THE RELATIVE INFLUENCE OF ABOVE AND BELOW GROUND COMPETITION ON THE GROWTH AND SURVIVAL OF RYEGRASS SEEDLINGS TRANSPLANTED INTO A HILL COUNTRY PASTURE.

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ABSTRACT

In many pasture improvement programmes, for example oversowing in hill country, seedling survival is influenced by competition from the existing vegetation. Competition between pasture plants occurs when resources are limited and may be for factors above or below ground, or both. Technically, the effective separation of above and below ground competition is difficult and considerable problems have been associated with previous studies. A technique developed for field studies combined the treatments of clipping herbage surrounding the transplanted seedling to prevent above ground competition and inserting a metal cylinder (root tube) into the ground to prevent below ground competition, resulting in conditions of shoot, root, full or no competition.

Ryegrass seedlings were transplanted in August 1986 into a pasture in summer dry hill country near Wanganui and subjected to shoot, root, full or no competition from the existing vegetation. The duration of the experiment was three months. The effect of competition on the growth of the ryegrass seedlings was assessed by non destructive measurements (plant height, tiller number) taken at approximately weekly intervals. On three occasions, destructive harvests were made and the dry weight of shoots and roots was recorded.

Below ground competition occurred before, and was more severe than above ground competition, as exemplified by changes in plant size. Ryegrass plants in the treatments with below ground competition were 80 % lighter, 64 % smaller and had 60 % fewer tillers than plants with either shoot competition or no competition. The distribution of plant size was highly skewed, and indicated that the stress plants encountered when subjected to below ground competition was severe. The effect of above ground competition on ryegrass growth was small except when root competition was also present. Shaded plants were usually taller than those that were unshaded. In conclusion, below ground competition, possibly for soil nutrients, was shown to be the major influence on growth and development of transplanted seedlings at the hill country site studied.

The survival of seedlings introduced into pasture was also dependent on environmental factors, especially soil moisture, and therefore important in summer dry hill country. In a second experiment during spring 1986, ryegrass seedlings were grown in tubes and transplanted into a hill pasture at Wanganui. The six treatments consisted of combinations of two planting dates, two tube lengths, two harvest dates and were arranged as a randomised complete block design Seedling survival was high over all treatments (98 %), probably because rainfall during the experimental period was high.

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Chapter 1
INTRODUCTION

Hill country farming is of major importance to New Zealand's economy in terms of land area, number of livestock carried and the volume of export meat and wool produced (Rattray, 1982). Nevertheless, the production, composition, quality and level of pasture utilisation by grazing animals, and moreover, the conversion of these to saleable products, is often capable of substantial improvement. Topographical constraints limit pasture development, renovation or improvement in steep hill country to oversowing by an aeroplane or helicopter (Lambert et al., 1985). The results of oversowing are unreliable due to the hostile conditions encountered by many seeds, these conditions include: environmental factors (mainly moisture and temperature), pest or fungal attacks and competition from the resident vegetation (Lambert et al., 1985). The experiments reported in this thesis were designed to investigate the effect of competition from the resident pasture on the survival and growth of establishing seedlings in hill country.

Many of the 'classical' competition experiments were based on the additive design (for example, Donald, 1958) or replacement design (for example, de Wit, 1960), but these were not considered appropriate. Instead, a recent technique developed by Cook and Ratcliff (1984) was used as this permitted separation of shoot and root competition between an establishing seedling and the resident vegetation. Perennial ryegrass (Lolium perenne L.) was transplanted into a hill country pasture at Wanganui, and the effect of above and below ground competition from the resident species (paspalum (Paspalum dilatatum Poir.) was of particular interest due to its high competitive ability) on ryegrass growth and development was studied. A concurrent experiment evaluated the transplanting technique and related seedling survival to environmental factors. A brief description of the growth characteristics of the species studied is given, followed by the experimental objectives.

The growth characteristics of perennial ryegrass in response to seasonal and management influences were described by Hunt and Field (1979). A survey of farmers in New Zealand by Sangakkara et al. (1982) showed that ryegrass was the most popular grass species used because 98 % of all seed mixtures incorporated one or more cultivars. Ellet, a ryegrass cultivar sown by 39 % of farmers (Sangakkara et al., 1982) was developed for its superior autumn and winter growth compared with older ryegrass cultivars, fast growth following rain after a dry summer period, as well as resistance to attack from Argentine stem weevil (Listronotus bonariensis (Kuschel)) (Barker et al., 1985). The cause of resistance to stem weevil was found in 1981 to be associated with the presence of an endophyte fungus (Acremonium loliae) in the ryegrass plant.

Paspalum, a perennial subtropical grass from South America was introduced to New Zealand in the early 1890's (Percival, 1977). Paspalum has a high potential for herbage dry matter production in summer because it is a C4 species and is therefore active in the warm season and resistant to drought, but is frost sensitive and dormant during the winter (Lambert et al., 1979). A survey of paspalum in New Zealand pastures by Percival (1977) indicated that the distribution limits were set by winter temperatures and in most districts, rapid growth of paspalum began in late November (range October to December) (Percival, 1977). A survey by Sangakkara et al. (1982) indicated that farmers considered the formation of a sod bound pasture (a dense mat of rhizomes and tillers at or just below the soil surface) was the least favoured characteristic of paspalum because other sward components were excluded. Thom et al. (1986a) demonstrated that paspalum offered severe competition to establishing plants due to its exceptional colonising ability, growth potential during summer and ability to withstand treading and grazing.

The experimental objectives were:

i) To determine whether above or below ground competition occurs first in the interaction between transplanted ryegrass and established paspalum plants in the field.

ii) To determine the rate of survival of ryegrass seedlings transplanted into a hill country pasture and to relate seedling survival to environmental factors.

Chapter 2 LITERATURE REVIEW

2.1 INTRODUCTION

Hill country pasture occurs throughout New Zealand and occupies 32 % of the 14 m ha sown pasture and tussock grassland (Anon, 1985). Sheep are the predominant form of livestock on hill country with lesser numbers of beef cattle and recently goats also being part of the farming system. The remaining pastoral land can be divided into the following categories: flat and rolling country (4 m ha), high country (5 m ha) and warm temperate regions incorporating some of the previous two regions (1.2 m ha) (Brougham, 1973).

Large increases in farm production from steep hill country are potentially possible because estimates suggest that stock numbers could more than double through land improvement and intensification of existing enterprises, but these changes are limited by economic and physical constraints (Chapman and Macfarlane, 1985). The main limitations to pasture growth in steep hill country are: soil fertility, soil moisture, temperature, and grazing management (Chapman and Macfarlane, 1985). Competition will occur when 'supply factors' are below the optimum level required for growth (Harper, 1977). Competition between plants may occur above and / or below ground and many experiments (for example Donald, 1958; Snaydon and Howe, 1986) have been designed to study such interactions. The experiments described in this thesis were undertaken on hill country, therefore, the review of literature will be limited to this land region and examples used will relate to pasture species wherever possible.

2.2 HILL COUNTRY

Hill country pastures occur over a wide range of soil types and climates resulting in large variations in pasture composition and production (Chapman and Macfarlane, 1985). On each farm, individual paddocks are not uniform but composed of a mixture of stock tracks / camps (1-12 ° slope), slopes (13-25 °), steep areas or banks (>26 °) and these differences influence pasture growth and species composition (Lambert et al., 1983; Chapman and Macfarlane, 1985). Stock camps are flatter areas where the animals tend to lie, especially overnight, so that high levels of nutrients (mainly nitrogen and phosphate) accumulate and annual pasture production may be in the range 20-25 t DM ha^{-1}, or equivalent to maximum lowland yields. Steep dry faces may produce less than 5 t DM $ha^{-1}yr^{-1}$, often of poor nutritive quality (Chapman and Macfarlane, 1985).

A MAF report divided hill country into two main groups according to the area; summer moist where rainfall during this period was reliable and summer dry where rainfall was variable and droughts often experienced (Thomson, 1983). Many regions of the North Island were found by Chapman and Macfarlane (1985) to be regularly affected by summer / autumn moisture deficits, including Wanganui. Within each land group, Lambert et al. (1983) showed that pasture production was altered according to the aspect, during summer and autumn herbage accumulation was greater on southern than northern facing slopes due to differences in soil moisture, even on summer moist hill country. Perennial plants may be killed by a period of severe moisture stress in summer dry or in localised areas of summer moist hill country, while others remained vegetative as moisture stress developed (Chapman and Macfarlane, 1985). Some perennial species were adapted to survive moisture stress (deep tap root, physiological mechanisms) whilst annuals avoided the summer period by existence as dormant seeds (Chapman and Macfarlane, 1985). Plant growth and botanical composition of the pasture was also influenced by temperature, north facing slopes (sunny) intercepted more radiation than south facing (shady) slopes and herbage production on the sunny face was greater than on the shady face in winter and spring because the temperature was higher and the ground warmed up more quickly. The minimum temperature required for growth of ryegrass and white clover (Trifolium repens L.) in southern North Island hill country was found to be 6-7 °C and 9 °C respectively (Chapman and Macfarlane, 1985) therefore their periods of active growth may be several weeks apart.

Botanical composition and pasture production in hill country was found by Suckling (1975), Grant et al. (1981) and Luscombe et al. (1981) to be largely determined by the nutrient status of the soil (often referred to as soil fertility), but modified by climatic conditions (temperature, rainfall), aspect, slope and management. Nitrogen deficiency was the principal nutrient limiting pasture growth in most hill country regions and many of these soils were also deficient in phosphorus (Chapman and Macfarlane, 1985). An application of fertiliser (increase in the concentration of available nutrients) led to improved seasonal and annual pasture production. As the nutrient status of the soil rose, species tolerant of low fertility (browntop (Agrostis capillaris L.), yorkshire fog (Holcus lanatus L.)) tended to decrease and those responsive to the higher levels increased (ryegrass), with a corresponding increase in productivity (Suckling, 1975; Grant et al., 1981). The changes in a browntop dominant hill pasture in response to fertiliser application were demonstrated by Luscombe et al. (1981). They found that addition of nitrogen resulted in a grass dominant pasture and of phosphate an increase in the clover content, accompanied by a reduction in the yield of sweet vernal (Anthoxanthum odoratum L.) and crested dogstail (Cynosurus cristatus L.) (normally found under conditions of low fertility) and of the weeds component. A corroborative study showed that ryegrass outyielded browntop by the greatest amount under high inputs of both nitrogen and phosphate (Grant et al., 1981).

