another in plant mixtures, resulting in superior growth of the mixture components than in their respective monocultures. As the results of this study indicate superior root growth of species in mixtures than in monocultures, this negative allelopathic effect could be another possible process of interaction between the species.

The observed behaviour of the selected species in mixtures may be due to chemical interactions, although the results do not indicate significant differences between treatments within a given species. This does not conclusively prove the existence or the absence of such chemical processes. However, chemical interactions offer a possible explanation for the observed growth patterns of the species during very early stages. These may have an important bearing upon the growth of species in mixtures during this stage although competitive effects seem to dominate within 4-5 weeks of planting. Thus detailed investigations using higher planting densities, with plant extractions and chemical analysis is warranted to confirm the existence of these chemical effects. Such experiments were not attempted as they were beyond scope of the objectives set for this study.



APPENDIX 10A

Agronomy Department

5 October, 1981

Dear Sir,

Survey on the use of pasture species in Central New Zealand

I am writing to ask for your help with my research. As a part of my Ph.D studies at Massey, I am trying to find out how farmers

- (1) Make decisions as to which grass species and varieties to use?
- (2) What are their sources of information on grass species?
- (3) Which species and varieties are most commonly used? and
- (4) Whether different methods of sowing down pastures give equally satisfactory results?

I promise that all information will be treated in strict confidence. Anonymity will be preserved as the results will only appear as general statements (e.g. 50% of the farmers surveyed used brand x).

If you find that some questions do not apply to you, please leave them unanswered and return the partly filled-in questionnaire.

I am aware that you are busy and the temptation to file this letter in the "usual place" will be great! I would only ask that you "give it a go" - it is quite easy really. To make the task a little easier, a ballot will be conducted among those who return the questionnaire even partly answered. The prize will be a Ralta SC2 crock-pot (retail value \$63:00) kindly donated by Wrightsons Grain and Seed. I hope to analyse this survey in late October or early November and would appreciate your prompt assistance.

Thanking you in advance for your kind and early attention,

Yours faithfully,

Ravi Sangakkara
(Ph.D Student)
Agronomy Department

Encl.



Massey University

PALMERSTON NORTH, NEW ZEALAND

TELEPHONES, 69-099, 69-089.

In reply please quote:

APPENDIX 10B



SURVEY ON THE USE OF PASTURE GRASS SPECIES IN CENTRAL DISTRICTS OF NEW ZEALAND

1. Please record the name of district and county the farm is situated in
District..... County.....
2. What is the total land area of the farm?.....Acres OR.....Hectares.
(Please include runoffs away from residential farm and exclude land
leased to others).
3. Out of the total land area, approximately what area is used for grazing?
.....Acres ORHectares.
4. Please indicate the types of livestock you currently have (Tick all
that apply).
 Sheep
 Beef
 Dairy stock
 Other (please specify.....)
 None.
5. The main livestock enterprise on the farm is (Please tick one)
 Sheep
 Beef
 Beef and sheep
 Dairy stock
 Other (please specify.....)
6. Please indicate the approximate proportion of your land which can be
cultivated using a wheeled tractor (Tick one).
 Less than 25%
 25-50%
 50-75%
 Over 75%
7. What type of pasture is grown on your farm? (Tick one)
 One grass species
 Mixture of grass species
 One grass species and 1 legume
 Mixture of grass species and legumes.
8. Have you established new pastures or developed existing pastures in the
last five years?
 Yes (IF YES, PLEASE PROCEED WITH QUESTION 9 - I.E. PAGE 2)
 No (IF NO, PLEASE GO TO QUESTION 20 - I.E. PAGE 4)

3.

17. What seed rates do you use in establishing pasture?.....lbs/acre OR
.....kg/ha
18. Have you noticed a change from the seed mixture in your newly established pasture?
 Yes
 No

If Yes please indicate the major grass/grasses now present
in your new pastures.....

19. Are you satisfied with performance of the pasture grass species you used the last time?
 Yes
 No

Why is that?

5.

28. When do you usually sow the pasture seeds (tick one)
 spring
 autumn
 other (specify)
29. If you have any additional information and/or comment to make that you consider important or relevant to the study, I would be grateful if you could kindly write them below:

FINALLY

30. If for some reason I want to clarify any of the information you have given, may I contact you again?
 Yes - please state name and address below
 No
31. Would you be interested in receiving a copy of the summary of results of this study?
 Yes - please enter name and address in space below.
 No.
32. Would you be interested in participating in the ballot?
 Yes - if yes please enter name and address in space below.
 No.

THANK YOU VERY MUCH FOR YOUR KIND ASSISTANCE. PLEASE USE THE ENCLOSED POSTAGE PAID ENVELOPE TO RETURN THE QUESTIONNAIRE.

NAME

ADDRESS

BIBLIOGRAPHY

- ABERG, E., JOHNSON, I.J. and WILSIE, C.P. (1943). Associations between species of grasses and legumes. *Journal of the American Society of Agronomy*. 35: 357-369.
- AIYER, A.K.Y.N. (1949). Mixed cropping in India. *Indian Journal of Agricultural Science*. 19: 439-543.
- ALBERDA, T. and SIMBA, L. (1968). Dry matter production and light interception of crop surfaces. 3. Actual herbage production in different years as compared with potential values. *Journal of the British Grasslands Society*. 23: 206-215.
- ALBERDA, T. and SIMBA, L. (1982). The influence of length of growing period, nitrogen fertilization and shading on tillering of perennial ryegrass (*Lolium perenne* L.). *Netherlands Journal of Agricultural Science*. 30: 127-135.
- ALCOCK, M.B. and MORGAN, E.W. (1966). The effect of defoliation on the yield of mixtures of S22 (diploid) and tetra (tetraploid) Italian ryegrass in early establishment. *Journal of the British Grassland Society*. 21: 62-64.
- ANDERSON, M.C. (1975). Solar radiation and carbon dioxide in plant communities - Conclusions. In "*Photosynthesis and productivity in different environments*". Edited by Cooper, J.P. Cambridge University Press. p. 345-354.
- ANDREWS, C.S. and JOHANSEN, C. (1978). Differences between pasture species in their requirements for nitrogen and phosphorus. In "*Plant relations in pastures*". Edited by Wilson, J.R. C.S.I.R.O., Melbourne. p. 111-127.
- ANDREWS, R.E. and NEWMAN, E.I. (1970). Root density and competition for nutrients. *Oecologia Plantarum*. 5: 319-334.
- ANONYMOUS (1980). *Scrub development*. Statistical Bureau Bulletin, New Zealand Institute of Valuers. November, 1980. p 2251.
- ANSLOW, R.C. (1966). The rate of appearance of leaves on tillers of the Graminae. *Herbage Abstracts*. 36: 149-155.
- ANSLOW, R.C. (1967). Frequency of cutting and sward production. *Journal of Agricultural Science (Cambridge)*. 68: 377-384.
- ANSLOW, R.C. and GREEN, J.O. (1967). The seasonal growth of pasture grasses. *Journal of Agricultural Science (Cambridge)*. 68: 109-122.
- APPLEBY, A.P., OLSON, P.D. and COLBERT, D.R. (1976). Winter wheat yield reduction from interference by Italian ryegrass. *Agronomy Journal*. 68: 463-466.
- ARENS, R. (1962). The effect of rate of seeding on competition between species on the productivity of the first year's pasture (In German). *Z. Acker-und Pflanzenbau*. 115: 357-374.

- ARNDT, W. (1965). The nature of mechanical impedance to seedlings by soil surface seals. *Australian Journal of Soil Research*. 3: 45-54.
- ARMSTRONG, C.S. (1977). "Grasslands Nui" perennial ryegrass. *N Z. Journal of Experimental Agriculture*. 5: 381-384.
- ARNOLD, G.C. Department of Mathematics and Statistics, Massey University, Palmerston North, New Zealand.
- ARNOTT, R.A. (1969). The effect of seed weight and depth of sowing on the emergence and early seedling growth of perennial ryegrass (*Lolium perenne*). *Journal of the British Grassland Society*. 24: 104-110.
- ASHER, C.J. and OZANNE, P.G. (1966). Root growth in seedlings of annual pasture species. *Plant and Soil*. 24: 423-436.
- ASPINALL, D.C. (1960). An analysis of competition between barley and white persicaria 2. Factors determining the course of competition. *Annals of Applied Biology*. 48: 637-654.
- ASPINALL, D. and MILTHORPE, F.L. (1959). An analysis of competition between barley and white persicaria. 1. Effects of growth. *Annals of Applied Biology*. 47: 156-172.
- AUSTENSON, H.M. and WALTON, P.D. (1970). Relationship between initial seed weight and mature plant characters in spring wheat. *Canadian Journal of Plant Science*. 50: 53-58.
- BAARS, J.A. (1982). Pasture production patterns in winter-early spring in New Zealand. In *Proceedings of the Conference on dairy production from pastures*. Edited by McMillan, K.L. and Taufa, V.K. p. 363-364.
- BAARS, J.A., DOUGLAS, J.A. and THOMSEN, E.J. (1976). An evaluation of "Grasslands Nui" perennial ryegrass in the Waikato. *Proceedings of the Ruakura Farmers Conference*. 28: 62-64.
- BAEUMER, K. and Wit, C.T. DE (1968). Competitive interference of plant species in monocultures and mixed stands. *Netherlands Journal of Agricultural Science*. 16: 103-122.
- BAKHUIS, J.A. and KLETER, H.J. (1965). Some effects of associated growth of grass and clover under field conditions. *Netherlands Journal of Agricultural Science*. 13: 280-310.
- BALDWIN, J.P. (1976). Competition for plant nutrients in a soil: A theoretical approach. *Journal of Agricultural Science (Cambridge)*. 87: 347-356.
- BALDWIN, J.P. and TINKER, P.B. (1972). A method of estimating the lengths and spatial patterns of two interpenetrating root systems. *Plant and Soil*. 37: 209-213.
- BALDWIN, J.P., NYE, P.H. and TINKER, P.B. (1972). Uptake of solutes by multiple root systems from soil 2. The theoretical effects of root density and pattern on uptake of nutrients from soil. *Plant and Soil*. 36: 693-708.

- BALDWIN, J.P., NYE, P.H. and TINKER, P.B. (1973). Uptake of solutes by multiple root systems from soil. 3. A model for calculating the solute uptake by a randomly dispersed root system developing in a finite volume of soil. *Plant and Soil*. 38: 621-635.
- BALDY, C. (1963). Cultures associées et productivité de l'eau. *Annales Agronomique*. 14: 489-534.
- BARLEY, K.P. (1970). The configuration of the root system in relation to nutrient uptake. *Advances in Agronomy*. 22: 159-201.
- BARLEY, K.P. and GREACEN, E.L. (1967). Mechanical resistance as a soil factor influencing the growth of roots and underground shoots. *Advances in Agronomy*. 19: 1-44.
- BARNARD, C. (1964). Form and structure. In *Cereals and Grasslands*. Edited by Barnard, C. McMillan, London. p. 47-72.
- BARRET, D.W. and CAMPBELL, N.A. (1974). An evaluation of effects of competition between Wimmera ryegrass (*Lolium rigidum*) during early stages of growth. *Australian Journal of Experimental Agriculture and Animal Husbandry*. 13: 581-586.
- BASKIN, I.M. and BASKIN, C.C. (1978). A discussion on the growth and competition ability of C₃ and C₄ plants. *Castanea*. 43: 71-76.
- BEBAWI, F.F. and NAYLOR, R.E. (1981). Performance of pure and mixed stands of forage grasses at the establishment phase. *New Phytologist*. 89: 347-356.
- BENEDICT, H.M. (1941). The inhibitory effect of dead roots on the growth of Brome grass. *Journal of the American Society of Agronomy*. 33: 1108-1109.
- BERENDSE, F. (1979). Competition between plant populations with different rooting depths. 1. Theoretical considerations. *Oecologia*. 43: 19-26.
- BERENDSE, F. (1981). Competition between plant populations with different rooting depth. 2. Pot experiments. *Oecologia*. 48: 334-341.
- BERENDSE, F. (1982). Competition between plant population with different rooting depths. 3. Field experiments. *Oecologia*. 53: 50-55.
- BERGH, J.P. VAN DEN (1968). An analysis of yields of grasses in mixed and pure stands. *Agricultural Research Report No. 714*, Pudoc, Wageningen. 71p.
- BERGH, J.P. VAN DEN (1979). Changes in the competition of mixed populations of grassland species. In "*The study of vegetation*". Edited by Werger, M.J.A., Dr W. Junk Publishers, Hague. p 59-80.

- BERGH, J.P. VAN DEN and WIT, C.T. DE (1960). Competition between timothy grass (*Phleum pratense* L.) and sweet vernal grass (*Anthoxanthum odoratum* L.) (in Dutch - with English summary). *Yearbook of the Institute for Biological and Chemical Research on Field Crops and Herbage*, Wageningen, 1960. p 155-165.
- BERGH, J.P. VAN DEN and ELBERSE, W.TH. (1962). Competition between *Lolium perenne* L. and *Anthoxanthum odoratum* L. at two levels of phosphate and potash. *Journal of Ecology*. 50: 87-95.
- BERGH, J.P. VAN DEN and ELBERSE, W.TH. (1970). Yields of monocultures and mixtures of two grass species differing in growth habit. *Journal of Applied Ecology*. 7: 311-320.
- BERGH, J.P. VAN DEN and BRAAKHEKKE, W.G. (1978). Coexistence of plant species by niche differentiation. In '*Structure and functioning of plant population*'. Edited by Woldendorp, J.W. Institute for Ecological research. The Netherlands. p 125-138.
- BEVERIDGE, J.L. and WILSIE, C.P. (1959). Influence of depth of planting, seed size and variety on emergence and seedling vigour in alfalfa. *Agronomy Journal*. 51: 731-734.
- BHAT, K.K.S. and NYE, P.H. (1973). Diffusion of phosphate to plant roots in soil. 1. Quantitative auto-radiography of the depletion zone. *Plant and Soil*. 38: 161-175.
- BHATTACHARYA, G.K. and JOHNSON, R.J. (1977). *Statistical concepts and methods*. John Wiley and Sons. p. 220-223.
- BIRCH, L.C. (1955). Selection in *Drosophila pseudobscura* in relation to crowding. *Evolution* 9: 389-399.
- BIRCH, L.C. (1957). The meaning of completion. *American Naturalist*. 41: 5-18.
- BLACK, C.C., CHEN, T.M. and BROWN, R.H. (1969). Biochemical basis for plant competition. *Weed Science*. 17: 338-344.
- BLACK, J.N. (1956). The influence of seed size and depth of sowing on pre-emergence and early vegetative growth of subterranean clover. *Australian Journal of Agricultural Research*. 7: 98-109.
- BLACK, J.N. (1957a). The early vegetative growth of three strains of subterranean clover (*Trifolium subterraneum* L.) in relation to size of seed. *Australian Journal of Agricultural Research*. 8: 1-14.
- BLACK, J.N. (1957b) Seed size as a factor in the growth of subterranean clover under spaced and sward conditions. *Australian Journal of Agricultural Research*. 8: 335-351.
- BLACK, J.N. (1957c). The influence of varying light intensity on the growth of herbage plants. *Herbage Abstracts*. 27: 89-98.

- BLACK, J.N. (1958). Competition between plants of different initial seed sizes in swards of subterranean clover (*Trifolium subterraneum* L.), with particular reference to leaf area and the micro climate. *Australian Journal of Agricultural Research*. 9: 299-318.
- BLACK, J.N. (1959). Seed size in herbage legumes - A review. *Herbage Abstracts*. 29: 235-241.
- BLACK, J.N. (1960a). An assessment of the role of planting density in competition between red clover (*Trifolium pratense* L.) and lucerne (*Medicago sativa* L.) in the early vegetative phase. *Oikos*. 11: 26-42.
- BLACK, J.N. (1960b). The significance of petiole length, leaf area and light interception in competition between strains of subterranean clover grown in swards. *Australian Journal of Agricultural Research*. 11: 277-291.
- BLACK, J.N. (1961a). Border and orientation effects and their elimination in experimental swards of subterranean clover. *Australian Journal of Agricultural Research*. 12: 203-211.
- BLACK, J.N. (1961b). Competition between two varieties of subterranean clover as related to the proportion of seeds sown. *Australian Journal of Agricultural Research*. 12: 810-820.
- BLACK, J.N. (1963). Defoliation as a factor in the growth of varieties of subterranean clover when grown in pure and mixed swards. *Australian Journal of Agricultural Research*. 14: 206-225.
- BLACK, J.N. (1966). Competition within grass and cereal communities. In "*The growth of cereals and grasses*". Edited by Milthorpe, F.L. and Ivins, G.D. University of Nottingham. p. 167-178.
- BLACK, J.N. and WILKINSON, G.E. (1963). The role of time of emergence in determining the growth of individual plants in swards of subterranean clover. *Australian Journal of Agricultural Research*. 14: 628-638.
- BLACKMAN, G.E. (1938). The interaction of light intensity and nitrogen supply in the growth and metabolism of grasses and clover. 1. The effects of light intensity and nitrogen supply on the clover content of a sward. *Annals of Botany*. 11: 257-280.
- BLACKMAN, G.E. and BLACK, J.N. (1959). Physiological and ecological studies in the analysis of plant environment. II. A further assessment of the influence of shading on the growth of different species in the vegetative phase. *Annals of Botany*. 23: 51-63.
- BLACKMAN, G.E. and TEMPLETON, W.G. (1938). The nature of competition between cereal crops and annual weeds. *Journal of Agricultural Science*. 28: 247-271.
- BLASER, R.E. and BRADY, N.C. (1950). Nutrient competition in plant associations. *Agronomy Journal*. 42: 128-135.

- BLASER, R.E., SKRDLA, W.H. and TAYLOR, T.H. (1952a). Ecological and physiological factors in compounding seed mixtures. *Advances in Agronomy*. 4: 179-216.
- BLASER, R.E., SKRDLA, W.H. and TAYLOR, T.H. (1952b). Advantages and disadvantages of simple and complex mixtures. *Proceedings of the 6th International Grasslands Congress I*: p. 349-355.
- BLASER, R.E., TAYLOR, T., GRIFFITH, W. and SKRDLA, W. (1956). Seedling competition in establishing forage plants. *Agronomy Journal*. 48: 1-6.
- BLEASDALE, K. (1960). Studies on plant competition. In "*The Biology of Weeds*". Edited by Harper, J.L. Blackwell Scientific Publications, Oxford, England. p. 133-142.
- BLIJENBURG, J.G. and SNEEP, J. (1975). Natural selection in a mixture of eight barley varieties grown in six successive years. I. Competition between the varieties. *Euphytica*. 24: 305-315.
- BOFFEY, T.B. and VEEVERS, A. (1977). Balanced designs for two component competition experiments. *Euphytica*. 26: 481-484.
- BOKHARI, U.G. (1978). Allelopathy among prairie grasses and its possible ecological significance. *Annals of Botany*. 42: 127-136.
- BRAAKHEKKE, W.G. (1980). On coexistence - A causal approach to diversity and stability in grassland vegetation. *Agricultural Research Report No. 902*, Pudoc, Wageningen. 164 p.
- BRADSHAW, A.D., LODGE, R.W., JOWETT, D. and CHADWICK, M.J. (1958). Experimental investigations into the mineral nutrition of several grass species. I. Calcium level. *Journal of Ecology*. 46: 749-757.
- BRADSHAW, A.D., LODGE, R.W., JOWETT, D. and CHADWICK, M.J. (1960a). Experimental investigations into the mineral nutrition of several grass species. 2. Calcium and pH level. *Journal of Ecology*. 48: 143-150.
- BRADSHAW, A.D., CHADWICK, M.J., JOWETT, D., LODGE, R.W. and SNAYDON, R.W. (1960b). Experimental investigations into the mineral nutrition of several grass species. 3. Phosphate level. *Journal of Ecology*. 48: 631-637.
- BRADSHAW, A.D., CHADWICK, M.J., JOWETT, D. and SNAYDON, R.W. (1964). Experimental investigations into the mineral nutrition of several grass species 4. Nitrogen level. *Journal of Ecology*. 52: 665-676.
- BRAY, R.H. (1954). A nutrient mobility concept of soil-plant relationships. *Soil Science*. 78: 9-22.

- BREESE, E.L. and HILL, J. (1973). Regression analysis of interactions between competing species. *Heredity*. 31: 181-200.
- BREMNER, P.M., ECKERSALL, R.M. and SCOTT, R.K. (1963). The relative importance of embryo size and endosperm size in causing the effects associated with seed size in wheat. *Journal of Agricultural Science*. 61: 139-145.
- BREWSTER, J.L. and TINKER, P.B. (1970). Nutrient cation flows in soil around plant roots. *Proceedings of the Soil Science Society of America*. 34: 421-426.
- BROCK, J.L. (1973). Effect of sowing depth and post-sowing compaction on the establishment of tall fescue varieties. *N.Z. Journal of Experimental Agriculture*. 1: 11-14.
- BROCK, J.L. and CHARLTON, D.F.L. (1977). *Lotus pedunculatus* establishment in intensive farming. *Proceedings of the N.Z. Grassland Association*. 39: 121-129.
- BROUGHAM, R.W. (1954a). Pasture establishment studies. 1. The effect of grass seeding rate on the establishment and development of pastures of short rotation ryegrass, red and white clovers. *N.Z. Journal of Science and Technology*. 35A: 518-538.
- BROUGHAM, R.W. (1954b). Pasture establishment studies. 2. The influence of herbage height at grazing and grass seeding rate on the establishment and development of pastures of short rotation ryegrass, red and white clovers. *N.Z. Journal of Science and Technology*. 35A: 539-549.
- BROUGHAM, R.W. (1956). Effect of intensity of defoliation on regrowth of pasture. *Australian Journal of Agricultural Research*. 7: 377-387.
- BROUGHAM, R.W. (1958). Interception of light by the foliage of pure and mixed stands of pasture plants. *Australian Journal of Agricultural Research*. 9: 39-52.
- BROUGHAM, R.W. (1959). The effect of frequency and intensity of grazing on the productivity of a pasture of short rotation ryegrass and red and white clover. *N.Z. Journal of Agricultural Research*. 2: 1232-1248.
- BROUGHAM, R.W. (1966). Aspects of light utilization, leaf development and senescence and grazing on grass legume balance and productivity of pastures. *Proceedings of the N.Z. Ecological Society*. 13: 58-65.
- BROUGHAM, R.W. (1969). Present position of pasture establishment research in New Zealand. *Proceedings of the N.Z. Grassland Association*. 31: 43-51.
- BROUGHAM, R.W. (1973). Pasture management and production. *Proceedings of the 25th Farmers Conference, Ruakura, New Zealand*. p. 169-183.

- BROUGHAM, R.W. and HARRIS, W. (1967). Rapidity and extent of changes in genotype structure induced by grazing in a ryegrass population. *N.Z. Journal of Agricultural Research.* 10: 56-65.
- BROUWER, R. (1963). Some aspects of the equilibrium between overground and underground plant parts. *Jaarboek 1963 Instituut von Biologisch en Scheikundig Onderzoek van Landbouwgewassen, Wageningen:* 31-39.
- BROWN, R.H. and BLASER, R.E. (1968). Leaf area index in pasture growth. *Herbage abstracts.* 38: 1-9.
- BUNTING, A.H. (1960). Some reflections on the ecology of weeds. In *The biology of weeds*". Edited by Harper, J.L. Blackwell Scientific Publications, Oxford. p 11-26.
- BURDON, J.J., GROVES, R.H. and CULLEN, J.M. (1981). The impact of biological control on the distribution and abundance of *Chondrilla juncea* in South eastern Australia. *Journal of Applied Ecology.* 18: 957-966.
- BURGESS, A.C. (1951). Value of prairie grass in North Taranaki. *N.Z. Journal of Agriculture.* 83: 29.
- BURTON, G.W. (1943). A comparison of the first year's root production of seven southern grasses established from seed. *Journal of the American Society of Agronomy.* 35: 192-196.
- CABLE, D.R. (1969). Competition in the semi-desert grass-shrub type as influenced by root systems, growth habits and soil moisture extraction. *Ecology* 50: 27-38.
- CAMERON, D.G. (1963). *Phalaris tuberosa* and soil conservation 2. *Journal of Soil Conservation, New South Wales.* 19: 220-233.
- CARTER, H.W., NORTON, H.W. and DUNGAN, G.H. (1957). Wheat and cheat. *Agronomy Journal.* 49: 261-267.
- CASHMORE, A.B. (1934). A comparative study of *Lolium perenne* L. and *Phalaris tuberosa* L. at varying stages of growth. *Commonwealth Science and Industrial Organization (Australia). Bulletin* 81. 28p.
- CAVERS, P.B. and HARPER, J.L. (1967). Studies in the dynamics of plant populations. 1. The fate of seed and grass plants introduced into various habitats. *Journal of Ecology.* 55: 59-71.
- CHARLES, A.H. (1961). Differential survival of cultivars of *Lolium*, *Dactylis* and *Phleum*. *Journal of the British Grassland Society.* 16: 69-73.
- CHARLES, A.H. (1964). Differential survival of plant types in swards. *Journal of the British Grassland Society.* 19: 198-204.

- CHARLES, A.H. (1965). Interactions of grass, clover and nurse crop in the seeding year. *Journal of the British Grassland Society*. 20: 241-247.
- CHARLES, A.H. (1966). Formation and maintenance of pastures. *Journal of the British Grassland Society*. 21: 93-96.
- CHIPPENDALE, H.G. (1932). The operation of interspecific competition in causing delayed growth of grasses. *Annals of Applied Biology*. 19: 221-242.
- CHIPPENDALE, H.G. (1949). Environment and germination of grass seeds. *Journal of the British Grassland Society*. 4: 57-61.
- CLEMENTS, F.E., WEAVER, J.E. and HANSON, H.C. (1929). Competition in cultivated crops. *Carnegie Institute, Washington Publication*. 398: 202-233.
- COCHRAN, W.G. and COX, G.M. (1957). *Experimental designs*. John Wiley and Sons, New York. 611p.
- COCKAYNE, A.H. (1919). Cocksfoot - its establishment and maintenance in pasture. *N.Z. Journal of Agriculture*. 18: 264-268.
- COCKS, P.S. (1969). Germination, establishment and interspecific competition in two annual pasture grasses. Ph.D Thesis, University of Adelaide, Australia.
- COCKS, P.S. (1974). The influence of density and nitrogen on the outcome of competition between two annual pasture grasses (*Hordeum leporinum* Link and *Lolium rigidum* Gaud.). *Australian Journal of Agricultural Research*. 25: 247-258.
- COCKS, P.S. and DONALD, C.M. (1973a). The early vegetative growth of two annual pasture grasses (*Hordeum leporinum* Link and *Lolium rigidum* Gaud). *Australian Journal of Agricultural Research*. 24: 11-19.
- COCKS, P.S. and DONALD, C.M. (1973b). The germination and establishment of two annual pasture grasses (*Hordeum leporinum* Link. and *Lolium rigidum* Gaud). *Australian Journal of Agricultural Research*. 24: 1-10.
- COOPER, J.P. (1951). Studies on the growth and development in *Lolium*. 2. Pattern of bud development of the shoot apex and its ecological significance. *Journal of Ecology*. 39: 228-270.
- CORKILL, W.S. (1954). A new improved strain of cocksfoot. *N.Z. Journal of Agriculture*. 89: 481-482.
- CORNFORTH, I.S. (1968). Relationship between soil volume used by roots and nutrient accessibilities. *Journal of Soil Science*. 19: 291-301.
- CROCKER, W. (1948). "Growth of plants - Twenty years research at Boyce Thompson Institute". Reinhold, New York. 459 p.