Individual paddocks were not uniform across the hillside and it was shown, for example, by Suckling (1960) that the botanical composition of the pasture varied accordingly. The steeper sites were generally of low fertility, and supported the growth of browntop on the moister areas, and ratstail (Sporobolus africanus Poir. Robyns Tourn) / danthonia (Rytidosperma sp. Steudal) on the dry faces with varying proportions of crested dogstail, chewings fescue (Festuca rubra L.), Kentucky bluegrass (Poa pratensis L.), sweet vernal, yorkshire fog and flatweeds (mainly Hydrocotyle sp.) (Suckling, 1960; Radcliffe, 1973). Ryegrass was usually dominant on the high fertility areas such as stock tracks and camps, valley bottoms (Suckling, 1960) and on these areas browntop cover was greatly reduced (Grant et al., 1973). The disproportionately high contribution of the track and camp areas to pasture production compared to the steeper areas was evaluated by Lambert et al. (1983). The results indicated that 39, 41 and 20 % of total dry matter was accumulated on stock tracks / camps, slopes and steep areas from a surface area of 28, 43 and 29 % respectively.

2.3 COMPETITION

An overview incorporating the historical development of definitions, ideas and experiments is presented followed by a more detailed account of competition between plants for above and below ground factors.

2.3.1 Definitions

The growth rate and morphology of plants in a community is influenced at some or all stages of development by biological and physical processes often referred to as competition (Hall, 1974; Harper, 1977). Donald (1963) amalgamated two earlier definitions to form the frequently quoted phrase "competition occurs when each of two or more organisms seeks the measure it wants of any particular factor or thing and when the immediate supply of the factor or thing is below the combined demand of the organisms". Harper (1961) felt that the word 'competition' should not be used because of its association with human activities such as sport, games and economics. Plant scientists associated with agronomy, ecology, genetics and evolution have very different preconceived ideas of the definition, therefore Harper suggested 'interference' should be used instead. The term interference is also imprecise and has not been subject to widespread use in the literature. Competition, if used according to Donald (1963) is well suited to a clearly defined set of biological situations and there is no reason to discontinue the use of this simple and effective term. There are often additions to scientific jargon, probably the most recent with respect to competition / ecological studies is the division between one sided or 'asymmetric' competition for light and two sided competition for nutrients (Weiner, 1985).

2.3.2 Competitive relationships between plants

Competition between plants can occur both above and below the ground, the outcome being dependent on the relative abilities of each species to capture and utilise available resources. The factors for which competition between plants can occur are water, nutrients, light, carbon dioxide, and perhaps, oxygen with the first three being most commonly deficient (Donald, 1963). These are described by Harper (1977) as 'supply factors' or consumable resources of the environment required for plant growth. 'Conditioning factors' are those which modify the plant's environment but are not directly used by the plant, for example, temperature, defoliation, presence of grazing animals and soil microbiological effects (Harper, 1977). The difficulties of isolating competitive effects in the field into individual components led de Wit (1960) to group these resources as 'biological space' and to identify competition between grasses, cereals and other crop combinations for biological space within their plant communities. The term 'space' evaded the need to pursue and recognise the real factors for which competition is occuring and its use has been discouraged (Donald, 1963). Supply factors are finite 'pools' of material so that "if the pool is of limited volume, or if it is subject to intermittent depletion by the competing plants, then the successful competitor is the plant which draws most rapidly from the pool, or which can continue to withdraw from the pool when it is at a low ebb or when its contents can no longer be tapped by other plants" (Donald, 1963).

Competitive relationships between plants occur due to 'neighbour effects' caused by other plants in the same environment (Harper, 1977). These effects can develop due to the presence of i) the same species (intraspecific competition) ii) different species (interspecific competition) and iii) within an individual plant (intraplant competition). Examples of these different types of competition in a hill pasture are between i) ryegrass plants ii) ryegrass and browntop plants iii) tillers within each ryegrass or browntop plant. At low plant densities there is unlikely to be any interference in the growth of one plant by another (Donald, 1963). Plants grown at high densities were smaller and of lower dry weight than those grown at the low density because competition for supply factors occurred early in their development (Donald, 1963; Harper, 1977; Snaydon and Howe, 1986).

Competitive interactions for a single growth requirement may occur in a specific situation, but generally competition between plants develops for several factors. The existence of one limiting growth factor may enhance the utilization of another to increase the growth of a component species and conceal the actual process of interference (Donald, 1963). Plant growth may be depressed by allelopathy - the exudation of harmful chemicals from one plant or species which inhibits the growth or may kill a neighbouring plant of the same or different species (Harper, 1977). Allelopathy is technically very difficult to research see Harper (1977) for a critical discussion.

2.4 INFLUENCE OF ABOVE GROUND FACTORS ON PLANT GROWTH

2.4.1 Light

Solar radiation largely governs the yield of a particular plant population and becomes the limiting factor to production when adequate supplies of water and nutrients are available. Production may be restricted in many situations due to inadequate utilisation of light after the increased use of fertilisers and irrigation, but even where there is a shortage of water or nutrients (as occurs for most of the world's crops) competition for light remains a factor of major importance (Donald, 1958, 1963). There is much confusion in the literature about the units that should be used for measurement of solar radiation, some definitions have been provided here. Solar radiation is propagated as waves of particles called photons and plants probably respond to light beyond the currently accepted range of 400-700 nm (Smith, 1982). Radiation has been incorrectly referred to in units of illumination (lux, foot candle), or total energy (Einstein) but is now superceded by photosynthetic photon flux density (PPFD) (photons / unit area / unit time) (Salisbury and Ross, 1978; Smith, 1982). Light quality perception depends on a comparison of the number of photons in two or more discrete wavebands and spectral data is now specified as the ratio of photon fluence rate in the red (R) to that in the far red (FR) range (Smith, 1982).

Competition for light

Light is intercepted by foliage in the plant canopy and a successful plant has leaves distributed in an advantageous position relative to that of its competitor (Donald, 1963). Solar radiation becomes reduced in energy and altered in spectral composition as it passes through the plant canopy by transmission and reflection and sometimes severe competition for light may occur in pastures (Ludlow, 1978; Rhodes and Stern, 1978). Competition for light occurs if the supply is reduced, for example, when one leaf or photosynthetically active organ overshadows another, with a corresponding reduction in photosynthetic rate of the shaded part. Shading may occur within an isolated plant (intraplant competition) and would be severe because light is not redistributed unlike other factors such as nutrients or water (Donald, 1961). During plant growth the lower leaves become shaded and may die if light levels are below the compensation point. The compensation point is the light intensity at which photosynthesis balances respiration and the net carbon dioxide exchange is zero (Salisbury and Ross, 1978). An increase in light intensity allows leaves lying deeper within the canopy to achieve a positive balance of photosynthesis over respiration (Donald, 1963).

Effect of shading on plant growth and development

The immediate response to shading is a reduction in leaf net photosynthetic rate due to decreased solar radiation. A further reduction results in modification of the photosynthetic and respiratory metabolism, hence the relative growth rate (Ludlow, 1978; Smith, 1982). Experiments to determine the effects of shading on the growth and development of plants have been carried out under a wide range of conditions: comparison of artificially shaded versus unshaded plants in controlled environment or glasshouse (Mitchell, 1953; Mitchell and Coles, 1955; Ludlow et al., 1974), clipped versus unclipped pastures in the field (Harris and Thomas, 1970; Cook and Ratcliff, 1984; Thom et al., 1986c), and in response to increased density (Rhodes, 1968a). Shaded plants allocated a greater proportion of dry weight to leaves and the leaf area ratio (leaf photosynthesis : leaf respiration) increased because the leaves were larger and thinner (Mitchell and Coles, 1955; Ludlow et al., 1974; Ludlow, 1978) probably partly as a result of increased leaf width (Mitchell, 1953; Rhodes, 1968a). The distribution of carbon to shoots at the expense of roots and reduced carbon balance increased the susceptibility of shaded plants to defoliation and environmental stress (Ludlow, 1978).

The rate of leaf appearance in ryegrass was lower when plants were shaded than unshaded and declined with a further decrease in irradiance levels (Mitchell and Coles, 1955), although Rhodes (1968a) found that it was unaffected by shading in four other grass species. The rate of tillering in grasses and branching in legumes was shown to be reduced by shading because the slow rate of leaf appearance provided less leaf axil sites from which tillers could develop and their subsequent growth was also restricted (Ludlow, 1978). The number of tillers per plant was reduced by shading treatments (Mitchell, 1953; Mitchell and Coles, 1955; Ludlow et al., 1974) analogous to an increase when the surrounding vegetation was clipped (Cook and Ratcliff, 1984; Thom et al., 1986c).

A marked reduction in the R : FR compared to daylight has been recorded under vegetation canopies (Smith, 1982). Reduced light quality affected plant growth and development: it promoted stem elongation, reduced leaf size and thickness, inhibited tillering or branching, decreased dry matter production of the whole plant (particularly the roots) and induced flowering (Ludlow, 1978). Shaded or crowded plants were taller than isolated unshaded plants as a result of longer internodes mediated by the phytochrome response (Ludlow, 1978) and shown experimentally (for example, Cook and Ratcliff, 1984; Thom et al., 1986c). It is important not to be confused by the changes in plant growth associated with flowering such as: cessation of leaf production on initiated tillers, reduction in tillering rate, stem elongation and inflorescence development (Jewiss, 1972). Few experiments have measured plant roots, but shading lowered the root : shoot ratio as a consequence of increased shoot growth (Ludlow, 1978) and reduced root weight per tiller in tropical grasses, and also in unclipped compared to clipped pastures (Ludlow et al., 1974; Thom et al., 1986c).

The characters which confer an ability to compete for light must be related to their ability to severely shade neighbouring plants (Rhodes and Stern, 1978). Plant height is probably the most important single attribute determining competitiveness for light (Ludlow, 1978). Plants with preferential access to radiation grow faster and improve their position relative to their competitors whereas shaded plants are disadvantaged by the reduced quantity and quality of radiation.

2.4.2 Carbon dioxide and oxygen

The concentration of carbon dioxide in the atmosphere is 0.03 % and the gas moves to the leaf surface by diffusion and turbulent transfer. The photosynthesising parts of the plant deplete the immediate neighbourhood of carbon dioxide. Competition will occur if carbon dioxide is in short supply and not replaced readily from the external atmosphere (Donald, 1963). Experiments have shown that carbon dioxide depletion may become a problem in dense plant populations in still weather (Donald, 1963; see Harper, 1977) but was unlikely to occur in pastures where grazing and wind movement combine to allow good redistribution of carbon dioxide. The supply of oxygen to the above ground parts of plants is unlikely to become deficient because both the mobility in the gaseous phase and concentration (about 20 %) are high (Harper, 1977).

2.5 INFLUENCE OF BELOW GROUND FACTORS ON PLANT GROWTH

2.5.1 Nutrients

Each new cell requires regulated amounts of mineral nutrients for growth, only some of which are obtained by retranslocation from older senescing parts of the plant. Consequently a net increase in the size of the plant must depend on the acquisition of appropriate quantities of mineral constituents by the roots (Clarkson and Hanson, 1980). These authors concluded that dependent on nutrient availability, transport systems in nature have a high affinity for their ions and the quantity of material absorbed is regulated by the quantity required irrespective of the energy cost involved. An excellent review article describes the properties of each nutrient element essential for plant growth (Clarkson and Hanson, 1980). Nutrient uptake is affected by factors apart from the supply, perhaps the most obvious is the size of the root system, but also temperature, oxygen availability, competing ions, water stress, rate of transpiration, and possibly allelopathy (Nye and Tinker, 1977). Uptake is not restricted to certain areas of the root surface although the movement of nutrients across the cortex by apoplastic or symplastic transport may change as the root ages (Clarkson and Hanson, 1980).

In New Zealand, pasture growth on most hill soils is likely to be limited by nutrients (Lancashire, 1984) due to: a lack of nutrients in the parent material, or strong adsorbtion onto the soil surface, or depletion by environmental conditions (for example, high rainfall leaches nutrients, especially nitrate). The supply of nutrients to the root surface depends on the concentration in the soil solution. This concentration is reliant on the buffering power of the soil (capacity of exchangeable pools to replenish the soil solution as nutrients are absorbed) and the rate of nutrient movement to the root surface by diffusion or mass flow (Nye and Tinker, 1977). Nutrient movement within the soil is either by mass flow of the soil solution towards the root surface as a result of the transpiration stream or by diffusion into the depleted root zone. Some ions (HPO_4^- > NH_4^+ > K^+) are readily adsorbed onto soil colloids and are present in such low concentrations in the soil solution that the rate of diffusion to the root surface determines uptake and is usually inadequate for optimum plant growth (Nye and Tinker, 1977; Chapin, 1980). Chapin (1980) concluded that soil processes form the main constraint to nutrient absorption by the root. The response of plants to varying concentrations of phosphate has been considered in some detail and response to nitrogen is probably similar although, in hill country both nitrogen and phosphate restrict pasture growth.

Studies by Barrow (1975) and Fox et al. (1986) demonstrated that there were minimum concentrations from which roots were able to absorb phosphate from the soil solution but also upper limits or saturation values (point where no additional phosphate was accumulated by plants when the external concentration was increased). More phosphate in solution was required to reach the saturation value for subterranean clover (Trifolium subterranean L.) than for annual ryegrass (Lolium rigidum Gaudin) (Barrow, 1975) and for white clover than for perennial ryegrass roots (Fox et al., 1986) therefore, the minimum concentration for absorption may also vary between species. That the nutrient requirement of plants varied during the different stages of growth and development was shown in wheat (Triticum aestivum L.) by Erdei et al. (1986). An indication of marked differences between species in the amount of phosphate required to produce maximum yield was found by Jackman and Mouat (1972), Parfitt et al. (1982) and Mouat (1983b) where clover appeared less efficient than grass in its response to phosphate. From these results it appeared that the differences between species in response to applied phosphate were large enough to strongly influence the botanical composition of the pasture and therefore fertiliser requirements.

Competition for nutrients

Competition between roots depends on their density in the soil, pattern of distribution and nutrient availability. Very limited data is available about root systems in pastures (Davidson, 1978). Relatively mobile nutrients (NO_3^-, SO_4^{2-}) are obtained from the whole volume of soil within the major part of the root system, whilst the more immobile nutrients (P, Zn, perhaps K) are acquired from small volumes of soil adjacent to each root or root hair surface (Bray, 1954). Competition for mobile nutrients occurs at a much lower root density than for immobile nutrients because depletion shells overlap (Nye and Tinker, 1977).

Nutrients are rarely evenly distributed with depth in the soil and it is possible that the different root morphologies of different plant species allow spatial avoidance in areas of conflicting soil exploration (Harper, 1977 from Weaver, 1919). These observations were in contrast to results from an experiment with browntop and white clover by Jackman and Mouat (1972) where 80 % of the total root activity for phosphate uptake of both species occurred in the top 2.5 cm of soil. Browntop reduced the growth of white clover indicating that competition for phosphate probably occurred, therefore the root systems of the two species were not spatially separated. Grass was found to have a finer root system (root length per unit weight) and longer root hairs than clover (Evans, 1977) and perhaps this gave a competitive advantage in nutrient uptake to the grass by allowing prior access to the available phosphate. In an establishing plant association, timing of growth may contribute to spatial avoidance, for example, Eagles (1972) suggested that one population of cocksfoot (*Dactylis glomerata* L.) may have exploited nutrients in successive soil horizons in advance of the other population.

Effect of nutrient shortage on plant growth and development

Under conditions of low nutrient availability (mainly nitrogen and phosphate in pastures), translocation of nutrients to the shoot is reduced and biomass is allocated to the root system in preference to the shoot system because the roots become a stronger sink for carbohydrates (Clarkson, 1985). An increase in root : shoot ratio as a result of low nutrient levels was found for New Zealand native species (Chapin et al., 1982), semi natural populations of white clover (Caradus, 1983), other pasture legumes (Hart et al., 1981) and nine pasture species (Mouat, 1983a). Differences in root : shoot ratio between species were found by Hart et al. (1981) and Mouat (1983a), and those that increase relative root growth under conditions of low phosphate would have a competitive advantage . Such a mechanism was found for browntop but not white clover in a study by Mouat (1983a) and this difference could be a considerable factor influencing the limitation of clover growth in hill country pastures under low phosphate supply.

Modification of the root system in response to a change in the nutrient concentration is of considerable practical importance since the deposition of excreta from the grazing animal or addition of fertiliser increases the nutrient status of the soil. Extreme clumping of roots may occur in spaces between impenetrable clods or around a high concentration of nutrients near a fertiliser granule, but is counterbalanced by reduced growth in other zones (Nye and Tinker, 1977). Experiments conducted on barley (Hordeum vulgare L.) under controlled laboratory conditions by Drew and Saker (1978) showed that the number of lateral roots and their rate of extension was considerably increased in response to a localised supply of phosphate and sufficient uptake occurred from this region to supply the remainder of the root system. The mechanism that brings about these localised responses to increased external nutrient concentrations is not fully understood (Scott Russell, 1977).

2.5.2 **Water and oxygen**

In soil, water and air occupy the spaces between the organic and mineral matter. Soil becomes waterlogged if drainage is impeded or is heavily textured and located in a wet area because the pores remain full of water and air is excluded (Simpson, 1983). Plant death may result from the anaerobic conditions due to build up of toxic gases and asphyxiation of roots. Under field conditions variations in water supply are frequently the major cause of differences in the distribution of roots, particularly the depth they attain in the soil. Plants have shallow root systems when dependent on current rain that does not penetrate deeply into the soil (Scott Russell, 1977) and plants are very sensitive to changes in their internal water status. The most obvious effect is a reduction in total herbage production (Harris and Chu, 1985) but even under relatively mild stress there is a reduction in leaf extension and under severe stress the above ground herbage will be killed. Quite short periods of warm, dry weather can cause large restrictions in the absorption of nutrients near the soil surface. Under such conditions the soil surface dries as a result of evapotranspiration and nutrients are unable to move due to breakage of the soil solution continuum (Scott Russell, 1977).

Many of the conditions that govern the availability of water as a resource for plant growth are similar to those affecting the availability of nutrients and are not repeated here. The growth of roots relative to shoots was increased by deficiencies of available moisture, nitrogen and phosphate in the soil (Davidson, 1969). The flow paths of water and hence nutrients are likely to be unevenly distributed among individuals and greatest towards plants that have the greatest growth so that the water resources will be used at different times, drawn from different zones in the soil, or both (Harper, 1977).

2.6 COMPETITION EXPERIMENTS

2.6.1 'Classical' experiments

Man has been aware of competition among plants since the early days of agriculture (Donald, 1963). For many decades plant ecologists have studied competition in natural populations, with much of this work being descriptive rather than experimental (Donald, 1963). Over the last 30 years a more quantitative approach has been taken in relation to studies of annual crops and pastures.

In 1960, de Wit devised a model to study the competitive abilities of plants in a mixture, based on a quantitative scale (de Wit, 1960). A mixture of two species is the simplest model for experimental study and two basic experimental designs have been used in classical competition studies where results are usually expressed as plant yield (seeds or dry matter) (Harper, 1977). First, the additive design where two species are grown together, one at a standard density the other at a range of densities, for example, to represent a weed invading a crop. Caution should be used in interpretation of these experiments because both the proportional composition and density of the mixture are changed and their effects may be completely confounded (Harper, 1977). Second, the replacement series or substitutive design where two species are sown in varying proportions while maintaining a constant overall density. These experiments are elegant for the study of plant interactions involving two species but have drawbacks because most plant populations that change in proportion over time also change in density (Harper, 1977). Results from substitution experiments (competitive ability of a species) are best illustrated by replacement diagrams (de Wit, 1960), the interpretation of these has been clearly explained by Harper (1977). Other terms which describe the competitive relationship between two species in a mixture compared to the monoculture include: relative crowding coefficient (aggressiveness), relative yield total, relative replacement rate and ratio diagrams (de Wit, 1960) and are explained by Harper (1977).