- CROCKER, R.L. and MARTIN, P.M. (1964). Competition between perennial ryegrass and meadow fescue under field plot conditions. *Journal of the British Grassland Society*. 19: 27-29.
- CROOKSTON, R.K. (1976). Intercropping - a new version of an old idea. *Crops and Soils*. 28(9): 7-9.
- CULLEN, N.A. (1964). Species competition in establishing swards - suppression effects of ryegrass on establishment and production of associated grasses and clovers. *N.Z. Journal of Agricultural Research*. 7: 678-693.
- DALY, G.T. (1973). The grasslands of New Zealand. In "*Pastures and pasture plants*". Edited by Langer, R.H.M. A.H. and A.W. Reed, Wellington. p. 1-40.
- DALRYMPLE, D.F. (1971). Survey of multiple cropping in less developed nations. Foreign Economic Development Service, U.S. Department of Agriculture, Co-operating with U.S.A.I.D. Washington D.C.
- DALRYMPLE, R.L. and DWYER, D.D. (1967). Root and shoot growth of five range grasses. *Journal of Range Management*. 20: 141-145.
- DAUBENMIRE, R. (1968). *Plant communities*. A textbook of plant synecology. Harper and Row, New York. 300p.
- DAVIDSON, R.L. (1978). Root systems - the forgotten component of pastures. In "*Plant relations in pastures*". Edited by Wilson, J.R. C.S.I.R.O., Melbourne. p. 86-94.
- DAVIES, J.G. (1936). Seed rates and interspecific competition in seed mixtures. *Australian and New Zealand Association for the Advancement of Science Congress Report*. 22: 316.
- DAVIES, M.S. and SNAYDON, R.W. (1976). Rapid population differentiation in a mosaic environment 3. Measures of selection pressure. *Heredity*. 36: 59-66.
- DAVIES, W. (1927). Seed mixture problems: Soil germination, seedling and plant establishment with particular reference to the effects of environment and agronomic factors. Field trials. *Welsh Plant Breeding Station Bulletin*. Series H6: 39-60.
- DAVIES, W. (1928). Seed mixture problems. The factor of competition between one species and another in seed mixtures. *Welsh Plant Breeding Station Bulletin*. Series H No. 8: 82-149.
- DAVIES, W. (1952). *The grass crop - Its development, use and maintenance*. E. & F.N. Spon Ltd., London. p. 104-138.
- DAVIES, W. and THOMAS, M.T. (1928). The behaviour of grasses in the seeding year, when sown in pure plots - Establishment, rate of growth and palatability. *Welsh Journal of Agriculture*. 4: 206-221.

- DITTMER, H.J. (1937). A quantitative study of the roots and root hairs of a winter rye plant (*Secale cereale*). *American Journal of Botany*. 24: 417-420.
- DOBLEN, W.H. VAN (1955). Concurrentie tussen haver en zomergest op een pH-trappen-proefveld (in Dutch). *Verslag. C.I.L.O.*, p. 128-131 (cit. by de Wit, 1960).
- DONALD, C.M. (1951). Competition among pasture plants. 1. Intra specific competition among annual pasture plants. *Australian Journal of Agricultural Research*. 2: 355-376.
- DONALD, C.M. (1954). Competition among pasture plants. 2. The influence of density on flowering and seed production in annual pasture plants. *Australian Journal of Agricultural Research*. 5: 585-597.
- DONALD, C.M. (1958). The interaction of competition for light and nutrients. *Australian Journal of Agricultural Research*. 9: 421-435.
- DONALD, C.M. (1961). Competition for light in crops and pastures. In "*Mechanisms in biological competition*". Edited by Milthorpe, F.L. Symposia of the Society of Experimental Biology. 15: 283-313.
- DONALD, C.M. (1963). Competition among crop and pasture plants. *Advances in Agronomy*. 15: 1-81.
- DONALD, C.M. and BLACK, J.N. (1958). The significance of leaf area in pasture growth. *Herbage Abstracts*. 28: 1-6.
- DOUGLAS, J.A. (1966). Grass species - Introduction in Central Otago. *Proceedings of the N.Z. Grassland Association*. 28: 86-95.
- DOUGLAS, J.A. (1974). A review of the grass species introductions into the tussock grasslands of the South Island, New Zealand. *Proceedings of the N.Z. Grassland Association*. 35: 224-239.
- DRAPALA, W.J. and JOHNSON, C.M. (1961). Border and competition effects in millet and sudangrass plots as characterized by different levels of nitrogen fertilization. *Agronomy Journal*. 53: 17-19.
- DRAWE, D.L. and PALMBALD, I.G. (1977). Competition between Russian wild rye seedlings and four common weeds. *Journal of Range Management*. 30: 223-226.
- DREW, M.C. and NYE, P.H. (1969). The supply of nutrient ions by diffusion to plant roots in soil. 2. The effect of root hairs on the uptake of potassium by roots of ryegrass (*Lolium multiflorum*). *Plant and Soil*. 31: 407-424.
- DUNCAN, W.G., LOOMIS, R.S., WILLIAMS, W.A. and HANALL, R. (1967). A model for stimulating photosynthesis in plant communities. *Hilgardia*. 38: 181-206.

- DUNHAM, R.J. and NYE, P.H. (1973). The influence of soil water content on the uptake of ions by roots. 1. Soil water content gradients near a plane of onion roots. *Journal of Applied Ecology*. 10: 585-598.
- DUNHAM, R.J. and NYE, P.H. (1974). The influence of soil water content on the uptake of ions by roots. II. Chloride uptake and concentration gradients in soil. *Journal of Applied Ecology*. 11: 581-595.
- DURRANT, A. (1965). Analysis of reciprocal differences in diallel crosses. *Heredity*. 20: 573-607.
- EAGLES, C.F. (1967). The effect of temperature on vegetative growth in climatic races of *Dactylis glomerata* in controlled environments. *Annals of Botany*. 31: 31-39.
- EAGLES, C.F. (1972). Competition for light and nutrients between natural populations of *Dactylis glomerata*. *Journal of Applied Ecology*. 9: 141-151.
- EAGLES, C.F. and OSTGARD, O. (1971). Variation in growth and development in natural populations of *Dactylis glomerata* from Norway and Portugal. 1. Growth analysis. *Journal of Applied Ecology*. 8: 367-381.
- EAGLES, C.F. and WILLIAMS, D.H. (1969). Effect of environment on competitive ability of two natural populations of *Dactylis glomerata* L. *Journal of Agricultural Science (Cambridge)*. 72: 271-272.
- EAGLES, C.F. and WILLIAMS, D.H. (1971). Competition between natural populations of *Dactylis glomerata* L. *Journal of Agricultural Science (Cambridge)*. 77: 187-193.
- EAGLES, C.F., WILLIAMS, D.H. and TOLER, R.J. (1982). Seasonal changes in competitive ability of contrasting populations of *Dactylis glomerata*. *Journal of Applied Ecology*. 19: 555-561.
- EDGE, E.A. (1977). A growth study of four species in four potting media with four nutrient solutions. *Internal report, Plant Physiology Division, D.S.I.R., Palmerston North*. pl-25.
- EDMOND, D.B. (1966). The influence of animal treading on pasture growth. *Proceedings of the 10th International Grasslands Congress*. p. 453-458.
- EDMOND, D.B. (1970). Effects of treading on pastures, using different animals and soils. *Proceedings of the 11th International Grasslands Congress*. p. 604-608.
- EDWARDS, K.J.R. and ALLARD, R.W. (1963). The influence of light intensity on competitive ability. *American Naturalist*. 97: 243-248.
- ELBERSE, W.TH and KRUYF, H.N.DE (1979). Competition between *Hordeum vulgare* L. and *Chenopodium album* L. with different dates of emergence of *Chenopodium album*. *Netherlands Journal of Agricultural Science*. 27: 13-26.

- ELLERN, S.J., HARPER, J.L. and SAGAR, G.R. (1970). A comparative study of the distribution of roots of *Avena fatua* and *A. stringosa* in mixed stands using a ^{14}C labelling technique. *Journal of Ecology*. 58: 865-868.
- ENGEL, R.E. and TROUT, J.R. (1977). Seedling competition of kentucky bluegrass, red fescue, colonial bentgrass and temporary grasses. *Proceedings of the 3rd International Turfgrass Research Conference*. Edited by Beard, J.B. Madison, Wisconsin, U.S.A. p. 379-389.
- ENGLAND, F.J.W. (1965). Interaction in mixtures of herbage grasses. *Scottish Plant Breeding Station Record*. 1965. p. 125-149.
- ENGLAND, F. (1968). Competition in mixtures of herbage grasses. *Journal of Applied Ecology*. 5: 227-242.
- ENNIK, G.C. (1960). The competition between white clover and perennial ryegrass with difference in light intensity and moisture supply. *Yearbook of the Institute for Biological and Chemical Research on Field Crops and Herbage, Wageningen*. (In Dutch). p. 37-50.
- ENNIK, G.C. (1970). White clover-grass relation strips: Competition effects in laboratory and field. In "*White clover research*" - *British Grassland Society Occasional Symposium*. No. 6. Edited by Lowe, J. p. 165-174.
- ERDMANN, M.H. and HARRISON, C.M. (1947). The influence of domestic ryegrass and redtop upon the growth of Kentucky bluegrass and chewing fescue in lawn and turf mixtures. *Journal of the American Society of Agronomy*. 39: 682-689.
- EVANS, L.T., WARDLAW, I.F. and WILLIAMS, C.N. (1964). Environmental control of growth. In "*Grasses and Grasslands*". Edited by Barnard, C. McMillan p. 102-125.
- EVANS, P.S. (1970). Root growth of *Lolium perenne* L. 1. Effect of plant age, seed weight and nutrient concentration on root weight, length and number of apices. *N.Z. Journal of Botany*. 8: 344-356.
- EVANS, P.S. (1973). Effect of seed size and defoliation at three development stages on root and shoot growth of seedlings of some common pasture species. *N.Z. Journal of Agricultural Research*. 16: 389-394.
- EVANS, P.S. (1977). Comparative root morphology of some pasture grasses and clovers. *N.Z. Journal of Agricultural Research*. 20: 331-335.
- EVANS, R.A. (1960). Differential responses of three species of the annual grassland type to plant competition and mineral nutrition. *Ecology*. 41: 305-310.
- EVANS, R.A. (1961). Effects of different densities of downy brome (*Bromus tectorum*) on growth and survival of crested wheatgrass (*Agropyron desertorum*) in the greenhouse. *Weeds*. 9: 216-223.

- EVANS, R.A. and YOUNG, J.A. (1972). Competition within the grass community. In *"The biology and utilization of grasses"*. Edited by Younger, V.B. and McKell, C.M. Academic Press, New York. p230-246.
- FINDLAY, W.M. (1913). Report on grass seed mixtures. 1907-1913. *North Scotland Agriculture Bulletin*. No. 18.
- FITTER, A.H. (1976). Effects of nutrient supply and competition from other species on root growth of *Lolium perenne* in soil. *Plant and Soil*. 45: 177-189.
- FITTER, A.H. (1979). Influence of mycorrhizal infection on competition for phosphorus and potassium by two grasses. *New Phytologist*. 79: 119-125.
- FITZPATRICK, E.A. and NIX, H.A. (1970). The climate factor in Australian grassland ecology. In *"Australian Grasslands"* Edited by Milton, R. Australian National University Press, Canberra. p. 3-26.
- FOTI, S. (1975). Agronomic aspects of plant competition (in Spanish with English Summary). *Rivista di Agronomia*. 11: 81-93.
- FOWLER, N. (1982). Competition and coexistence in a North Carolina Grassland. 3. Mixtures of component species. *Journal of Ecology*. 70: 77-92.
- FRAME, J. and HUNT, I.V. (1964). The effect of a companion grass and seed rate on the productivity of a tall fescue sward. *Journal of the British Grassland Society*. 19: 330-335.
- FRIEND, D.J.C. (1966). The effect of light and temperature on the growth of cereals. In *"The growth of cereals and grasses"*. Edited by Milthorpe, F.L. and Ivins, G.D. University of Nottingham. p. 181-199.
- GARDNER, A.L. and HUNT, I.V. (1963). Intervarietal competition in perennial ryegrass swards. *Journal of the British Grassland Society*. 18: 285-291.
- GARWOOD, E.A. (1966). Studies on roots of grasses. *Annual report, Grassland Research Institute, Hurley, England*. 1966. p72-79.
- "GENSTAT" - A general statistical program. Alvey, N.G. et al., Rothamstead Experimental Station, United Kingdom.
- GIST, G.R. and SMITH, R.M. (1948). Root development of several common forage grasses to a depth of eight inches. *Journal of the American Society of Agronomy*. 40: 1036-1042.
- GLAUNINGER, J. and HOLZNER, W. (1982). Interference between weeds and crops - A review of literature. In *"Biology and ecology of weeds"*. Edited by Holzner, W. and Numata, N. Monographie Biologicae, Junk Publications, The Hague, p. 149-159.