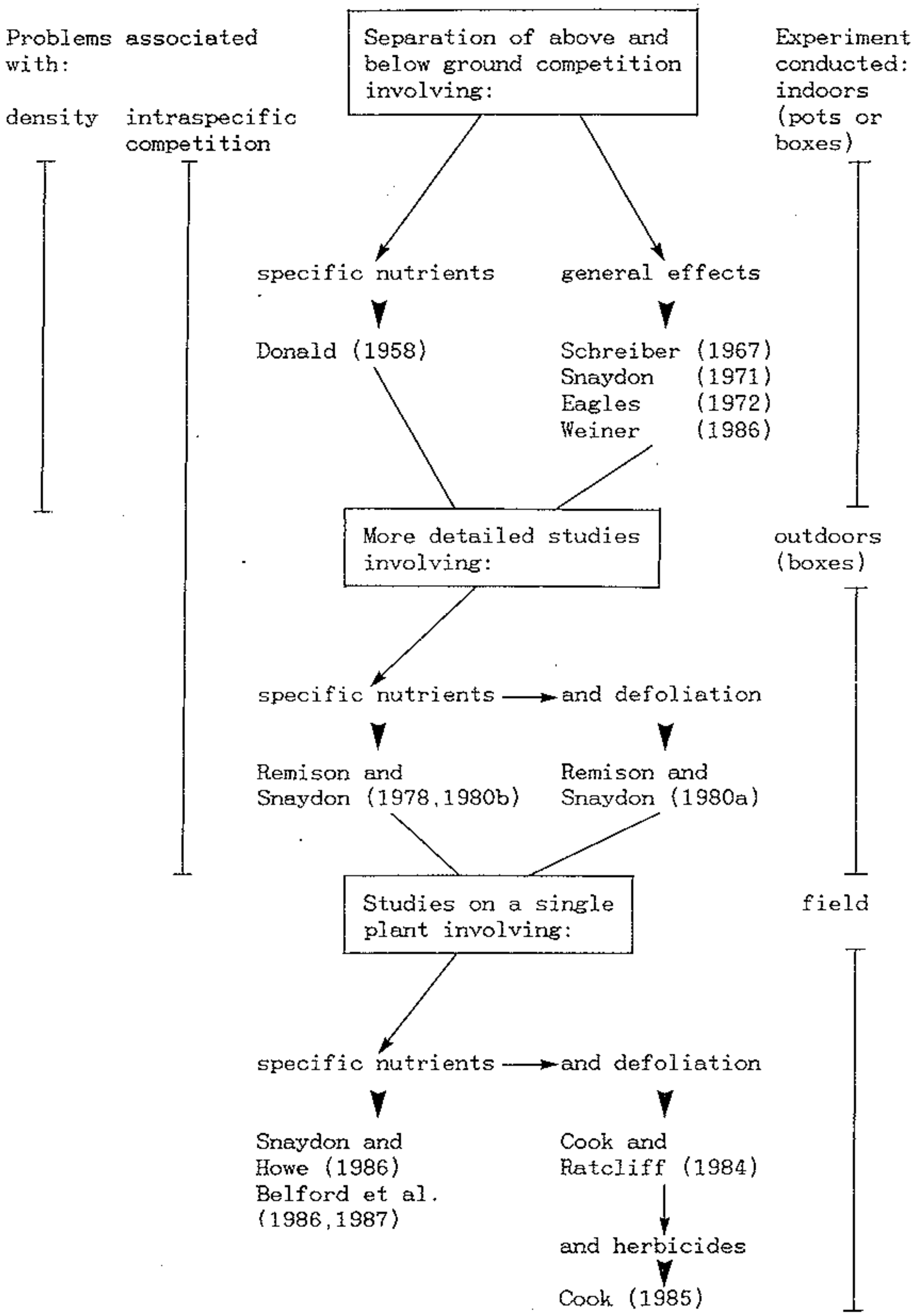
2.6.2 Competition experiments studying above and below ground interactions

The original model proposed by de Wit (1960) referred to competition for 'space' without attempting to define the limiting factors. Over the last 30 years experiments have been designed to quantify competition between and within plants for specified limiting factors or resources. A search for more precision in defining the interaction of two species in competition for limiting resources was initiated by the work of Donald (1958) who pioneered a study of competition between plants for two defined factors (light and nitrogen).

Donald (1958) attempted to separate the individual and interacting effects of competition for light and a nutrient through the use of aerial and soil partitions (see Table 2.1). The partitions in the pot were arranged so that competition between plants occurred for light, nutrients, light and nutrients or there was no competition. Schreiber (1967) grew plants in rows in boxes to study weed competition in forage legume establishment. Both Donald's and Schreiber's experiments were criticised by Eagles (1972) due to the problem of density effects associated with the additive design, similarly that by Weiner (1986), because the abundance of environmental resources per plant was reduced as well as permitting competition. Modification of the original technique resulted in a similar experiment using aerial and soil partitions except that the same number of plants were grown in each compartment (Snaydon, 1971; Rennie, 1974). Rows of plants have been sown in boxes to create a simulated pasture, with aerial and soil partitions to separate competition as described by Donald (1958). This variation of the original technique (see Table 2.1) was used to study: competition between two populations of cocksfoot (Eagles, 1972), yield and seasonal changes in root competitive ability among four grass species (Remison and Snaydon, 1978), effect of defoliation and fertilisers on root competition between cocksfoot and perennial ryegrass (Remison and Snaydon, 1980a), and to compare shoot and root competition between cocksfoot and ryegrass (Remison and Snaydon, 1980b).

The technique has been used to investigate the effect of specific limiting nutrients: of nitrogen (Donald, 1958), of nitrogen and phosphate (Remison and Snaydon, 1980a), of nitrogen, phosphate and potassium (Remison and Snaydon, 1978, 1980b) or of defoliation (Remison and Snaydon, 1980a). These and other studies, for example, Rhodes (1968c) indicated that the effects of root competition were usually greater than those of shoot competition, at least during the first few months after planting.

Table 2.1: Historical development of experimental designs and techniques: separation of above and below ground competition between plants.



Root competitive ability, changes in which were due in part to the nutrients applied, was determined from the experiments by Remison and Snaydon (1978, 1980a, 1980b) where different species of plants were grown in monocultures and mixtures. The greater root competitive ability of ryegrass at high nutrient levels compared to yorkshire fog, sweet vernal (Remison and Snaydon, 1978) and cocksfoot (Remison and Snaydon, 1980a) was associated with the abundance of ryegrass on highly fertile field soils. Similarly, for the greater root competitive ability between yorkshire fog and cocksfoot, also for yorkshire fog collected from a heavily fertilised versus an unfertilised pasture (Remison and Snaydon, 1980b). Root competitive ability was reduced by defoliation (Remison and Snaydon, 1980a) when perennial ryegrass and cocksfoot were grown in a mixture, but the effect was modified by application of nitrogen fertiliser. Many experiments have been undertaken in the glasshouse or controlled environment because isolation of competitive effects in a field situation is difficult.

Recent studies of plant interactions have combined the additive design (Donald, 1958) and the subtitution design (de Wit, 1960) techniques (Snaydon, 1979). Nevertheless, there have been two major areas of criticism of many of the competition experiments undertaken similar to that of Donald (1958) and others. These criticisms revolve around the lack of recognition of intraspecific competition and the confounding effects of shoot and root partitions.

Intraspecific competition

A major problem in all these experiments that appears, on the whole, not to have been recognised, is where interspecific (or interpopulation (Eagles, 1972)) competition has been separated yet intraspecific (intrapopulation) competition remains (see Table 2.1). Milthorpe (1961), referring to the effects of competition between species states that "many of the arguments advanced here also apply to intraspecific competition, the distinction between inter and intraspecific competition is rather artificial as both always operate in a mixed association and the differences are usually of a degree rather than a kind". Some degree of doubt must therefore be attached to results from previous studies where the confounding effect of intraspecific competition was present.

Aerial and soil partitions

Inevitably, some artificiality will be involved in an experiment designed to gain a quantitative measure of competition for light and nutrients on plant growth. Pot cultures force the plants to use the same limited root space and soil resources whereas in the field different root zones may be penetrated, also the use of partitions introduce serious complications (Harper, 1977). Researchers have been criticised for using aerial partitions to control the spread and intermingling of shoots in studies of competition because the partitions could influence the environment and hence growth rate of plants by changing air flow or the radiation climate (Warren and Lill, 1975). Aerial partitions when tested by Warren and Lill (1975) were found to influence evaporation and light conditions. Therefore, they concluded that shoot interaction had not been defined from experiments using aerial shields. Materials used for aerial partitions have included glass (Rhodes, 1968c; Eagles, 1972) and metal (Donald, 1958; Schreiber, 1967; Snaydon, 1971). To prevent reduction of light quantity and quality, a reflective surface was attached to the metal partition (Schreiber, 1967) or a reflective aluminium material used (Remison and Snaydon, 1980a, 1980b; Snaydon and Howe, 1986). Partitions below the ground that prevent two root systems from intermingling also divide soil resources (nutrients, water) therefore, a vigorous plant would be deprived of potential supply factors (Harper, 1977). Some problems associated with the use of soil partitions were illustrated by Hall (1978) with reference to competition for nutrients between a grass / legume mixture. However, results appeared variable because an experiment on cotton (*Gossypium hirsutum* L.) indicated that plant growth was not affected by root partitions (Rennie, 1974).

Oversowing and field competition techniques

In a newly sown pasture, competition will occur once the plants are large enough to interact by the proximity of one shoot or root system to its neighbour. The oversowing of pasture species into undisturbed pasture has the potential to reduce establishment costs markedly and allow pasture improvement in areas such as steep hill country where conventional cultivation is impracticable (Lambert et al., 1985). Successful establishment of the introduced species will depend on the seed reaching a favourable site, its ability to germinate and subsequent growth rate compared to the growth rate and proximity of neighbouring established plants (Harper, 1977). Competition from existing vegetation is a major factor limiting the survival of seedlings established by oversowing methods where seedlings are required to establish and compete with an existing plant community containing a developed root system (Macfarlane, 1987). Cook and Ratcliff (1984) devised a method for studying shoot / root interactions suitable for field conditions which created minimal soil and root disturbance and had little effect on the growth of existing plants (see Table 2.1). Competition between roots was prevented by thin walled steel tubes driven into soil between the native species and seedlings of the introduced pasture species were grown within these tubes. Above ground competition was present or absent depending on whether the native pasture was unclipped or clipped. The various combinations of the treatments imposed gave conditions similar to those of Donald (1958) where competition occurred between shoots, roots, shoot and roots or there was no competition. The use of steel tubes was evaluated in the studies by Cook and Ratcliff (1984) and Cook (1985) and was found to be a suitable method for separation of root competition between seedlings and established plants.

The relative importance of above and below ground competition from established plants on the growth of seedlings under well watered conditions and with or without fertiliser was determined by Cook and Ratcliff (1984), and Cook (1985) (see Table 2.1). Their experiments showed that root competition was the main factor that determined the growth of green panic

(*Panicum maximum* Jacq. var. *trichloglume* Eyles ex Robyns) seedlings in a native pasture of *Heteropogon contortus*. Both leaf and tiller production were found by Cook and Ratcliff (1984) to increase following clipping but only where root competition was controlled with the use of root tubes, similarly, Cook (1985) showed that after an application of herbicide to reduce root competition from the native pasture, leaf and tiller production was increased. There are considerable technical problems associated with the sampling of roots apart from being immensely time consuming, nevertheless, it was unfortunate that root measurements were not an integral part of the competition studies by Cook and Ratcliff (1984) and Cook (1985).

The paucity of information about root growth in the field was realised and acted upon by Belford *et al*. (1986). These workers developed a technique for collection and isolation of intact root and shoot systems in field grown winter wheat similar to the root tubes used by, for example, Cook and Ratcliff (1984). Square hollow sections were constructed so that one side could be easily removed to provide access to the soil core and intact root system after the section was removed from the ground. The technique was labour intensive but gave considerably more information about individual root axes and their branching pattern down the profile than measurement of bulk root systems from conventional soil cores. The usefulness of this technique for field sites was demonstrated by Belford *et al*. (1986) because the physical and chemical environment inside the section was similar to that outside.

2.6.3 **Concluding comments on experimental techniques**

In practice it is difficult to isolate the mechanisms involved when plants are interfering with the growth of each other and to interpret these results. For example, plant growth may be speeded up following an application of nutrients to the the vegetation, and consequently the time at which light becomes limiting (Harper, 1977). Studies of the interaction between pairs of species have repeatedly shown that the balance between them can be altered by conditions such as addition of a particular nutrient and yet Harper (1977) doubts whether these experiments have contributed significantly to understanding the mechanism of competition or merely been of historical importance to emphasise that an interaction was a function of the experimental environment.

Since 1984 some experiments have been designed to alleviate many of the criticisms of previous methods (see Table 2.1). The techniques described by Cook and Ratcliff (1984), Belford et al. (1986) and Snaydon and Howe (1986) permitted the study of single plants subjected to above and / or below ground competition from neighbouring plants of native vegetation, the same species and ryegrass respectively. There are no confounding effects from density or 'unintentional' intraspecific competition as in previous work (Donald, 1958; Schreiber, 1967; Snaydon, 1971; Eagles, 1972; Remison and Snaydon, 1978, 1980a, 1980b) (see Table 2.1) and the experiments were carried out in the field which is a more relevant situation considering that competition has been demonstrated under controlled conditions for many years (Harper, 1977).

The technique involving the use of root tubes and clipping the surrounding vegetation to study competition between plants for above and below ground factors in the field is probably the most relevant and accurate method currently available. Caution should still be used in the choice of experimental design because "if experiments are designed to discover whether plants compete for nutrients, it is highly likely that nutrients will turn out to be important and the same is true of light, water, toxins, predators, pathogens etc." (Harper, 1977).

Chapter 3 COMPETITION EXPERIMENT

A study to determine the relative influence of above and below ground competition from established pasture plants on the growth of ryegrass seedlings transplanted into a hill country pasture.

3.1 INTRODUCTION

Oversowing is the accepted practice for pasture development, renovation and improvement on hill country (Lambert *et al.*, 1985). The introduction of improved plants to existing hill pastures is considered to be beneficial because species can be selected for attributes such as tolerance to drought and to pest attack, suitability to extreme soil fertility levels, improved annual or seasonal herbage production, and better quality feed presumably leading to increased animal performance (Lambert *et al.*, 1985). The importance of management practices to reduce competition from the existing pasture during renovation of hill country pastures has been emphasised, for both pre and post oversowing control of competition (Macfarlane, 1987). In particular, to provide suitable conditions for establishment of plants developed from oversown seed, Macfarlane (1987) recommended a period of controlled grazing management for 9-12 months.

Competition between plants mainly occurs for light, nutrients and water, but perhaps also carbon dioxide and oxygen in some circumstances (Donald, 1963). Experiments have been undertaken (often using seedlings) to study the effect of competition for limiting resources on plant growth, for example Donald (1958) and Rhodes (1968c), but the techniques used were not considered suitable for hill country (see section 2.6). Cook and Ratcliff (1984) developed a novel method for separating above and below ground competition in the field, as a result of their study of competition from native vegetation on the establishment of oversown grasses. Metal tubes were inserted into the soil and herbage surrounding the seedling was clipped to separate root and shoot competition respectively (Cook and Ratcliff, 1984). A similar technique was used in the experiment described in this chapter to determine whether above or below ground competition from resident vegetation occurred first on ryegrass seedlings transplanted into a hill country pasture. Paspalum was anticipated to be the main competitive species from the resident vegetation.

3.2 MATERIALS AND METHODS

3.2.1 Site description and management

The experiment was conducted at Long Acre (a Ministry of Agriculture and Fisheries Research Area, 11 km ENE from Wanganui) New Zealand between May and December 1986. The topography of the Research Area was reported by Wilde (1985) as being rugged, steep hills leading to narrow ridges and soils formed from parent material of mainly siltstones and mudstones of the Kai-iwi Group. The predominant soil type was an Okoia steepland soil, characterised by a firm silty clay loam subsoil overlain with a friable silty topsoil (Wilde, 1985). The paddock used for the experiment was composed of approximately equal proportions of track, slope and steep areas. The inclination of the track was $17 \pm 6^{\circ}$ and slopes was $43 \pm 6^{\circ}$, steep areas were not studied. The experimental site chosen was a north facing slope. Ryegrass, white clover and paspalum constituted the main resident vegetation on tracks while the slopes included ratstail, danthonia and browntop. The whole paddock was grazed down to 5-10 cm stubble before the initial transplanting of ryegrass seedlings in mid August. Subsequently, an area was fenced to enclose the competition experiment and twenty ewes grazed the remainder of the paddock for 7 days in mid October (to 3-5 cm on the tracks). A plan of the experimental site is presented in Appendix 1. The nutrient status of the soil was determined by the Ministry of Agriculture and Fisheries laboratory, Ruakura on soil taken from the transplant holes.

3.2.2 Plant culture

Ryegrass (cultivar Ellett) was used as the test plant and grown in a mixture of 60 % soil (taken from the site), 25 % peat and 15 % sand. Plastic tubes (3 cm diameter and 10 cm length) were filled with the soil mixture, stacked in seed boxes on capillary matting and placed in an unheated glasshouse. The soil in the tubes was watered from above as well as from the capillary matting. To test this watering system the soil in the tubes was

Plate 1 General view of field site at Wanganui with fenced competition experiment in foreground.

Plate 2 View of track with pegs marking paspalum patches and a root tube prior to insertion.

watered twice daily for five days and then examined. The soil was found to be evenly moist throughout the tube. On 16 July, two seeds of ryegrass were placed in each tube and covered by 1 cm soil mixture. Plants were watered daily. A germination test proved the seed to be 100 % viable and generally two seedlings emerged, these were thinned to one plant per tube. The seedlings were transplanted 9 weeks from sowing.

3.2.3 Transplanting procedure

A soil corer (3 cm diameter) was used to make a hole 10 cm deep and the soil sample retained for nutrient analysis. To ensure that the soil on the sides of the hole were not smeared the surface was roughened with a 'scraper' to allow good contact with the transplant (seedling and soil mixture). The scraper consisted of a piece of wood with nails that projected sufficiently from the lower 15 cm to touch the sides of the hole. A plunger was used to push the transplant from the plastic tube, onto a holding dish, before it was tipped into the prepared hole and lightly tamped in.

3.2.4 Experimental technique

The interaction of the surrounding vegetation on the transplanted ryegrass seedling was studied by separating shoot and root competition. The methods used were:

i) shoot competition was prevented by clipping the vegetation surrounding the transplanted seedling approximately weekly with shears to a height of 3 cm in a 15 cm radius of the seedling. The clippings were removed.

ii) root competition was prevented by insertion of a metal tube where the seedling was to be transplanted. Each steel tube (9 cm diameter, 16 cm length) was driven into the soil to a depth of 15 cm. The 1 cm protrusion above the soil surface prevented growth of rhizomatous or stoloniferous species into the tube. Once the tube was in place, existing herbage was killed with an application of 40 ml Roundup (1.5 ml active ingredient l^{-1}) and any subsequent unwanted growth was physically removed.

The four possible combinations of with or without clipping and with or without root tubes gave treatments of shoot competition, root competition, full competition or no competition (Figure 3.1). Throughout the thesis the following terms will be used for the various combinations of competition treatment:

shoot competition - root tube prevented root competition
root competition - clipping surrounding vegetation prevented shoot competition
full competition - competition not prevented
no competition - root tube and clipping prevented all shoot and root competition

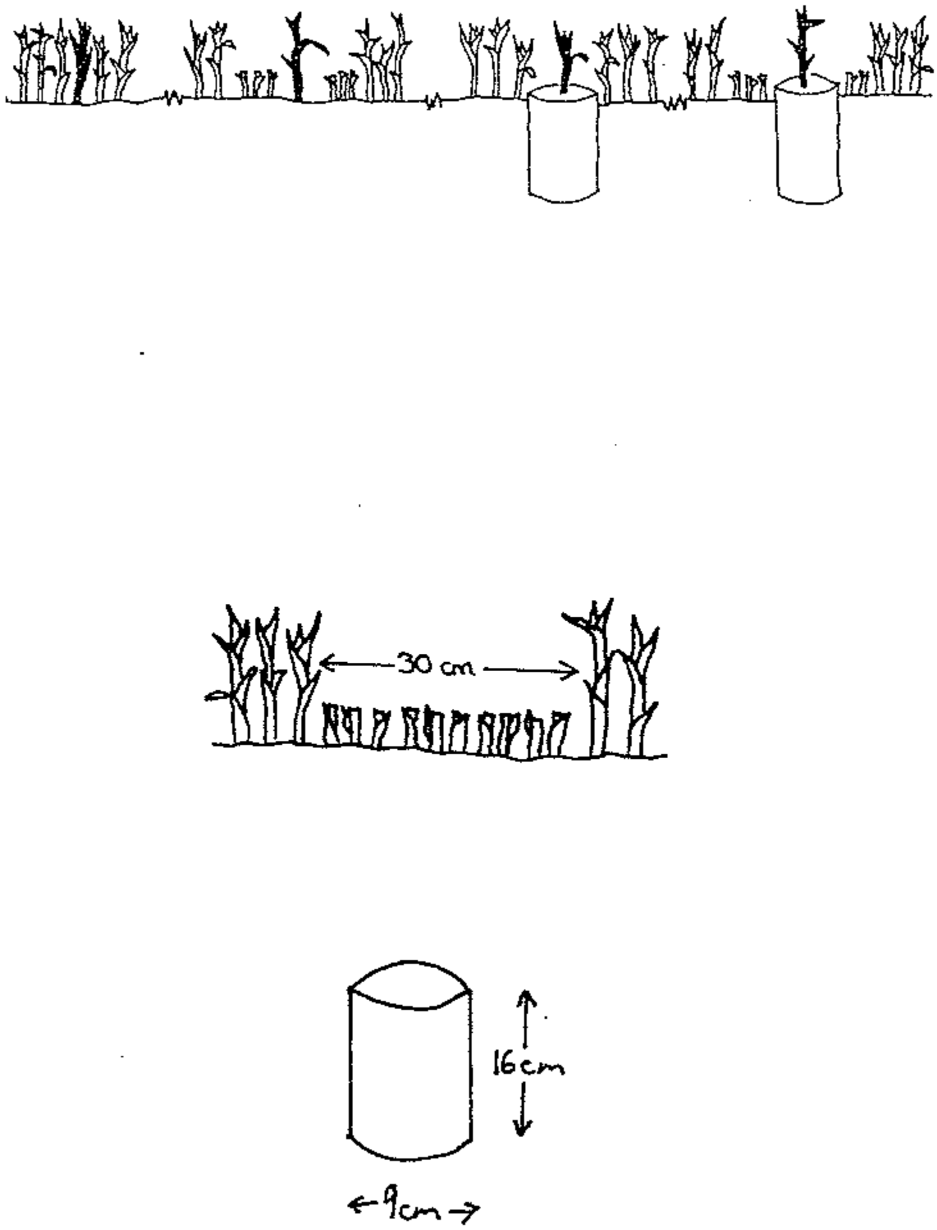
Above ground competition - referred to treatments with either shoot competition or full competition
Below ground competition - referred to treatments with either root competition or full competition