- GLEESON, A.C. and MC GILCHRIST, C.A. (1978). Analysis of plant competition data from an incomplete mixture diallel experiment. *Journal of Agricultural Science (Cambridge)*. 91: 419-426.
- GLEESON, A.C. and MC GILCHRIST, C.A. (1980). Mixture diallel experiments with unequal proportions of genotypes. *Journal of Agricultural Science (Cambridge)*. 95: 525-532.
- GOH, B.S. (1979). Stability in models of mutualism. *American Naturalist*. 113: 261-275.
- GOMEZ, K.A. and GOMEZ, A.A. (1976). *Statistical procedures for agricultural research - with emphasis on rice*. International Rice Research Institute, Los Baños, Phillipines. 294p.
- GRANT, E.A. and SALLANS, W.G. (1964). Influence of plant extracts on germination and growth of eight forage species. *Journal of the British Grassland Society*. 19: 191-197.
- GRAY, B., DRAKE, M. and COLBY, W.G. (1953). Potassium competition in grass-legume associations as a function of root cation exchange capacity. *Proceedings of the American Society of Soil Science*. 17: 235-239.
- GREENAWAY, T.E. and BUDDEN, M. (1960). The use of perennial ryegrass sown at 1 lb per acre in a standard seed mixture. *Journal of the British Grassland Society*. 15: 235-237.
- GREENWOOD, D.J. (1969). Effect of oxygen distribution in the soil on plant growth. In "*Root growth*". Edited by Whittington, W.J. Butterworth, London. p. 202-223.
- GREENWOOD, R.M. (1950). Physiological studies on the germination and early growth of clovers. *Proceedings of the N.Z. Grassland Association*. 12: 122-131.
- GREIG-SMITH, P. (1964). *Quantitative plant ecology*. Butterworths, London 256p.
- GRIME, J.P. (1966). Shade avoidance and shade tolerance in flowering plants. In "*Light as an ecological factor*". Edited by Bainbridge, R., Evans, G.C. and Rackham, O. Oxford. p 187-207.
- GRIME, J.P. (1973). Competitive exclusion in herbaceous vegetation. *Nature (London)*. 242: 344-347.
- GRIME, J.P. (1974). Vegetative classification by reference to strategies. *Nature (London)*. 250:26-31.
- GRIME, J.P. (1977). Evidence for the existence of primary strategies in plants and its relevance to ecological and evolutionary theory. *American Naturalist*. 111: 1169-1194.
- GRIME, J.P. (1978). Interpretation of small scale patterns in the distribution of plant species in space and time. In "*Structure and functioning of plant populations*". Edited by Freyden, A.H.J. and Woldendorp, J.W. North Holland Publishing Co., Amsterdam. p.125-138.
- GRUBB, P.J. (1977). The maintenance of species richness in plant communities: The importance of the regeneration niche. *Biological Review*. 52: 107-145.

- GULMON, S.L. (1979). Competition and coexistence - Three annual grass species. *American Midland Naturalist*. 101: 403-416.
- GUPTA, P.L. and RORISON, I.H. (1975). Seasonal differences in the availability of nutrients down a podzolic profile. *Journal of Ecology*. 63: 521-534.
- GUSTAFSSON, A. (1951). Introduction of changes in genes and chromosomes. 2. Mutalines, environment and evolution. *Cold Spring Harbour Symposium on Quantitative Biology*. 16: 263-280.
- HAGGAR, R.J. (1979). Competition between *Lolium perenne* and *Poa trivialis* during establishment. *Grass and Forage Science*. 34: 27-36.
- HALL, R.L. (1974a). Analysis of the nature of interference between plants of different species. 1. Concepts and extension of the de Wit analysis to examine effects. *Australian Journal of Agricultural Research*. 25: 739-747.
- HALL, R.L. (1974b). Analysis of the nature of interference between plants of different species. 2. Nutrient relations in a Nandi *Setaria* and Greenleaf *Desmodium* association with particular reference to potassium. *Australian Journal of Agricultural Research*. 25: 749-756.
- HALL, R.L. (1978). Analysis and significance of competitive and non competitive interference between species. In "*Plant Relations in pastures*". Edited by Wilson, J.R., C.S.I.R.O., Melbourne. p. 163-174.
- HANKS, R.J. and THORPE, F.C. (1956). Seedling emergence of wheat as related to soil moisture content, bulk density, oxygen diffusion rate and crust strength. *Proceedings of the Soil Science Society of America*. 20: 307-308.
- HARKESS, R.D. (1965). The effect of seed size on early growth of diploid and tetraploid Italian ryegrass. *Journal of the British Grassland Society*. 20: 190-193.
- HARKESS, R.D. (1970). Competition between tall fescue and perennial ryegrass in pure and mixed swards under simulated field conditions. *Journal of Applied Ecology*. 7: 497-506.
- HARPER, J.L. (1961). Approaches to the study of biological competition. In "*Mechanisms in biological competition*". Edited by Milthorpe, F.L. Symposium of the Society of Experimental Biology. 15: 1-39.
- HARPER, J.L. (1964). The individual in the population. *Journal of Ecology*. 52 (supplement): 149-158.
- HARPER, J.L. (1965). The nature and consequence of interference amongst plants. In "*Genetics Today*". Proceedings 11th International Congress of Genetics. 2: 465-482.
- HARPER, J.L. (1967). A Darwinian approach to plant ecology. *Journal of Ecology*. 55: 247-270.

- HARPER, J.L. (1977). *Population biology of plants*. Academic Press, London. 892 p.
- HARPER, J.L. and CLATWORTHY, J.N. (1963). The comparative biology of closely related species. 6. Analysis of the growth of *Trifolium repens* and *T. fragiferum* in pure and mixed populations. *Journal of Experimental Botany*. 14: 172-190.
- HARRIES, J.H. and NORRINGTON-DAVIES, J. (1977). Competition studies in diploid and tetraploid varieties of *Lolium perenne* L. 2. The inhibition of germination. *Journal of Agricultural Science (Cambridge)*. 88: 411-415.
- HARRIS, A.J., BOYD, A.F., ANDERSON, L.B., VARTHA, E.W. and RYAN, D.L. (1977). Performance of four ryegrass cultivars under cutting. *N.Z. Journal of Experimental Agriculture*. 5: 391-395.
- HARRIS, G.A. (1967). Some competitive relationships between *Agropyron spicatum* and *Bromus tectorum*. *Ecological Monographs*. 37: 89-111.
- HARRIS, G.A. (1976). Root phenology as a factor of competition among grass seedlings. *Journal of Range Management*. 30: 172-177.
- HARRIS, G.A. and WILSON, A.M. (1970). Competition for moisture among seedlings of annual and perennial grasses as influenced by root elongation at low temperature. *Journal of Ecology*. 51: 530-534.
- HARRIS, W. (1968). Pasture seed mixtures, competition and productivity. *Proceedings of the N.Z. Grassland Association*. 30: 143-153.
- HARRIS, W. (1970a). Competition effects on yield and plant and tiller density in mixtures of ryegrass cultivars. *Proceedings of the N.Z. Ecological Society*. 17: 10-17.
- HARRIS, W. (1970b). The prospects for mixing varieties of the *Lolium multiflorum* Lam. - *Lolium perenne* L. complex. *Proceedings of the 11th International Grasslands Congress*. p. 654-657.
- HARRIS, W. (1972). Shading, defoliation, temperature, growth stage and residual fertility effects on competition between *Rumex acetosella*, *Trifolium repens* and *Lolium (multiflorum x repens)*. *N.Z. Journal of Agricultural Research*. 15: 687-705.
- HARRIS, W. (1973). Competition among pasture plants 4. Cutting frequency, nitrogen and phosphorus interactions and competition between two ryegrass cultivars. *N.Z. Journal of Agricultural Research*. 16: 399-413.
- HARRIS, W. (1974). Competition among pasture plants 5. Effects of frequency and height of cutting on competition between *Agrostis tenuis* and *Trifolium repens*. *N.Z. Journal of Agricultural Research*. 17: 251-256.
- HARRIS, W. (1977). An approach to evaluate a large number of mixtures under grazing. *Proceedings of the 13th International Grassland Congress*. p. 389-393.
- HARRIS, W. (1978). Defoliation as a determinant of the growth persistence and composition of pasture. In "*Plant relations in pastures*". Edited by Wilson, J.R. C.S.I.R.O., Melbourne. p. 67-85.

- HARRIS, W. (Dr). Director, Botany Division, Department of Scientific and Industrial Research, Private Bag, Lincoln, Christchurch, New Zealand.
- HARRIS, W. and BROCK, J.L. (1972). Effect of Porina caterpillar (*Wiseana* Spp.) infestation on yield and competitive interactions of ryegrass and white clover varieties. *N.Z. Journal of Agricultural Research*. 15: 723-740.
- HARRIS, W. and BROUGHAM R.W. (1968). Some factors affecting change in botanical composition in a ryegrass-white clover pasture under continuous grazing. *N.Z. Journal of Agricultural Research*. 11: 15-38.
- HARRIS, W. and HOGLUND, J.H. (1977). Influences of seasonal growth periodicity and N-fixation on competitive combining abilities of grasses and legumes. *Proceedings of the 13th International Grassland Congress*. p. 239-243.
- HARRIS, W. and LAZENBY, A. (1974). Competitive interaction of grasses with contrasting temperature responses and water stress balances. *Australian Journal of Agricultural Research*. 25: 227-246.
- HARRIS, W. and SEDCOLE, J.R. (1974). Competition and moisture stress effects on genotypes in three grass populations. *N.Z. Journal of Agricultural Research*. 17: 443-454.
- HARRIS, W. and THOMAS, V.J. (1970). Competition among pasture plants. 1. Effects of frequency and height of cutting on competition between two ryegrass cultivars. *N.Z. Journal of Agricultural Research*. 13: 833-861.
- HARRIS, W. and THOMAS, V.J. (1972). Competition among pasture plants. 2. Effects of frequency and height of cutting on competition between *Agrostis tenuis* and two ryegrass cultivars. *N.Z. Journal of Agricultural Research*. 15: 19-32.
- HARRIS, W. and THOMAS, V.J. (1973). Competition among pasture plants. 3. Effects of frequency and height of cutting on competition between white clover and two ryegrass cultivars. *N.Z. Journal of Agricultural Research*. 16: 49-56.
- HARRIS, W., FORDE, B.J. and HARDACRE, A.K. (1981a). Temperature and cutting effects on the growth and competitive interactions of ryegrass and paspalum. 1. Dry matter production, tiller numbers and light interception. *N.Z. Journal of Agricultural Research*. 24: 299-307.
- HARRIS, W., FORDE, B.J. and HARDACRE, A.K. (1981b). Temperature and cutting effects on the growth and competitive interactions of ryegrass and paspalum. 2. Interspecific competition. *N.Z. Journal of Agricultural Research*. 24: 309-320.
- HASLEMORE, R.H. and ROUGHAN, P.G. (1976). Rapid chemical analysis of some plant constituents. *Journal of the Science of Food and Agriculture*. 27: 1171-1178.
- HAYNES, R.J. (1980). Competitive aspects of the grass legume association. *Advances in Agronomy*. 33: 227-261.

- HERRIOT, J.B.D. (1958). The establishment of herbage species in Great Britain. *Herbage Abstracts*. 28: 73-82.
- HIGGINS, J.J., HAUN, J.R. and KOCH, E.J. (1964). Leaf development: Index of plant response to environmental factors. *Agronomy Journal*. 56: 489-492.
- HILL, J. (1972). Competition in herbage plants. *Annual Report, Welsh Plant Breeding Station*. 1972. p. 27-30.
- HILL, J. (1973). Methods of analysing competition with special reference to herbage plants. 2. Effects of associate plants. *Journal of Agricultural Science (Cambridge)*. 81: 91-98.
- HILL, J. (1974). Methods of analysing competition with special reference to herbage plants. 3. Monocultures v. binary mixtures. *Journal of Agricultural Science (Cambridge)*. 83: 57-65.
- HILL, J. and SHIMAMOTO, Y. (1973). Methods of analysing competition with special reference to herbage plants. 1. Establishment. *Journal of Agricultural Science (Cambridge)*. 81: 77-89.
- HOFFMANN, T. BANN and ENNIK, G.C. (1980). Investigations into plant characters affecting the competitive ability of perennial ryegrass (*Lolium perenne* L.). *Netherlands Journal of Agricultural Science*. 28: 97-109.
- HOLLIDAY, R.J. (1960). Plant population and crop yield. *Field Crop Abstracts*. 13: 159-167.
- HOVE, H.J. TEN and KLEINENDORST, A. (1957). The influence of seed size on the youth development of *Lolium perenne* L. *Mededeling Instituut Biol. Scheikundig. Onderz. Land. Wageningen*. 179: 39-46.
- HULBERT, L.C. (1955). Ecological studies of *Bromus tectorum* and other annual brome grasses. *Ecological Monographs*. 25: 181-213.
- IDRIS, H. and MILTHORPE, F.L. (1966). Light and nutrient supplies in the competition between barley and charlock. *Oecologia Plantarum*. 1: 143-164.
- INTERNATIONAL SEED TESTING ASSOCIATION. International rules for seed testing. *Seed Science and Technology*. 1976. p. 98-134.
- IVENS, G.W. and MLOWE, F. (1980). A study of competition between seedlings of gorse (*Ulex europaeus* L.) and perennial ryegrass (*Lolium perenne* L.) by means of a replacement series experiment. *Weed Research*. 20: 183-191.
- JACKMAN, R.H. and MOUAT, M.C.H. (1972a). Competition between grass and clover for phosphate. 1. Effect of browntop (*Agrostis tenuis* Sibth) on white clover (*Trifolium repens* L.) growth and nitrogen fixation. *N.Z. Journal of Agricultural Research*. 15: 653-666.