3.2.5 Experimental procedure

One hundred patches of paspalum growing on the tracks (>30 cm diameter) were marked on 14 May 1986 before the period of winter dormancy. At the end of August, fifty patches were selected according to the criteria that the markers were at least 40 cm apart and the total area was compact and homogenous to enable easy erection of temporary fencing, finally five tracks were chosen. The experimental design was completely random with twelve replicates per treatment (48 plants total), and twenty four root tubes were driven into place accordingly. The soil in the tubes was allowed to settle for several weeks before the ryegrass seedlings (2-3 tillers) were transplanted into the centre of a marked paspalum patch. After transplanting, the surrounding vegetation was trimmed to a height of 3 cm as this simulated the recommended procedure of hard grazing prior to oversowing (Macfarlane, 1987). Competition treatments were imposed on 30 September and this was referred to as day 0. At the beginning of the measurement period (day 0) there was no difference between treatments ($P<0.05$) in the height or number of

Figure 3.1: Diagramatic representation of techniques used to control competition in the experiment.

Competition treatment	Full	Root	Shoot	None



tillers per ryegrass plant (Tables 3.2, 3.4).

3.2.6 Measurements

3.2.6.1 Non destructive sampling

Non destructive estimates of ryegrass growth and the degree of shading from the surrounding vegetation were made on ten occassions at approximately weekly intervals (days 0, 8, 14, 22, 30, 42, 52, 58, 63 and 83).

Ryegrass growth

Plant height was measured as the distance between the soil surface and ligule of the youngest leaf. A tiller was counted once its first leaf had unfolded and for each plant the three tallest tillers were measured. The number of tillers per plant was recorded and each tiller marked with a plastic ring. A different coloured ring was used for each measurement date, to facilitate identification of dead tillers. The number of tillers that became reproductive was also recorded (see Sections 3.2.6.1, 3.2.6.2).

Shading from the surrounding vegetation

The degree of shading at the base of the pasture was assessed by two methods:

i) Between 12.00-13.00 hours the photosynthetic photon flux density (PPFD) in the 400-700 nm waveband was measured at the base of each ryegrass plant by an LZ-170 Quantum / Radiometer / Photometer fitted with a LI-190S Quantum Sensor (Lambda Instrument Co.). The quantity of PPFD transmitted to 4 cm above the soil surface was expressed as a percentage of the total available PPFD.

ii) A 'shading index' was developed and based on a graded scale of 0-5 where 0 represented no shading and 5 where the transplanted ryegrass was overtopped by the surrounding vegetation.

3.2.6.2 Destructive sampling

Four ryegrass plants chosen at random from each treatment were destructively sampled on days 30 and 63. Samples were also taken at the time of transplanting.

Above ground determinations

The shoot was cut at ground level, placed in a plastic bag and transported to the laboratory. Each shoot was dissected into leaf, stem and dead material then dried in a forced draught oven at 80 °C for 48 hours. Prior to drying, the leaf area of each shoot was determined using a portable leaf area meter (LiCor 3000). The stage of growth was determined by examining the apex under a binocular microscope.

Below ground determinations

Root tubes (where present) contained soil and roots of the ryegrass plants. Two treatments did not require root tubes (root competition and full competition) therefore a spare tube was inserted into the soil to surround these ryegrass plants before extraction of the tube and contents from the ground. Soil and roots were removed from each tube and the sample frozen for later analysis. After thawing, soil was washed from the roots with water that continuously flowed through two sieves (mesh sizes 2.75 and 4.0 mm). Roots from plants other than ryegrass were removed wherever possible. A weighed subsample of approximately 0.5 g was used to determine root length according to the method described by Tennant (1975) and dry weight was recorded for the total root sample after drying in a forced draught oven for 48 hours at 80 °C. The ash free dry weight was calculated following burning in a muffle furnace at 500 °C for 3 hours and all root data was expressed on this basis.

3.2.7 Meteorological data collection

On 27 August 1986 a meteorological unit was established on the experimental site from which readings were taken approximately weekly at 10.00 hours. A Stevenson screen was constructed to support the maximum and minimum thermometers. The 5 and 20 cm soil thermometers were situated in a bare patch of ground nearby, also situated nearby was a grass minimum thermometer under which the herbage was trimmed to 1-2 cm. An anemometer was installed at the top of the site. Daily rainfall was measured at the bottom of the valley by staff from the Research Area. Meteorological observations from Wanganui town were also obtained. Five samples of soil for moisture analysis (later bulked) were taken at regular intervals along each track on the measurement days. The corer used was 3 cm diameter and samples from 10 and 20 cm depth were taken in late afternoon, and placed in grip-top plastic bags for transit to the laboratory. The samples were weighed then dried at 105 °C for 48 hours, then weighed again.

3.2.8 Statistical analysis

Standard statistical procedures as recommended by Steele and Torrie (1981) and Snedecor and Cochran (1967) were used for analysis of the experiment. A $\log_{10}$ transformation stabilized the variance and was found to be necessary according to Bartlett's Test for Homogeneity of Variances. The transformed values were presented unless stated otherwise. The data was analysed as a split plot in time (when repeated measurements were taken on plants) hence the experimental treatments formed the main plots and sampling time the split plots. Where appropriate a more detailed analysis was undertaken. The Duncans new multiple range test was used to separate treatment means when the F test for the particular source of variance was significant at or below the 1 % level unless stated otherwise. Multiple regression was used according to the method outlined by Snedecor and Cochran (1967). The use of other statistical methods are described below or in the text where appropriate. The computer programme used for the analyses was the Statistical Analysis System (SAS) available on the Prime at Massey University.

3.2.8.1 Further statistical methods

An analysis of covariance showed that there was no difference between the tracks in the growth of ryegrass plants for example, plant height, leaf area and shoot dry weight, even at the 10 % level (Appendix 2). This information validates the use of the completely random experimental design.

The relationship of plant height versus time was expressed by the regression equation $Y = a + bX + cX^2$ (Figure 3.2) as this resulted in a significantly better fit than the linear function for treatments with above ground competition. Therefore the quadratic equation was used throughout the data set to express all functions on the same basis.

For the duration of the experiment there was no significant difference in the number of tillers per plant when subjected to full competition. A good fit for the regression of total tiller number versus time for the whole data set was not therefore possible, and only the linear phase was fitted for ryegrass plants in the treatments with shoot, root and no competition. The results from an analysis of variance was used as the criteria for selection of the linear phase where means similar to the final value (day 83) were excluded.

Mean relative tillering rate was calculated for each time interval between measurement dates from the following equation derived from that for mean relative growth rate (Hunt, 1982).

$$\text{Mean relative tillering rate} = \frac{\log_e(TN_2) - \log_e(TN_1)}{t_2 - t_1}$$

where TN = $\log_{10}$ tiller number and $t_2 - t_1$ was the time interval (days) between measurements.

Plant size for each ryegrass plant was obtained from Bellotti (1984) as follows:

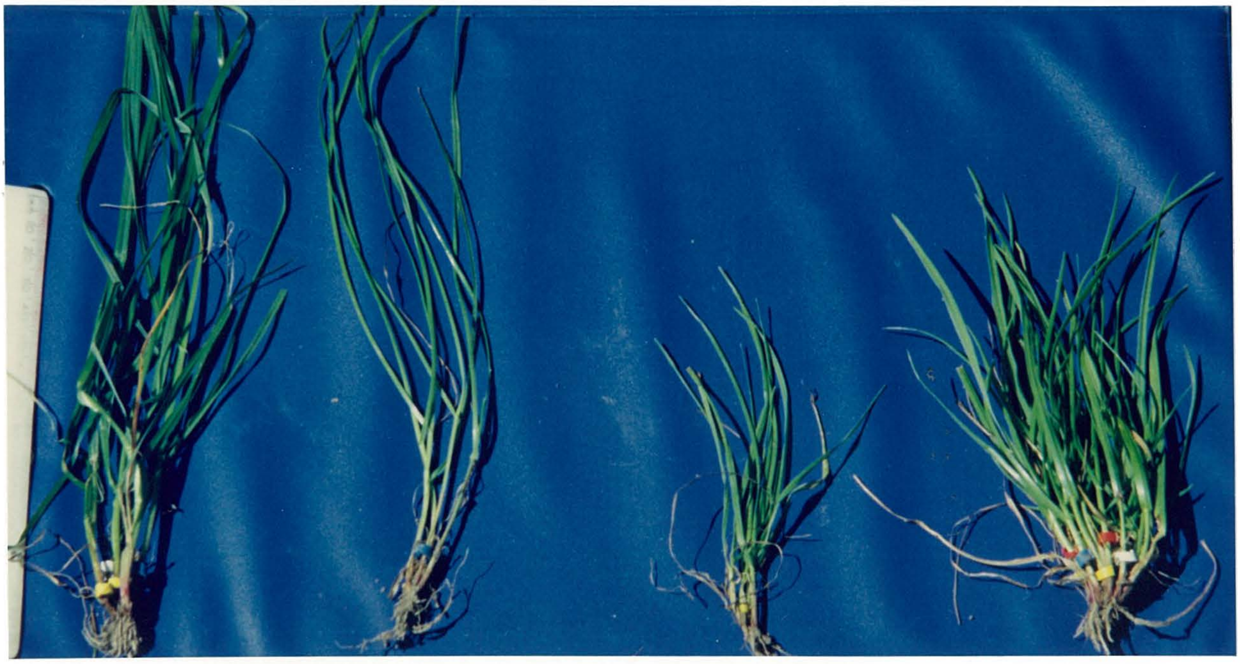
Size = plant height x tiller number

Plant size was chosen for the study of skewness (see Bellotti, 1984) where the frequency distribution was analysed as discrete size classes from the raw data and presented as histograms (Figure 3.6). Size class intervals were calculated from the values attained at day 83 after the method by Harris and Sedcole (1974), later modified by Bellotti (1984) and the number of classes required (15) was determined from Koyama and Kira (1956).

$$\text{Size class interval} = (S_{max} + a) - (S_{min} + a) / 15$$

where S_{max} and S_{min} were the mean of the five largest or smallest size index values (the mean was used to reduce the influence of one or two very large or small plants on the overall analysis) and the a value is a small number to prevent the calculated sizes falling on a class interval border. Statistical tests, for example, skewness and kurtosis (Snedecor and Cochran, 1967) could not be applied because too few plants were measured and the data was based on repeated observations (T. Moore, pers. comm.).