- JACKMAN, R.H. and MOUAT, M.C.H. (1972b). Competition between grass and clover for phosphate. 2. Effect of root activity, efficiency of response to phosphate and soil moisture. *N.Z. Journal of Agricultural Research*. 15: 667-675.
- JACQUARD, P. (1965). Study of the biological interferences in forage mixtures. *Proceedings of the 9th International Grassland Congress*. p. 349-355.
- JAGANNATH, M.K. (1978). A modified model for plant competition under varying plant geometry. *Current Science*. 47: 251-254.
- JEWISS, O.R. (1966). Morphological and physiological aspects of growth of grasses during the vegetative phase. In "*The growth of cereals and grasses*". Edited by Milthorpe, F.L. and Ivins, J.D. Nottingham University. p. 39-54.
- JEWISS, O.R. (1972). Tillering in grasses. Its significance and control. *Journal of the British Grassland Society*. 27: 65-82.
- JONES, D.J.C. (1957). Early stages in ley establishment. *Agriculture (London)*. 63: 509-513.
- JONES, M. (1933). Grassland management and its influence on the sward. *Journal of the Royal Agricultural Society (England)*. 94: 21-41.
- JONES, M. (1958). Grassland management. *Transactions of the Royal Highland Agricultural Society of Scotland*. 6th Series 3. 73-86.
- JORDAN, B.T. (1957). Prairie grass used to advantage in dairy pastures. *N.Z. Journal of Agriculture*. 94: 135.
- JUSKA, F.V., TYSON, J. and HARRISON, C.M. (1955). The competitive relationship of Merion bluegrass as influenced by various mixtures, cutting heights and level of nitrogen. *Agronomy Journal*. 47: 513-518.
- KALTON, R.R., DELONG, R.A. and MC LEOD, D.S. (1959). Cultural factors in seedling vigour of smooth brome grass and other forage species. *Iowa State Journal of Science*. 34: 47-80.
- KANEMASU, E.G., THURTELL, G.W. and TANNER, C.B. (1969). Design, calibration and field use of a stomatal diffusion porometer. *Plant Physiology*. 44: 881-885.
- KAUFMANN, M.L. and GUITARD, A.A. (1967). The effect of seed size on early plant development in barley. *Canadian Journal of Plant Science*. 47: 73-78.
- KAYS, S. and HARPER, J.L. (1974). The regulation of plant and tiller density in a grass sward. *Journal of Ecology*. 62: 97-105.
- KIDD, F. and WEST, C. (1969). Physiological predetermination: The influence of the physiological condition of the seed upon the course of subsequent growth and upon the yield. *Annals of Applied Biology*. 5: 112-142.

- KING, J. (1971). Competition between established and newly sown grass species. *Journal of the British Grassland Society*. 26: 221-229.
- KING, J., LAMB, W.I.C. and MCGREGOR, M.T. (1979). Regrowth of ryegrass swards subject to different cutting regimes and stocking densities. *Grass and Forage Science*. 34: 107-118.
- KIRA, T., OGAWA, H. and SHINOZAKI, K. (1953). Intraspecific competition among higher plants. 1. Competition-density-yield inter-relationships in regularly dispersed populations. *Journal of the Institute of Polytechnics, Osaka University* D4: 1-16.
- KITTOCK, D.L. and LAW, A.G. (1968). Relationship of seedling vigour to respiration and tetrazolium chloride by germinating wheat seed. *Agronomy Journal*. 60: 286-288.
- KITTOCK, D.L. and PATTERSON, J.K. (1962). Seed size effects on performance of dryland grasses. *Agronomy Journal*. 54: 277-278.
- KNAPP, R. (1959). Reciprocal influence of a plant species in a dry sward and a deciduous woodland (in German). *Berichte der Deutschen Botanischen Gesellschaft*. 72: 368-382.
- KNEEBONE, W.R. and CREMER, C.L. (1955). The relationship of seed size to seedling vigour in some native grass species. *Agronomy Journal* 47: 472-477.
- KOYAMA, H. and KIRA, T. (1956). Intraspecific competition among higher plants. 8. Frequency distribution of individual plant height as affected by the interaction between plants. *Journal of the Institute of Polytechnics, Osaka City University*. 7: 73-94.
- KUJIRA, Y. and KANDA, M. (1977). Competition among individual plants in crop population 3. Competition from the point of root behaviour. *The reports of the Institute for Agricultural Research*. Tohoku University. 28: 29-39.
- LAMBERT, D.A. (1968). Competition between plants of cocksfoot (*Dactylis glomerata*) grown for seed. *Journal of the British Grassland Society*. 23: 274-279.
- LAMBRECHTSEN, N.C. (1975). *What grass is that?* New Zealand D.S.I.R. Information Series No. 87. 136 p.
- LANCASHIRE, J.A. (1977). Growing more pasture when we need it. *Massey University Dairy Farming Annual*. 29: 40-50.
- LANCASHIRE, J.A. (1978). Improved species and seasonal pasture production. *Proceedings of the N.Z. Agronomy Society*. 8: 123-127.
- LANCASHIRE, J.A. (1982). Plant growth in dairy pastures during the winter. In "*Proceedings of the Conference on dairy production from pastures*". Edited by McMillan, K.L. et al. p 347-358.

- LANCASHIRE, J.A. and BROCK, J.L. (1983). Management of new cultivars for dry land. *Proceedings of the N.Z. Grassland Association*. 44: 61-73.
- LANCASHIRE, J.A. and HARRIS, A.J. (1977). Evaluation of new herbage cultivars. *Proceedings of the N.Z. Grassland Association*. 39: 108-120.
- LANCASHIRE, J.A., HARRIS, A.J., ARMSTRONG, C.S. and RYAN, D.L. (1978). Perennial ryegrass cultivars. *Proceedings of the N.Z. Grassland Association*. 40: 114-124.
- LANGER, H.J. (1973). A method for analysing of plant competition experiments. *Mauri Ora* (University of Canterbury). 1: 73-77.
- LANGER, R.H.M. (1963). Tillering in herbage grasses. *Herbage Abstracts*. 33: 141-148.
- LANGER, R.H.M. (1972). *How grasses grow*. Edward Arnold, London. 66p.
- LANGER, R.H.M. (1973). Grass species and strains. In "*Pastures and pasture plants*". Edited by Langer, R.H.M. A.H. & A.W. Reed, Wellington. p. 65-84.
- LANGER, R.H.M., RYLE, S.M. and JEWISS, O.R. (1964). The changing plant and tiller populations of timothy and meadow fescue swards. 1. Plant survival and patterns of tillering. *Journal of Applied Ecology*. 1: 197-208.
- LAZENBY, A. and ROGERS, H.H. (1962). Selective criteria in grass breeding 1. *Journal of Agricultural Science*. 59: 51-62.
- LEE, J.A. (1960). A study of plant competition in relation to development. *Evolution*. 14: 18-28.
- LEMON, E.R. and WEIGAND, C.L. (1962). Soil aeration and plant and root relations. 2. Root respiration. *Agronomy Journal*. 54: 171-175.
- LEON, J.A. and TUMPSON, D.B. (1975). Competition between two species for two complementary or substitutable resources. *Journal of Theoretical Biology*. 50: 185-201.
- LEVY, E.B. (1922). Principles of pasture establishment. *New Zealand Journal of Agriculture*. 25: 65-75.
- LEVY, E.B. (1970). *Grasslands of New Zealand* (3rd Edition). Government Printer, Wellington, New Zealand. p. 173-217.
- LEVY, E.B. and MADDEN, E.A. (1933). The point method of pasture analysis. *N.Z. Journal of Agriculture*. 46: 267-279.
- LITAV, M. and HARPER, J.L. (1967). A method for studying the spatial relationship between the root system of two neighbouring plants. *Plant and Soil*. 26: 389-392.
- LITAV, M. and SELIGMAN, N. (1970). Competition between *Oryopsis holciformis* (M.B.) Hack. and annual plants. 2. Performance of *O. holciformis* and two annuals when grown in mixtures of differing ratios. *Israel Journal of Botany*. 19: 517-528.

- LITAV, M. and WOLOVITCH, S. (1971). Partial separation of roots as a means of reducing the effect of competition between two grass species. *Annals of Botany*. 35: 1163-1178.
- LODGE, R.W. (1964). Autecology of *Cynosurus cristatus* L. 4. Competitive ability and yield. *Journal of Ecology*. 52: 53-61.
- LUDLOW, M.M. (1978). Light relations in pastures. In "Plant relations in pastures". Edited by Wilson, J.R. C.S.I.R.O., Melbourne. p. 35-49.
- MAC DIARMID, B.N. and WATKIN, B.R. (1971). The cattle dung patch. Part 1. *Journal of the British Grassland Society*. 26: 239-246.
- MAC DIARMID, B.N. and WATKIN, B.R. (1972). The cattle dung patch. Part 2. Effect of a dung patch on the chemical status of the soil, and ammonia nitrogen losses from the patch. 3. Distribution and rate of decay of dung patches and their influences on grazing behaviour. *Journal of the British Grassland Society*. 27: 43-54.
- MACHIN, D. and SANDERSON, B. (1977). Computing maximum - likelihood estimates for the parameters of the de Wit competition model. *Applied Statistics*. 26: 1-8.
- MAHMOUD, A. and GRIME, J.P. (1976). An analysis of competitive ability in three perennial grasses. *New Phytologist*. 77: 431-435.
- MARTEN, G.C. and JORDAN, R.M. (1974). Significance of palatability differences among *Phalaris arundinacea* L. *Bromus inermis* Leyss. and *Dactylis glomerata* L. grazed by sheep. *Proceedings of the 12th International Grassland Congress*. 1: 305-312.
- MARTIN, F.B. (1973). Beehive designs for observing variety competition. *Biometrics*. 29: 397-402.
- MARTIN, M.P.L.D. and SNAYDON, R.W. (1982). Root and shoot interaction between barley and field beans when intercropped. *Journal of Applied Ecology*. 19: 263-272.
- MATHER, K. (1961). Competition and cooperation. In "Mechanisms in Biological Competition". Edited by Milthorpe, F.L. Symposia of the Society for Experimental Biology. 15: 264-281.
- MC COWN, R.L. and WILLIAMS, W.A. (1968). Competition for nutrients and light between the annual grass species *Bromus mollis* and *Erodium botrys*. *Ecology*. 49: 981-990.
- MC GILCHRIST, C.A. (1965). Analysis of competition experiments. *Biometrics*. 21: 975-985.
- MC GILCHRIST, C.A. and TRENBATH, B.R. (1971). A revised analysis of plant competition experiments. *Biometrics*. 27: 659-671.
- MC KELL, C.M. (1972). Seedling vigour and seedling establishment. In "The biology and utilization of grasses". Edited by Younger, V.B. and McKell, C.M. Academic Press, New York. p. 74-89.

- MC KELL, C.M., DUNCAN, C. and MULLER, C.H. (1969). Competitive relationships of annual ryegrass (*Lolium multiflorum* Lam.). *Ecology*. 50: 653-657.
- MC WILLIAM, J.R. (1978). Response of pasture plants to temperature. In "*Plant relations in pastures*". Edited by Wilson, J.R. C.S.I.R.O., Melbourne. p. 17-34.
- MC WILLIAM, J.R. and DOWLING, P.M. (1970). Factors influencing the germination and establishment of pasture seed on the soil surface. *Proceedings of the 11th International Grassland Congress*. p. 579-583.
- MC WILLIAM, J.R., CLEMENTS, R.J. and DOWLING, P.M. (1970). Some factors influencing the germination and early seedling development of pasture plants. *Australian Journal of Agricultural Research*. 21: 19-32.
- MEAD, R. (1979). Competition experiments. *Biometrics*. 35: 41-54.
- MEAD, R. and STERN, R.D. (1980). Designing experiments for intercropping research. *Experimental Agriculture*. 16: 329-342.
- MEAD, R. and RILEY, J. (1981). A review of statistical ideas relevant to intercropping. *Journal of the Royal Statistical Society*. 144: 462-509.
- MILLER, R.S. (1967). Pattern and processes in competition. *Advances in Ecological Research*. 4: 1-74.
- MILNE, A. (1961). Definitions of competition among annuals. In "*Mechanisms in biological competition*". Edited by Milthorpe, F.L. Symposia of the Society for Experimental Biology. 15: 40-61.
- MILTHORPE, F.L. (1961). The nature and analysis of competition. In "*Mechanisms in biological competition*". Edited by Milthorpe, F.L. Symposia of the Society for Experimental Biology. 15: 330-355.
- "MINITAB" - Reference manual. Ryan T.A. (Jr). Pennsylvania State University, U.S.A.
- MITCHELL, K.J. (1953a). Influence of light and temperature on the growth of ryegrass (*Lolium* spp.). I. Pattern of vegetative development. *Physiologia Plantarum*. 6: 21-46.
- MITCHELL, K.J. (1953b). Influence of light and temperature on the growth of ryegrass (*Lolium* spp.) 2. The control of lateral bud development. *Physiologia Plantarum*. 6: 425-443.
- MITCHELL, K.J. (1954). Growth of pasture species. 1. Short rotation and perennial ryegrass. *N.Z. Journal of Science and Technology*. 36A: 193-206.
- MITCHELL, K.J. (1955). Growth of pasture species. 2. Perennial ryegrass (*Lolium perenne*), cocksfoot (*Dactylis glomerata*) and paspalum (*Paspalum dilatatum*). *N.Z. Journal of Science and Technology*. 37A: 8-26.