Plate 3 Shoots of ryegrass plants subjected to shoot, full, root and no competition (from left to right).



3.3 RESULTS

3.3.1 Site classification

During August, September and October, precipitation was greater and for the first two months temperatures were lower than the long term average (Table 3.1). November and December were considerably drier than, but temperatures were similar to the long term average. The moisture content (mean for each month) of the soil was 28, 32, 19 and 25 % for the samples taken from September to December respectively. The nutrient analysis showed that the soil on the experimental site was less than optimum in phosphorus and sulphur (Appendix 3).

3.3.2 Plant height

Ryegrass plants subjected to shoot competition were approximately 50 % taller after 83 days compared to those in the treatment with root competition (see Table 3.2) and this difference occurred from day 8. Throughout the experiment, plants in the treatment with full competition were similar in height ($P<0.01$) to those grown with no competition (Table 3.2). Final plant height (detransformed data) was recorded as 17, 9, 6 and 5 cm for ryegrass plants in the treatments with shoot competition, no competition, full competition and root competition respectively. From day 22 to day 63 plants subjected to root competition were shorter than those in the other treatments (Table 3.2).

The interaction between treatment and time was significant ($P<0.0001$) and clearly shown in Figure 3.2. From day 42, ryegrass plants in all treatments (except full competition) were exhibiting reproductive growth (see Section 3.3.3.3). Coefficients from the fitted functions were similar for treatments with above ground competition (Figure 3.2). Ryegrass plants in the treatment with shoot competition were taller than those with root competition or no competition (Table 3.2) and comparison of the regression coefficients also showed similar

Table 3.1: Selected monthly climatic data from the experimental site and Wanganui town during the period August to December 1986 and the long term mean values for Wanganui town.

	Month				
	August	September	October	November	December
Rainfall (mm)					
Site 1986	136	96	116	67	55
Town 1986	101	82	97	42	30
Town 1890-1980	67	64	70	72	72
Temperature (°C) (Town only)					
Minimum 1986	5.0	6.0	11.0	11.2	12.6
Minimum 1937-1980	5.8	7.6	9.2	10.8	12.5
Maximum 1986	12.4	14.5	17.4	18.2	20.7
Maximum 1937-1980	13.6	15.1	16.8	18.8	20.5

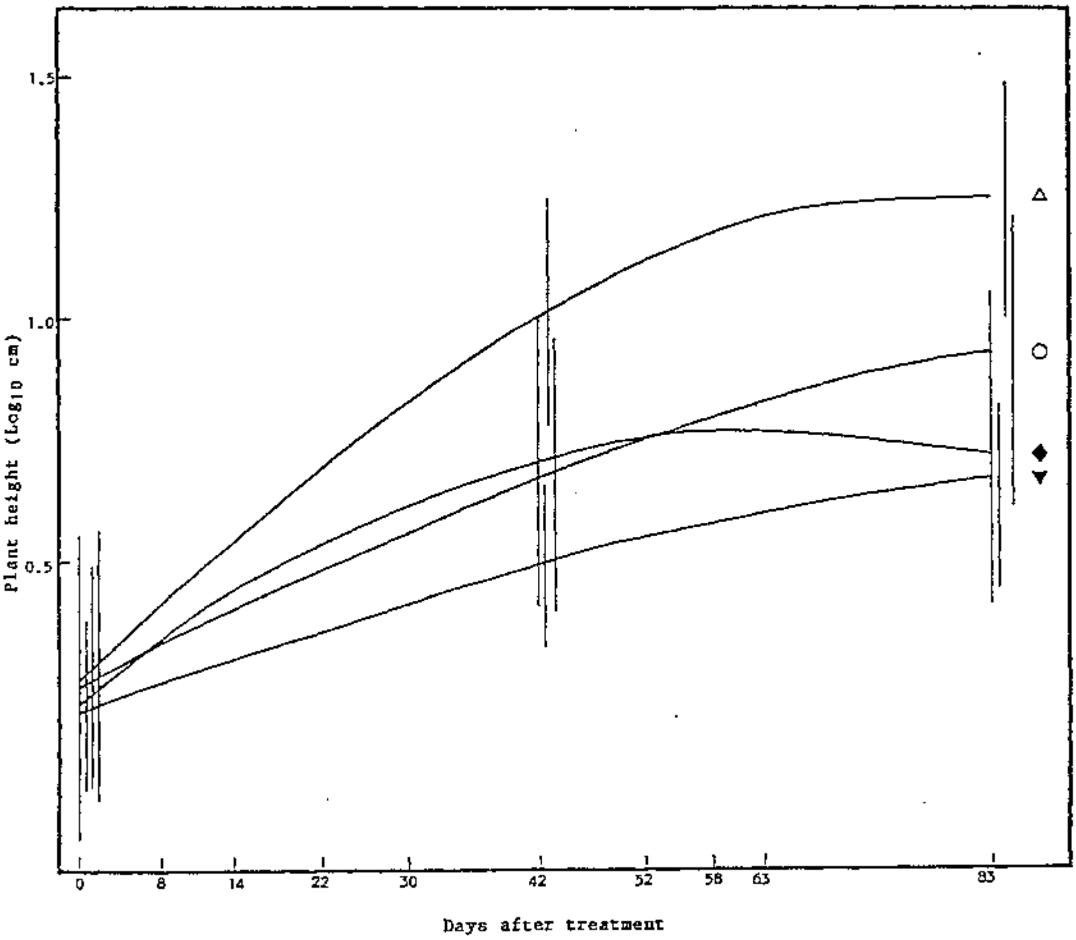
Table 3.2: Height ($\log_{10}$ cm) of ryegrass plants subjected to full, root, shoot and no competition from a hill country pasture over 83 days during August to December 1986. Means within each row are signficantly different (P<0.01) when not followed by the same letter (df=33). LSD = 0.04 days 0-63, 0.06 day 83. D = R (LSD) where D is Duncans new multiple range test and R values were obtained from Table A.5 (Little and Hills, 1978).

Days after	Competition treatment			
treatment	Full	Root	Shoot	None
0	0.24 a	0.26 a	0.29 a	0.32 a
8	0.40 ab	0.29 c	0.44 a	0.34 bc
14	0.44 b	0.32 c	0.57 a	0.41 bc
22	0.53 b	0.36 c	0.74 a	0.48 b
30	0.63 b	0.47 c	0.83 a	0.60 b
42	0.74 b	0.53 c	1.04 a	0.73 b
52	0.76 b	0.58 c	1.10 a	0.76 b
58	0.74 b	0.57 c	1.13 a	0.78 b
63	0.76 b	0.55 c	1.20 a	0.80 b
83	0.78 bc	0.69 c	1.23 a	0.93 b

Table 3.3: Comparison of regression coefficients (P<0.05) for functions relating the height of ryegrass plants subjected to full, root, shoot and no competition to time (df=2). See Figure 3.1 for further details.

Comparison of	Regression coefficient		
treatment	a	bX	cX^2
Full vs none	ns	ns	ns
Full vs shoot	ns	ns	ns
Full vs root	ns	ns	ns
Root vs none	ns	ns	ns
Root vs shoot	ns	*	*
Shoot vs none	ns	*	*

Figure 3.2: Predicted plant height ($\log_{10}$ cm) and regression coefficients ($\pm$ S.E.) from fitted quadratic functions ($Y = a + bX + cX^2$, where Y = plant height and X = days) for ryegrass plants subjected to full, root, shoot and no competition from a hill country pasture over 83 days during August to December 1986. Bars denote 95% confidence limits. ◆ full, ▼ root, △ shoot, ○ no competition.



Coefficients from the fitted functions

Terms included in regression	Competition treatment Full	Root	Shoot	None
r^2	0.6***	0.7***	0.9***	0.7***
Constant (a)	0.257	0.238	0.276	0.281
Coefficient (bX)	0.016	0.007	0.023	0.011
S.E.	0.033	0.019	0.026	0.030
Coefficient (cX^2)	-0.00010	-0.00003	-0.00010	-0.00004
S.E.	0.00003	0.00002	0.00002	0.00003

*** = P<0.0001

differences between treatments (Table 3.3). The wide confidence limits shown in Figure 3.2 reflect the relatively low coefficient of determination (r^2). The large within treatment variability of ryegrass plants subjected to full competition probably contributed to the lack of significant results ($P<0.05$) (Table 3.3).

The number of days until 90 % maximum height was calculated from the fitted function to be 41 for plants in the treatment with full competition, 53 for shoot competition, 64 for root competition and 65 days for plants without competition (see Figure 3.2). The relative rate of height increase was computed for half of the 90 % maximum height. The values obtained were 1.108, 1.770, 0.534 and 0.834×10^{-2} cm day^{-1} for ryegrass plants under the influence of full, shoot, root or no competition respectively (see Figure 3.2). Overall, the treatments that included above ground competition resulted in a rapid increase in plant height over a short period relative to those plants without above ground competition. The lowest relative rate of height increase was recorded for ryegrass plants in the treatment with root competition.

3.3.3 Tillers

3.3.3.1 Total tiller number

After 83 days, the maximum number of tillers was recorded for ryegrass plants without competition and this was 62 % greater than those in the treatment with full competition (Table 3.4). Similar trends were shown by the mean relative tillering rate (Table 3.5). The interaction of treatment and time was significant ($P<0.0001$) for tiller number. The interaction was exemplified by ryegrass plants subjected to root competition where, by day 83, a similar number of tillers (0.869) was present compared to plants in the treatment with no competition between days 8-14 (Table 3.4). The importance of below ground competition in reducing the tiller number of ryegrass plants was shown in Table 3.4. From day 8, plants in the root competition treatment had fewer tillers than those in

Table 3.4: Tiller number (log_{10}) of ryegrass plants subjected to full, root, shoot and no competition. LSD = 0.04 days 0-30, 0.05 days 42-63, 0.07 day 83. See Table 3.2 for further details.