- MITCHELL, K.J. (1956a). Growth of pasture species under controlled environment. 1. Growth at various levels of constant temperatures. *N.Z. Journal of Science and Technology*. 38A: 203-216.
- MITCHELL, K.J. (1956b). Influence of light and temperature on the growth of pasture species. *Proceedings of the 7th International Grassland Congress*. p. 58-69.
- MITCHELL, K.J. (1970). A look at the future technical potential of New Zealand farming. *Proceedings of the Lincoln College Farmers Conference*. 20: 72-79.
- MITCHELL, K.J. and COLES, S.T.J. (1955). Effects of defoliation and shading on short rotation ryegrass. *N.Z. Journal of Science and Technology*. 36A: 586-604.
- MITCHELL, K.J. and GLENDAY, A.C. (1958). The tiller population of pastures. *N.Z. Journal of Agricultural Research*. 1: 305-318.
- MOLISH, C. (1937). Der einfluss einer pflanze auf die andere-allelopathie. *Gustav Fischer Verlag. Jena*. (Cited by Rice, E.L., (1980).
- MONSI, M. and SAEKI, T. (1963). Uber den lichtfaktor in den pflanzengesellschaften und seine bedeutung für die Stoffproduktion. (in German). *Japanese Journal of Botany*. 14: 22-52. (Cited by Harper, J.L., 1977).
- MOSS, G.R. (1962). Prairie grass seed mixtures. *N.Z. Journal of Agriculture*. 104: 35.
- MOUAT, M.C.H. and WALKER, T.W. (1959). Competition for nutrients between grasses and white clover. 1. Effects of grass species and nitrogen supply. *Plant and Soil*. 11: 30-40.
- MUSGRAVE, D.J. (1981). Evaluation of grassland cultivars in fertilized tussock grasslands. *Research Report, Agricultural Division, Southern North Island, Ministry of Agriculture and Fisheries, New Zealand*. p. 48-49.
- NAQVI, H.H. (1972). Preliminary studies of interference exhibited by Italian ryegrass. *Biologia (Lahore)*. 18: 201-210.
- NAQVI, H.H. and MULLER, C.H. (1975). Biochemical inhibition (allelopathy) exhibited by Italian ryegrass (*Lolium multiflorum* L.) *Pakistan Journal of Botany*. 7: 139-147.
- NAYLOR, R.E. (1980). Effects of seed size and emergence time on subsequent growth of perennial ryegrass. *New Phytologist*. 84: 313-318.
- NEWBERY, D.Mc. C. (1979). The affect of decomposing roots on the growth of grassland plants. *Journal of Applied Ecology*. 16: 613-622.
- NEWBERY, D. Mc.C. and NEWMAN, E.I. (1978). Competition between grassland plants of different initial size. *Oecologia*. 33: 136-380.

- NEWMAN, E.I. and ANDREWS, R.E. (1973). Uptake of phosphorus and potassium in relation to root growth and root density. *Plant and Soil*. 38: 49-69.
- NEWMAN, E.I. and MILLAR, M.H. (1977). Allelopathy among some British grassland species. 2. Influence of root exudates on phosphorus uptake. *Journal of Ecology*. 65: 399-411.
- NEWMAN, E.I. and ROVIRA, A.D. (1975). Allelopathy among some British grassland species. *Journal of Ecology*. 63: 727-737.
- NEW ZEALAND STATISTICS YEARBOOKS 1973-1982. Government Printer, Wellington, New Zealand.
- NICHOL, H. (1935). Mixed cropping in primitive agriculture. *Empire Journal of Experimental Agriculture*. 3: 189-195.
- NICHOLS, A.O. (Dr) Division of Land Use. Research, C.S.I.R.O., Canberra, Australia.
- NORMAN, M.J.T. (1960). The relationship between competition and defoliation in pasture. *Journal of the British Grassland Society*. 15: 145-149.
- NORRINGTON-DAVIES, J. (1967). Application of diallel analysis to experiments in plant competition. *Euphytica*. 16: 391-406.
- NORRINGTON-DAVIES, J. (1968). Diallel analysis of competition between some grass species. *Journal of Agricultural Science (Cambridge)*. 71: 223-231.
- NORRINGTON-DAVIES, J. (1972). Diallel analysis of competition between some barley species and their hybrids. *Euphytica* 21: 292-308.
- NORRINGTON-DAVIES, J. and CROWLEY, J.G. (1969). Effect of density and fertility on the competitive interactions of diploid and tetraploid ryegrasses during early growth. *Irish Journal of Agricultural Research*. 8: 359-374.
- NORRINGTON-DAVIES, J. and HARRIES, J.H. (1977). Competition studies in diploid and tetraploid varieties of *Lolium perenne*. 1. The influence of density and proportion of sowing. *Journal of Agricultural Science (Cambridge)*. 88: 405-410.
- NORRINGTON-DAVIES, J., MOORE, K. and BLIJENBURG, J.G. (1981). The yield and competitive ability of euploid and aneuploid genotypes of tetraploid *Lolium perenne* in two seasons at two locations. *Euphytica*. 30: 675-686.
- NYE, P.H. (1966). The effect of the nutrient intensity and buffering pattern of a soil and the absorbing power, size and root hairs of a root on nutrient absorption by diffusion. *Plant and Soil*. 25: 81-105.

- NYE, P.H. (1968). The soil model and its application to plant nutrition. In *"Ecological aspects of the mineral nutrition of the plant"*. Edited by Rorison, I.H. 9th Symposium of the British Ecological Society. Blackwell, Oxford, p. 105-114.
- NYE, P.H. and FOSTER, W.N.M. (1961). The relative uptake of phosphorus by crops and natural fallow from differing parts of their root zones. *Journal of Agricultural Science*. 56: 299-306.
- NYE, P.H. and TINKER, P.B. (1969). The concept of a root demand coefficient. *Journal of Applied Ecology*. 6: 293-300.
- O'BRIEN, T.A. (1960). The influence of nitrogen on seedling and early growth of perennial ryegrass and cocksfoot. *N.Z. Journal of Agricultural Research*. 3: 399-411.
- O'BRIEN, T.A., MOORBY, J. and WHITTINGTON, W.J. (1967). The effect of management and competition on the uptake of ³²Phosphorus by ryegrass, meadow fescue and their natural hybrid. *Journal of Applied Ecology*. 4: 513-520.
- ODUM, E.P. (1959). *FUNDAMENTALS OF ECOLOGY*. W.B. Saunders, Philadelphia. 574 p.
- OLSEN, S.R. and KEMPER, W.D. (1968). Movement of nutrients to plant roots. *Advances in Agronomy*. 20: 91-151.
- ONG, C.K. (1978). The physiology of tiller death in grasses. 1. The influence of tiller age, size and position. *Journal of the British Grassland Society*. 33: 197-203.
- ONG, C.K., MARSHALL, C. and SAGAR, G.R. (1978). The physiology of tiller death in grasses. 2. Causes of tiller death in a grass sward. *Journal of the British Grassland Society*. 33: 205-211.
- PALMER, P.C. (1970). The presence of other grasses in ryegrass/white clover pastures. *Proceedings of the 23rd Weed and Pest Control Conference*: 51-56.
- PANTALL, A.W. (1961). Prairie grass as a substitute for short rotation ryegrass. *Proceedings of the N.Z. Grassland Association*. 23: 92-99.
- PATEL, A.S. and COOPER, J.P. (1961). The influence of seasonal changes in light energy on leaf and tiller development in ryegrass, timothy and meadow fescue. *Journal of the British Grassland Society*. 16: 299-308.
- PAVLYCHENKO, T.K. (1937). Quantitative studies of the entire root systems of weed and crop plants under field conditions. *Ecology*. 18: 62-79.
- PAVLYCHENKO, T.K. and HARRINGTON, J.B. (1934). Competitive efficiency of weeds and cereal crops. *Canadian Journal of Research*. 10: 77-94.
- PEARCE, S.C. and GILLIVER, B. (1979). Graphical assessment of inter-cropping methods. *Journal of Agricultural Science (Cambridge)*. 93: 51-58.

- PETERSON, H.L. (1976). Competition in *Lolium perenne* L. as measured by yield and persistency. *Department of Crop Husbandry and Plant Breeding, Royal Veterinary and Agricultural University, Copenhagen, Denmark.* p. 129-140.
- PINEIRO, J. and HARRIS, W. (1978a). Performance of mixtures of ryegrass cultivars and prairie grass with red clover under two grazing frequencies. I. Herbage production in the establishment year. *N.Z. Journal of Agricultural Research.* 21: 83-92.
- PINEIRO, J. and HARRIS, W. (1978b). Performance of mixtures of ryegrass cultivars and prairie grass with red clover under two grazing frequencies. 2. Shoot populations and natural re-seeding of prairie grass. *N.Z. Journal of Agricultural Research.* 21: 665-673.
- PLUMMER, A.P. (1943). The germination and early seedling development of twelve range grasses. *Journal of the American Society of Agronomy.* 35: 19-34.
- POLLOK, J.A. (1975). A comparative study of certain New Zealand and German soil formed from loess. PH.D Thesis, Friedrich-Wilhelms Universität, Bonn.
- POTTINGER, R.P. (1973). Pests of grassland and small seed crops. In "*Pastures and pasture plants*". Edited by Langer, R.H.M. A.H. & A.W. Reed, Wellington. p. 409-426.
- REITH, J.W.S., INKSON, R.H.E., HOLMES, W., MACLUSKY, D.S., REID, D., HEDDLE, R.G. and COPEMAN, G.J.F. (1964). The effects of fertilizer on herbage production. 2. The effect of nitrogen, phosphorus and potassium on botanical and chemical composition. *Journal of Agricultural Science.* 63: 209-220.
- REMISON, S.U. (1978). The effects of mineral nutrition and density on root interactions in three grass species. *Annals of Botany.* 42: 277-283.
- REMISON, S.U. and SNAYDON, R.W. (1978). Yield, seasonal changes in root competitive ability and competition for nutrients among grass species. *Journal of Agricultural Science (Cambridge).* 90: 115-124.
- REMISON, S.U. and SNAYDON, R.W. (1980). Effects of defoliation and fertilizers on root competition between *Dactylis glomerata* and *Lolium perenne*. *Grass and Forage Science.* 35: 81-93.
- RENNIE, J.C. (1974). Some effects of competition and density of plants on dry weight produced. *Annals of Botany.* 38: 1003-1012.
- RERKASEM, K., STERN, W.R. and GOODCHILD, N.A. (1980a). Associated growth of wheat and annual ryegrass. 1. Effect of varying total density and proportion in mixtures of wheat and annual ryegrass. *Australian Journal of Agricultural Research.* 31: 649-658.
- RERKASEM, K., STERN, W.R. and GOODCHILD, N.A. (1980b). Associated growth of wheat and annual ryegrass. 2. Effect of varying the time of ryegrass germination in stands of wheat. *Australian Journal of Agricultural Research.* 31: 659-672.

- RERKASEM, K., STERN, W.R. and GOODCHILD, N.A. (1980c). Associated growth of wheat and annual ryegrass. 3. Effects of early competition on wheat. *Australian Journal of Agricultural Research*. 31: 1057-1067.
- RHODES, I. (1967). Studies on the effect of competitive stress on the growth and development of some grass species and populations. Ph.D Thesis, University of New England, Armidale, Australia.
- RHODES, I. (1968a). The growth and development of some grasses under competitive stress. 1. Competition between seedlings, and between seedlings and established plants. *Journal of the British Grassland Society*. 23: 129-136.
- RHODES, I. (1968b). The growth and development of some grass species under competitive stress. 3. The nature of competitive stress and characters associated with competitive ability during seedling growth. *Journal of the British Grassland Society*. 23: 330-335.
- RHODES, I. (1970). Competition between herbage grasses. *Herbage Abstracts*. 40: 115-121.
- RHODES, I. (1973). Relationship between canopy structure and productivity in herbage grasses and its implications for plant breeding. *Herbage Abstracts*. 43: 129-133.
- RHODES, I. and HARRIS, W. (1979). The nature and basis of differences in sward composition and yield in ryegrass-white clover mixtures. In "*Changes in sward composition and productivity*". British Grassland Society Occasional Symposium No. 10., Edited by Charles A.H. and Haggard, R.J. p. 55-60.
- RHODES, I. and STERN, W.R. (1978). Competition for light. In "*Plant relations in pastures*". Edited by Wilson, J.R. C.S.I.R.O. Melbourne. p. 175-189.
- RICE, E.L. (1974). *Allelopathy*. Academic Press, New York. 353p.
- RICE, E.L. (1979). Allelopathy - an update. *Botanical Review*. 45: 15-109.
- RICE, E.L. (1980). Some roles of allelopathy in pasture and forage crops. In "*Proceedings of the 37th Southern pasture and forage crop improvement conference, Tennessee*". Science and Education Administration, U.S.D.A. p. 56-63.
- RICHARDS, D., GOUBRAN, F.H., GARWOLI, W.N. and DALY, M.W. (1979). A machine for determining root length. *Plant and Soil*. 52: 69-76.
- RISSER, P.G. (1969). Competitive relationships among herbaceous grassland plants. *The Botanical Review*. 35: 251-284.
- RITCHIE, I.M. (1975). "Grasslands Nui" ryegrass. *Annual report, Research Division, Ministry of Agriculture and Fisheries, Wellington, 1974-1975*. p. 144-145.

- ROBERTS, J.L. and OLSEN, F. (1942). Inter-relationships of legumes and grass grown in association. *Journal of the American Society of Agronomy*. 34: 695-701.
- ROBERTSON, J.H. and PEARCE, C.K. (1945). Artificial reseeding in the closed community. *North West Science*. 19: 58-66.
- ROGERS, H.H. and LAZENBY, A. (1966). The evaluation of grasses in microplots. *Journal of Agricultural Science (Cambridge)*. 66: 147-151.
- ROGLER, G.A. (1954). Seed size and seedling vigour in crested wheat grass. *Agronomy Journal*. 46: 216-220.
- ROSS, M.A. and HARPER, J.L. (1972). Occupation of biological space during seedling establishment. *Journal of Ecology*. 60: 77-88.
- ROSSITER, R.C. (1974). The relative success of strains of *Trifolium subterraneum* L. in binary mixtures under field conditions. *Australian Journal of Agricultural Research*. 25: 757-766.
- ROSSITER, R.C. and PALMER, M.J. (1981). An analysis of seed yield in some strains of subterranean clover (*Trifolium subterraneum* L.) When grown in binary mixtures. *Australian Journal of Agricultural Research*. 32: 445-452.
- ROVIRA, A.D. (1978). Microbiology of pasture soils and some effects of microorganisms on pasture plants. In "Plant relations in pastures". Edited by Wilson, J.R. C.S.I.R.O., Melbourne. p. 95-110.
- RUMBALL, W. (1969). Pasture species and their performance in the Wairarapa. *Proceedings of the N.Z. Grassland Association*. 31: 35-42.
- RUMBALL, W. (1974). "Grasslands Matua" Prairie grass (*Bromus catharticus* vahl.). *N.Z. Journal of Experimental Agriculture*. 2: 1-5.
- RUMMEL, R.S. (1946). Some effects of competition from cheat grass brome on crested wheat grass and blue stem wheat grass. *Ecology*. 27: 159-167.
- RYLE, G.J.A. (1964). A comparison of leaf and tiller growth in seven perennial grasses as influenced by nitrogen and temperature. *Journal of the British Grassland Society*. 19: 281-290.
- SAKAI, K.I. (1955). Competition in plants and its relation to selection. *Cold Spring Harbour Symposia on Quantitative Biology*. 20: 137-157.
- SAKAI, K.I. (1957). Studies on competition in plants 7. Effects on competition of a varying number of competing and non competing individuals. *Journal of Genetics*. 35: 227-234.

- SAKAI, K.I. (1961). Competitive ability in plants - its inheritance and some related problems. In *"Mechanisms in biological competition"*. Edited by Milthorpe, F.L. Symposia of the Society for Experimental Biology. 15: 245-263.
- SALISBURY, E.J. (1942). *The reproductive capacity of plants*. G.Bell and Sons., London. 244p.
- SANDERS, F.E., TINKER, P.B. and NYE, P.H. (1970). Uptake of solutes by multiple root systems from soil. 1. An electrical analog of diffusion to root systems. *Plant and Soil*. 34: 453-466.
- SANDFAER, J. (1954). On the influence of natural selection - inter-plant competition on breeding work with self fertilized small grains. (in Danish with English Summary) *Tidsskrift for Planteavl*. 58: 334-354.
- SANDFAER, J. (1970). An analysis of the competition between some barley varieties. *Riso Report*. 230: 114p.
- SANGSTER, B. (1981). Finding a role for prairie grass. *N.Z. Farmer*. September 24, 1981: 102-107.
- SANTHIRASEGARAM, K. (1962). Competition between wheat and undersown pastures with particular reference to the light factor. Ph.D. Thesis, University of Adelaide, Australia.
- SCARISBRICK, D.H. and IVINS, J.D. (1970). Some aspects of competition between pasture species: The effect of environment and defoliation. *Journal of Applied Ecology*. 7: 417-428.
- SCHREIBER, M.M. (1967). A technique for studying weed competition in forage legume establishment. *Weeds*. 15: 1-4.
- SCOTT, D. (1974). Interactions between resident vegetation and oversown seed in improving New Zealand tussock grasslands. *Proceedings of the 12th International Grasslands Congress*. p. 831-840.
- SCOTT, D. (1975). Allelopathic interactions of resident tussock grassland species on germination of oversown seed. *N.Z. Journal of Experimental Agriculture*. 3: 135-141.
- SCOTT, R.S. (1975). Nutrient efficiency of some grasses and legumes in relation to environmental stress. Ph.D Thesis, Massey University, Palmerston North, New Zealand.
- SCOTT, R.S. and LOWTHER, W.L. (1980). Competition between white clover 'Grasslands Huia' and *Lotus pedunculatus* 'Grasslands Maku'. 1. Shoot and root competition. *N.Z. Journal of Agricultural Research*. 23: 501-507.
- SCOTTER, D.R. (Dr). Department of Soil Science, Massey University, Palmerston North, New Zealand.
- SCOTTER, D.R., CLOTHIER, B.E. and TURNER, M.A. (1979a). Soil water in a fragiaqualf. *Australian Journal of Agricultural Research*. 17: 443-453.

- SCOTTER, D.R., CLOTHER, B.E. and TURNER, M.A. (1979b). Soil water balance in a fragiaqualf and its effect on pasture growth in Central New Zealand. *Australian Journal of Agricultural Research*. 17: 455-465.
- SEARS, P.D. (1956). The effect of the grazing animal on pasture. *Proceedings of the 7th International Grasslands Congress*. p. 92-103.
- SHEARD, R.W. and WINCH, J.E. (1966). The use of light interception, grass morphology and time as a criterion for the harvesting of timothy, smooth brome and cocksfoot. *Journal of the British Grassland Society*. 21: 231-237.
- SHEATH, G.W. and GREENWOOD, P.B. (1982). Suitability of some pasture species in the sub humid areas of Otago. 1. Grasses. *N.Z. Journal of Experimental Agriculture*. 10: 23-30.
- SHEATH, G.W., GALLETLY, W.S. and GREENWOOD, P.B. (1976). An evaluation of several grass and legume cultivars under dryland and irrigation in North Otago. *Proceedings of the N.Z. Grassland Association*. 38: 140-150.
- SHIBUYA, K., YAMADA, T., HIROTA, H. and ITO, M. (1979). Transition of competitive superiority from a primary pasture canopy to the succeeding canopies. 1. Seed size and emergence earliness as initial factors causing competition. *Journal of the Japanese Society of Grassland Science*. 24: 259-269.
- SIMMONDS, N.W. (1962). Variability in crop plants, its use and conservation. *Biological Reviews*. 37: 442-465.
- SITHAMPARANATHAN, J. (1979). Seasonal growth patterns of herbage species on high rainfall hill country in northern North Island. *N.Z. Journal of Experimental Agriculture*. 7: 157-162.
- SMITH, E.M., EWEN, L.S. and LOEWER, O.J. (Jr.). (1981). Growth of fescue and red clover as influenced by environment and interspecific competition. *Paper Number 81 - 4020, American Society of Agricultural Engineers*. Michigan, U.S.A. 18p.
- SMOLIAK, S. and JOHNSTON, A. (1975). Seedling competition of some grasses in mono and mixed culture under greenhouse conditions. *Canadian Journal of Plant Science*. 55: 935-940.
- SNAYDON, R.W. (1962). The growth and competitive ability of contrasting natural populations of *Trifolium repens* L. on calcareous and acid soils. *Journal of Ecology* 50: 439-447.
- SNAYDON, R.W. (1971). An analysis of competition between plants of *Trifolium repens* L. populations collected from contrasting soils. *Journal of Applied Ecology*. 8: 687-697.
- SNAYDON, R.W. (1978). Genetic changes in pasture populations. In "Plant relations in pastures" Edited by Wilson, J.R. C.S.I.R.O., Melbourne. p 253-272.
- SNAYDON, R.W. (1979). A new technique for studying plant interactions. *Journal of Applied Ecology*. 16: 281-286.

- SNAYDON, R.W. and BAINES, R.N. (1981). Factors affecting interactions between white clover and grasses. In *British Grassland Society Occasional Symposium No. 13*. Edited by Wright, C.E. p. 178-184.
- SNAYDON, R.W. and BRADSHAW, A.D. (1962a). Differences between natural populations of *Trifolium repens* in response to mineral nutrients. 1 Phosphate. *Journal of Experimental Botany*. 13: 422-434.
- SNAYDON, R.W. and BRADSHAW, A.D. (1962b). The performance and survival of contrasting natural populations of white clover when planted into an upland *Festuca/Agrostis* sward. *Journal of the British Grassland Society*. 17: 113-118.
- SNAYDON, R.W. and BRADSHAW, A.D. (1969). Differences between natural populations of *Trifolium repens* L. in response to mineral nutrients 2. Calcium, Magnesium and Potassium. *Journal of Applied Ecology*. 6: 185-202.
- SNAYDON, R.W. and HARRIS, P.M. (1979). Interactions below ground - the use of nutrients and water. In "*Proceedings of the International Workshop on Intercropping*". Edited by Willey, R.W. I.C.R.I.S.A.T., India. p. 188-201.
- SNEDECOR, G.W. and COCHRAN, W.G. (1967). *Statistical methods* (6th Edition) Iowa State University Press, Ames, Iowa, U.S.A. 593p.
- SPITTERS, C.J.T. (1979). Competition and its consequences for selection in barley breeding. *Agricultural Research Report No. 893*. Pudoc, Wageningen. 268p.
- SPITTERS, C.J.T. (1980). Competition effects within mixed stands. In "*Opportunities for increasing crop yields*" Edited by Hurd, R.G., Biscoe, P.V. and Dennis, C. Pitman Publishers, London p. 219-231.
- SPITTERS, C.J.T. and BERGH, J.P. VAN DEN (1982). Competition between crops and weeds. A systems approach. In "*Biology and Ecology of Weeds*". Edited by Holzner, W. and Numata, N. Monographie, Biologicae, Junk Publications, The Hague, p.137-147.
- SPRAGUE, V.G. (1943). The effects of temperature and daylength on seedling emergence and early growth of several pasture species. *Proceedings of the Soil Science Society of America*. 1943. p. 287-294.
- STADLER, L.J. (1921). Experiments in field plot technique for the preliminary determination of comparative yields in small grains. *University of Missouri, Agricultural Experiment Station Research Bulletin*. 49: 78p. (Cited by Spitters 1979).
- STAPLEDON, R.G. and DAVIES, W. (1927). Seed mixture problems. 3. Establishment in relation to the drawing up of seed mixtures - being general summary of the evidence from garden and field trials. *Welsh Plant Breeding Station Bulletin*. H5: 64-68.

- STAPLEDON, R.G. and DAVIES, W. (1928). Seed mixture experiments with special reference to the influence of environmental factors. *Welsh Plant Breeding Station Bulletin Series H8*: 7-81.
- STAPLEDON, R.G., DAVIES, W. and BEDDOWS, A.R. (1927). Seed mixture problems: Soil germination, seedling and plant establishment with particular reference to the effects of environmental and agronomic factors. *Welsh Plant Breeding Station Bulletin. Series H6*: 5-38.
- STEEL, R.G.D. and TORRIE, J.H. (1981). *Principles and procedures of statistics*. McGraw Hill Book Company Inc. London 481p.
- STERN, W.R. (1960) The light factor in grass and clover swards. Ph.D Thesis, University of Adelaide, Adelaide, Australia.
- STERN, W.R. (1962). Light measurements in pastures. *Herbage Abstracts*. 32: 91-96.
- STERN, W.R. (1965). The effect of density on the performance of individual plants in subterranean clover swards. *Australian Journal of Agricultural Research*. 16: 541-555.
- STERN, W.R. and DONALD, C.M. (1962). Light relationships in grass clover swards. *Australian Journal of Agricultural Research*. 13: 599-614.
- STEVENSON, D.S. (1967). Effective soil volume and its importance to root and top growth of plants. *Canadian Journal of Soil Science*. 47: 163-174.
- STEWART, G. and HULL, A.C. (1949). Cheat grass (*Bromus tectorum* L.) - An ecological intruder in Southern Idaho. *Ecology*. 30: 58-74.
- THOMAS, H. and DAVIES, A. (1978). Effect of shading on the regrowth of *Lolium perenne* in the field. *Annals of Botany*. 42: 705-715.
- THOMAS, M.T. (1945). The establishment and early management of sown pastures (Great Britain). In the establishment and early management of sown pastures. *Imperial Bureau of Pasture and Forage Crops Bulletin*. No. 34. p. 22-47.
- THOMAS, N. and STEPPLER, H.A. (1970). Intraspecific competition in timothy (*Phleum pratense* L.) and orchard grass (*Dactylis glomerata* L.). *Proceedings of the 11th International Grassland Congress*. 1970. p. 668-672.
- THOMAS, R.L. (1966). The influence of seed weight on seedling vigour in *Lolium perenne*. *Annals of Botany*. 30: 111-122.
- THOMAS, V.J. (1970). A mathematical approach to fitting parameters in a competition model. *Journal of Applied Ecology*. 7: 487-496.
- THOMSON, A.J. (1970). Analysis of yield from a competition trial with perennial ryegrass. *Journal of the British Grassland Society*. 25: 309-313.

- TINNIN, R.O. (1972). Interference or competition? *American Naturalist*. 106: 672-675.
- TISDALE, E.W. (1947). The grasslands of the southern interior of British Columbia. *Ecology*. 28: 348-382.
- TORSSEL, B.W.R. and NICHOLLS, A.O. (1976). A comparison between two models for plant competition. *Australian Journal of Ecology*. 1: 29-35.
- TRENBATH, B.R. (1974a). Biomass productivity of mixtures. *Advances in Agronomy*. 26: 177-210.
- TRENBATH, B.R. (1974b). Neighbour effects in the genus *Avena*. 2. Comparison of weed species. *Journal of Applied Ecology*. 11: 111-125.
- TRENBATH, B.R. (1974c). Application of a growth model to problems of the productivity and stability of mixed swards. *Proceedings of the 12th International Grassland Congress*. p.546-558.
- TRENBATH, B.R. (1975). Neighbour effects in the genus *Avena*. 3. A diallel approach. *Journal of Applied Ecology*. 12: 189-200.
- TRENBATH, B.R. (1976). Plant interactions in mixed crop communities. In "*Multiple Cropping*". Edited by Papendick, R.I. et al., A.S.A. Special Publication No. 27 p. 129-170.
- TRENBATH, B.R. (1978). Models and interpretation of mixture experiments. In "*Plant relations in pastures*". Edited by Wilson, J.R. C.S.I.R.O., Melbourne. p. 145-162.
- TRENBATH, B.R. and HARPER, J.L. (1973). Neighbour effects in the genus *Avena*. 1. Comparison of crop species. *Journal of Applied Ecology*. 10: 379-400.
- TRENBATH, B.R., ELBERSE, W.TH and BRAAKHEKKE, W.G. (1977). Competition for water and light in mixed plant communities. *Annual Report, Research School of Biological Sciences, Australian National University, Canberra*. p. 61-62.
- TROUGHTON, A. (1956). Studies on the growth of young grass plants with special reference to the relationship between the shoot and root systems. *Journal of the British Grassland Society*. 11: 56-65.
- TROUGHTON, A. (1957). *The underground organs of herbage grasses*. Bulletin 44, Commonwealth Bureau of Pasture and Field Crops., Commonwealth Agricultural Bureau 163p.
- TROUGHTON, A. (1960). Further studies on the relationship between shoot and root systems of grasses. *Journal of the British Grassland Society*. 15: 41-47.
- TUKEY, H.B. (Jr) (1969). Implications of allelopathy in agricultural plant science. *Botanical Review*. 35: 1-16.

- TUKEY, H.B. (Jr). (1970). The leaching of substances from plants. *Annual Review of Plant Physiology*. 21: 305-324.
- TURNER, N.C. and BEGG, J.E. (1978). Responses of pasture plants to water deficits. In "*Plant relations in pastures*". Edited by Wilson, J.R. C.S.I.R.O., Melbourne. p. 50-66.
- VALLIS, I. (1978). Nitrogen relationships in grass/legume mixtures. In "*Plant relations in pastures*". Edited by Wilson, J.R. C.S.I.R.O., Melbourne. p. 190-201.
- VARTHA, E.W. (1975). Comparative annual and seasonal growth of three ryegrass varieties and cocksfoot at Lincoln, Canterbury. *N.Z. Journal of Experimental Agriculture*. 3: 319-323.
- VARTHA, E.W. (1977). Comparative growth of "Grasslands Matua" prairie grass, 'S23' ryegrass, an experimental cocksfoot and "Grasslands Kahu" timothy at Lincoln, Canterbury. *N.Z. Journal of Experimental Agriculture*. 5: 137-141.
- VEEVERS, A. (1978). *Experimental design for observing variety competition* - Paper presented to the British region of the Biometrics Society. University of Liverpool - Department of Computational and Statistical Science. 18p.
- VEEVERS, A. and BOFFEY, T.B. (1975). On the existence of levelled beehive designs. *Biometrics*. 31: 963-967.
- VEEVERS, A. and ZAFAR-YAAB, A. (1980). Balanced designs for two component competition experiments on a square lattice. *Euphytica*. 29: 459-464.
- WALKER, T.W. and ADAMS, A.F.R. (1958). Competition for sulphur in a grass-clover association. *Plant and Soil*. 9: 353-366.
- WALKER, T.W., ORCHISTON, H.D. and ADAMS, A.F.R. (1954). The nitrogen economy of grass-legume associations. *Journal of the British Grassland Society*. 9: 249-274.
- WARREN, J.F. and LILL, W.J. (1975). The influence of ariel shields on plant growth environment in competition experiments. *Annals of Botany*. 39: 1141-1142.
- WATKIN, B.R. and CLEMENTS, R.J. (1978). The effects of grazing animals on pastures. In "*Plant relations in pastures*". Edited by Wilson, J.R. C.S.I.R.O., Melbourne. p. 273-289.
- WATKINSON, A.R. (1981). Interference in pure and mixed populations of *Agrostemma githago*. *Journal of Applied Ecology*. 18: 967-976.
- WEAVER, J.E. (1926). *Root development of field crops*. McGraw Hill, New York 291p.
- WEAVER, J.E. and FLORY, E.L. (1934). Stability of climax prairie and some environmental changes resulting from breaking. *Ecology*. 15: 333-347.

- WEIRSUM, L.K. (1961). Utilization of soil by the plant root system. *Plant and Soil*. 15: 189-192.
- WELBANK, P.J. (1961). A study of the nitrogen and water factors in competition with *Agropyron repens* L. Beauv. *Annals of Botany*. 25: 116-137.
- WELBANK, P.J. (1962). The effect of competition with *Agropyron repens* and nitrogen and water supply on the nitrogen content of *Impatiens parviflora*. *Annals of Botany*. 26: 361-373.
- WELBANK, P.J. (1964). Competition for nitrogen and potassium in *Agropyron repens*. *Annals of Botany*. 28: 1-16.
- WHALLEY, D.R.B., MC KELL, C.M. and GREEN, L.R. (1966). Seedling vigour and early non-photosynthetic stage of seedling growth in grasses. *Crop Science*. 6: 147-150.
- WHITE, J.G.H. (1973). Pasture establishment. In "Pastures and pasture plants". Edited by Langer, R.H.M. A.H. & A.W. Reed, Wellington. p. 129-158.
- WHITTINGTON, W.J. and O'BRIEN, T.A. (1968). A comparison of yields from plots sown with a single species or a mixture of grass species. *Journal of Applied Ecology*. 5: 209-213.
- WILDIN, J.H. and HALL, R.L. (1980). Replacement interaction diagrams in interspecific competition experiments. *Australian Journal of Ecology*. 5: 205-210.
- WILKINSON, S.R. and GROSS, C.F. (1964). Competition for light, soil moisture and nutrients during Ladino clover establishment in orchard grass. *Agronomy Journal*. 56: 389-392.
- WILLEY, R.W. (1979a) Intercropping - Its importance and research needs. Part 1. Competition and yield advantages. *Field Crop Abstracts*. 32: 1-10.
- WILLEY, R.W. (1979b). Intercropping - Its importance and research needs. Part 2. Agronomy and research approaches. *Field Crop Abstracts*. 32: 73-85.
- WILLIAMS, E.J. (1962). The analysis of competition experiments. *Australian Journal of Biological Science*. 15: 509-525.
- WILLIAMS, R.F. (1955). Redistribution of mineral elements during development. *Annual Review of Plant Physiology*. 6: 25-42.
- WILLIAMS, W. (1947). The germination and establishment of red clover under conditions of direct reseeding. *Journal of the British Grassland Society*. 2: 30-44.
- WILLIAMSON, M.H. (1957). An elementary theory of interspecific competition. *Nature (London)*. 180: 422-425.
- WILSON, G.F. (1977). "Grasslands Matua" prairie grass. *N.Z. Agricultural Science*. 11: 47-48.

- WILSON, P.W. (1940). *"The biochemistry of nitrogen fixation"*.
University of Wisconsin Press, Madison.
- WILSON, D.B. and PEAKE, R.W. (1956). Seasonal yield and nitrogen content of three grasses grown singly and in mixtures. *Canadian Journal of Agricultural Science*. 36: 221-232.
- WIT, C.T. DE. (1960). On competition. *Verslagen von Landbouwkundig Onderzoekingen*. 66.8 Pudoc, Wageningen. 82.p.
- WIT, C.T. DE (1965). Photosynthesis of leaf canopies. *Agricultural Research Reports - No. 663.*, Wageningen. pl-57.
- WIT, C.T. DE (1970). On the modelling of competitive phenomena. *Proceedings of the Advanced Study Institute, Dynamics, Numbers, Population*. Oosterbeek, Netherlands. p. 269-281.
- WIT, C.T. DE and BERGH, J.P. VAN DEN (1965). Competition between herbage plants. *Netherlands Journal of Agricultural Science*. 13: 212-221.
- WIT, C.T. DE., DJIKSHOORN, W. and NOGGLE, J.C. (1963). Ionic balance and growth of plants. *Agricultural Research Report 69.15*, Wageningen. pl-69.
- WIT, C.T. DE., TOW, P.G. and ENNIK, G.C. (1966). Competition between legumes and grasses. *Agricultural Research Report No. 687*. Pudoc, Wageningen. pl-30.
- WRIGHT, A.J. (1971). The analysis and prediction of some two factor interactions in grass breeding. *Journal of Agricultural Science (Cambridge)*. 76: 301-306.
- WRIGHT, A.J. (1975). Methods of analysis of a competition diallel in Italian ryegrass with varying mixture populations. *Journal of Agricultural Science (Cambridge)*. 84: 431-444.
- WRIGHT, L.N. (1971). Drought influence on germination and seedling emergence. In *"Drought injury and resistance to crops"*. Edited by Lawson, K.L. and Eastin, J.D. C.S.S.A. Special Publication No. 2., Crop Science Society of America. p.19-44.
- WRIGHT, D.L., BLASER, R.E. and WOODRUFF, J.M. (1978). Seedling emergence as related to temperature and moisture tension. *Agronomy Journal*. 70: 709-712.
- WRIGHT, J.L. and LEMON, E.R. (1966). Photosynthesis under field conditions 8. Analysis of windspeed fluctuation data to evaluate turbulent exchange within a sown crop. *Agronomy Journal* 58: 255-261.
- YAMADA, T. and HORIUCHI, S. (1960). On the basis of quantitative characters and the change of their distribution in a population due to interplant competition. *Proceedings of the 8th International Grassland Congress*. p. 297-301.
- YAMANE, T. (1973). *Statistics - An introductory analysis*. Harper and Row Publishers, New York.

- YODA, K., KIRA, T. and HOZUMI, K. (1957). Intraspecific competition among higher plants. 9. Further analysis of the competitive interaction between adjacent individuals. *Journal of the Institute of Polytechnics, Osaka City University* 8: 161-178.
- YODA, K., KIRA, T., OGAWA, H. and HOZUMI, K. (1963). Self thinning in overcrowded pure stands under cultivated and natural conditions. *Journal of Biology, Osaka City University*. 14: 107-129.
- ZAVITZ, C.A. (1908). The relations between the size of seeds and the yield of plants of farm crops. *Proceedings of the American Society of Agronomy*. 1: 98-105.
- ZIMDHAL, R.L. (1980). *Weed-crop competition - A review*.
Published by the International Plant Protection Centre; Oregon State University, Oregon, U.S.A. 195.p.

Examples of analysis of variance tables used in different experiments.

A1. An example of analysis of variance tables used in analysing plant characters in Experiments 1, 2 and 3 (Chapter 3).

A1.1 Analysis of variance of shoot weights per plant of cocksfoot at 4 weeks after transplanting (Experiment 2).

Variate: CF1

Source of variation	DF	S.S	SS%	MS	V.R
Reps. stratum	2	0.0040498	12.34	0.0020249	10.155
Reps Treatment stratum					
Treatment	6	0.0263683	80.36	0.0043947	22.039**
Residual	12	0.0023929	7.29	0.0001994	
Total	18	0.0287611	87.66	0.0015978	
Grand Total	20	0.0328110	100.00		

A2. An example of analysis of variance used in analysing plant characters in Experiments 4 and 5. (Chapters 4, 5).

A.2.1 Analysis of variance of tiller number per plant of ryegrass at the 5th harvest. (Experiment 5 - Chapter 5).

Variate: Rye 5

Source of variation	DF	S.S	SS%	MS	V.R
Reps stratum	1	1.4464	2.37	1.4464	7.181
Reps Treatment stratum					
Treatment	6	58.3200	95.65	9.7200	48.255**
Residual	6	1.2086	1.98	0.2014	
Total	12	59.5286	97.63	4.9607	
Grand Total	13	60.9750	100.00		

A3 An example of analysis of variance tables used in analysing plant characters in Experiment 6 (Chapter 6).

A3.1 Analysis of variance of leaf area per plant of ryegrass, prairie grass and cocksfoot at the 4th harvest.

Variate H4

Source of variation	DF	S.S	SS%	MS	V.R
Reps stratum	5	1210.1	2.10	242.0	0.351
Reps Treatment stratum					
Treatment	2	49428.5	85.90	24714.3	35.799**
Residual	10	6903.7	12.00	690.4	
Total	12	56332.2	97.90	4694.3	
Grand Total	17	57542.3	100.00		

A4. An example of analysis of variance tables used in analysing dry matter yields per plot in Experiments 1, 2, 3 (Chapter 3).

A4.1 Analysis of variance of dry matter yields per pot at the warm temperature, at the 3rd harvest.

Variate H3

Source of variation	DF	S.S	SS%	MS	V.R
Reps stratum	2	1.04581	0.90	0.52291	13.980
Reps Treatment stratum					
Treatment	11	114.31538	98.39	10.39231	277.834**
Residual	22	0.82290	0.71	0.03740	
Total	33	115.13829	99.10	3.48904	
Grand Total	35	116.18410	100.00		

A5. Regression analysis based on $\text{Log}_e y = a + \beta x$, where y = growth parameter, and x = time in days. (Experiment 4 - Chapter 4)

A5.1 Primary tiller appearance rates of ryegrass - Analysis of the monoculture.

Y variate - Log tillers (1)

	Estimate	SE	T
Constant	-0.24342	0.06353	-3.83
Time	0.22744	0.00863	26.35

Analysis of variance

Y variate - Log tillers (1)

	DF	SS	MS
Regression	1	14.7951	14.79505
Residual	22	0.4688	0.02131
Total	23	15.2639	0.66365
Change	-1	-14.7951	14.79505

% variance accounted for (r^2) = 96.8

A6. Analysis of variance of relative yield totals

A6.1 Analysis of relative yield totals of ryegrass-prairie grass combinations at the 6th harvest (Experiment 5), based on root weight per plant.

Variate RYT 6

Source of variation	DF	S.S	SS%	MS	V.R
Reps stratum	1	0.00002400	25.18	0.00002400	1.778
Reps Treatment stratum					
Treatment	2	0.00004433	46.50	0.00002217	1.642 NS
Residual	2	0.00002700	28.32	0.00001350	
Grand Total	5	0.00009533	100.00		

A7. Analysis of variance of aggressivity indices

A7.1 Analysis of aggressivity indices of prairie grass when grown with cocksfoot at the 1st harvest (Experiment 5), based on shoot weight per plant.

Variate Aggres 1

Source of variation	DF	S.S	SS%	MS	V.R.
Reps stratum	1	0.0021169	8.83	0.0021160	7.778
Reps Treatment stratum					
Treatment	2	0.0213204	88.90	0.0106602	39.169 *
Residual	2	0.0005443	2.27	0.0002722	
Total	4	0.0218647	91.17	0.0054662	
Grand Total	5	0.0239816	100.00		