Days after treatment	Competition treatment Full	Root	Shoot	None
0	0.53 a	0.50 a	0.57 a	0.60 a
8	0.62 b	0.56 b	0.74 a	0.78 a
14	0.67 b	0.63 b	0.90 a	0.96 a
22	0.68 c	0.67 c	0.95 b	1.08 a
30	0.68 c	0.75 c	0.98 b	1.18 a
42	0.63 d	0.79 c	1.03 b	1.29 a
52	0.62 d	0.81 c	1.01 b	1.31 a
58	0.54 d	0.82 c	1.01 b	1.33 a
63	0.52 d	0.84 c	1.00 b	1.34 a
83	0.54 c	0.87 b	0.92 b	1.43 a

Table 3.5: Mean relative tillering rate per ryegrass plant ([TN TN^{-1}] day^{-1}) when subjected to full, root, shoot and no competition (see Section 3.2.8.1). LSD = $1.58x10^{-3}$ periods 1-4, $1.94x10^{-3}$ periods 5-8, $2.74x10^{-3}$ period 9. See Table 3.2 for further details.

Period	Competition treatment			
	Full	Root	Shoot	None
1	†0.12 c	0.07 d	0.21 b	0.23 a
2	0.08 d	0.11 c	0.26 b	0.30 a
3	0.02 d	0.05 c	0.06 b	0.15 a
4	0.00 d	0.10 b	0.03 c	0.13 a
5	0.02 c	0.10 b	0.12 a	0.14 a
6	-0.01 b	0.02 a	-0.02 b	0.01 a
7	-0.13 c	0.03 a	0.00 b	0.04 a
8	-0.04 b	0.03 a	-0.02 b	0.03 a
9	0.11 a	0.07 b	0.02 c	0.09 ab

†multiply all values by 10^{-1}

Table 3.6: Comparison of regression coefficients (P<0.05) for functions relating the tiller number of ryegrass plants subjected to root, shoot and no competition to time (df=2). See Figure 3.2 for further details.

Comparison of treatment	Regression coefficient a	bX
Root vs none	ns	*
Root vs shoot	ns	*
Shoot vs none	ns	ns

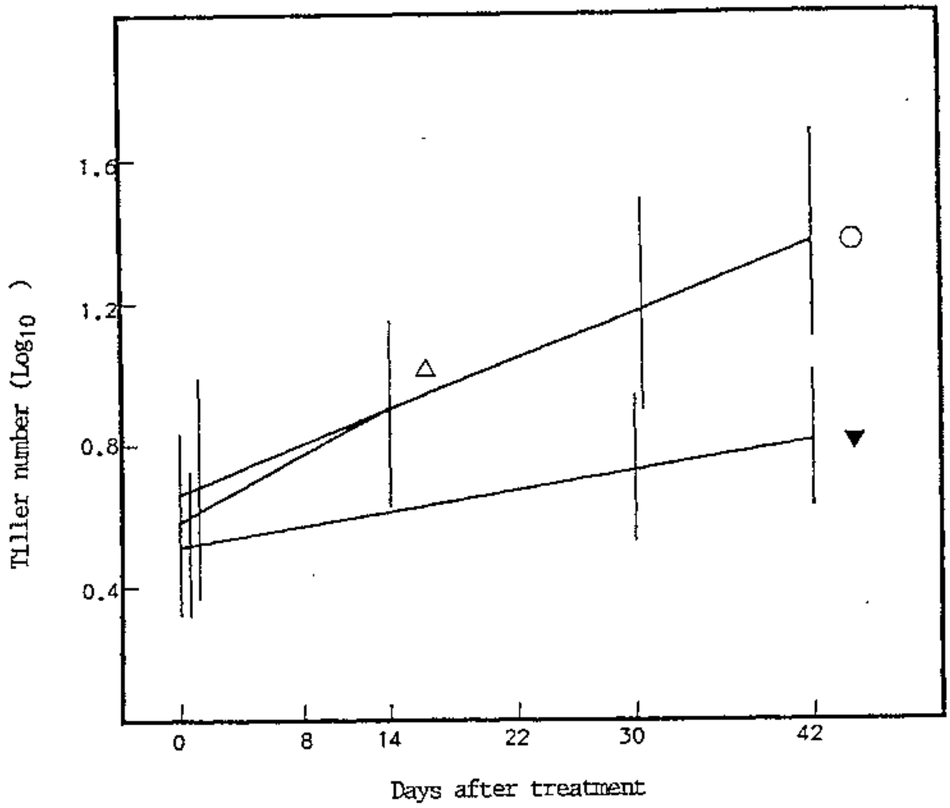
the treatment with shoot competition or no competition. A similar conclusion was drawn from the t-test between regression coefficients (Table 3.6). The fitted functions predicted from the regression equation were shown in Figure 3.3. The exclusion of ryegrass plants in the treatment with full competition was due to the large variation between plants, probably as a result of the severe stress imposed.

Ryegrass plants subjected to above ground competition exhibited a marked phase of tiller death and this occurred earlier in the treatment with full competition than with shoot competition (Table 3.4). Differences between treatments in the peak of tiller production was highlighted by the number of days to 90 % maximum tiller number, for plants subjected to full competition being 10, 31 days for those with shoot competition , 59 days for root competition and 73 days for plants without competition. The corresponding tillering rate obtained from this phase was 4.6, 12.0, 5.7 and 10.0×10^{-3} $tillers^{-1}$ (see Figure 3.3), and demonstrated the reduction in tillering of plants subjected to below ground competition. The maximum number of tillers observed were 27, 11, 7, and 5 for ryegrass plants in the treatments with no competition, shoot competition, root competition and full competition respectively (detransformed data).

3.3.3.2 New tillers

The relationship between the number of new tillers and environmental factors was examined by multiple regression for data from all treatments, but was poor (Appendix 4). The independent variables were time and the following 'weather variables' measured per week from town data: daily rainfall, total rainfall, maximum temperature, minimum temperature, grass minimum, 20 cm soil temperature, windrun and soil moisture at 10 and 20 cm depths from the site. All factors were poorly related to the number of new tillers as the 'weather variables' accounted for 30 % of the variation in tiller number and time for 36 %. Inclusion of all independent variables in the model did not significantly improve the

Figure 3.3: Predicted tiller number ($\log_{10}$) and regression coefficients (± S.E.) from fitted linear functions (Y = a + bX, where Y = tiller number and X = days) for ryegrass plants subjected to root, shoot and no competition. Bars denote 95% confidence limits. ▼ root, △ shoot, ○ no competition. See Figure 3.2 for further details.



Coefficients from the fitted functions

Terms included in regression	Competition treatment Root	Shoot	None
r^2	0.5***	0.6***	0.7***
Constant (a)	0.512	0.569	0.653
S.E.	0.021	0.033	0.030
Coefficient (bX)	0.007	0.023	0.017
S.E.	0.0009	0.0035	0.0014

*** = P<0.0001

regression (R^2=37 %). (Similar results were obtained for plant height).

3.3.3.3 Tiller dynamics

Dead tillers

Tiller death in ryegrass plants subjected to root competition was less (0.1 tiller $plant^{-1}$) than for those in the other three treatments (0.3 tillers $plant^{-1}$), presented as the detransformed values. The treatment by time interaction was not significant. The number of dead tillers, expressed as a percentage of total tillers, was greatest for ryegrass plants grown under full competition ($P<0.05$) at days 58 and 63 only. The interaction between treatment and time was significant, for example by days 30 and 58 the same percentage of dead tillers was reached by ryegrass plants in the treatments with full competition and no competition.

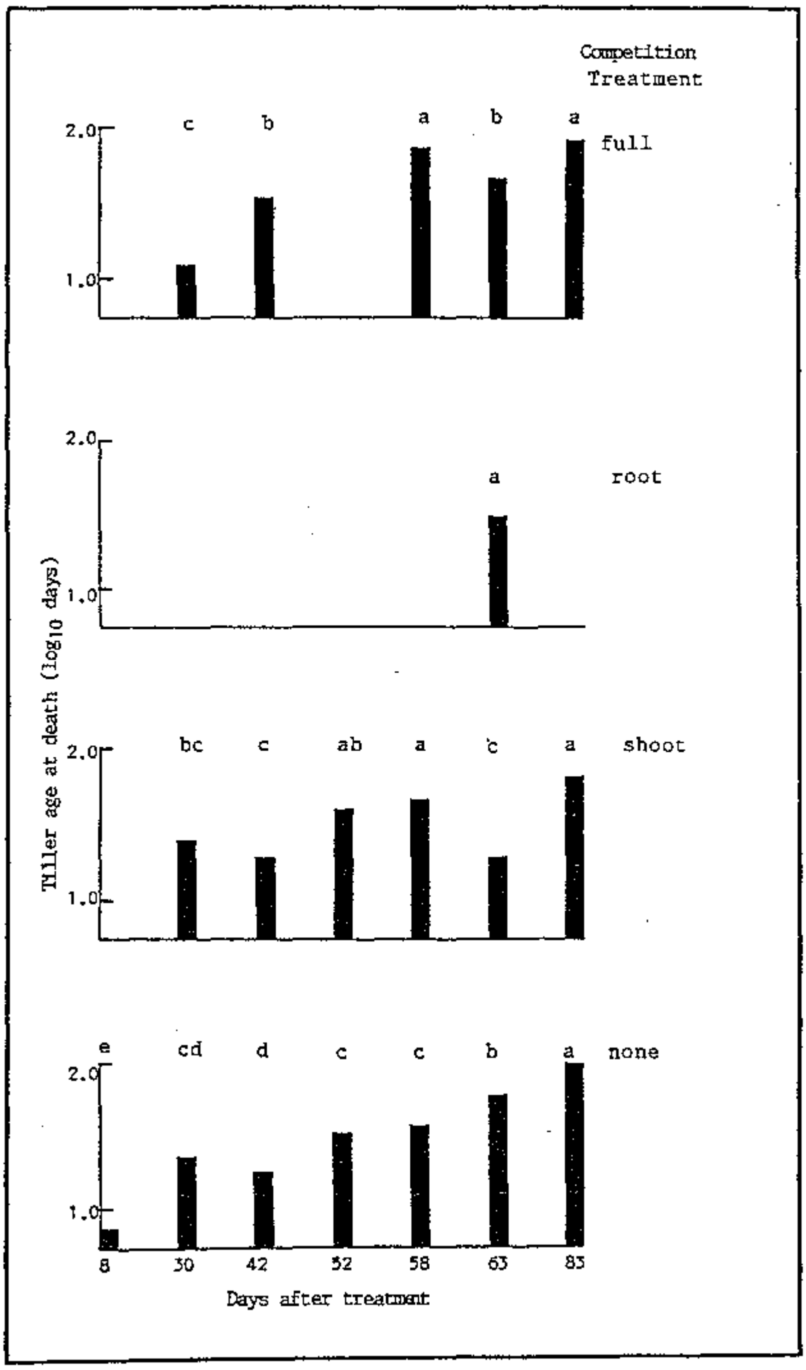
Tiller life cycle

Tiller age at death was obtained from records of tiller turnover, there was no difference between treatments or in the interaction of treatment and time ($P<0.05$). Towards the end of the experiment, the older tillers died in ryegrass plants subjected to the treatments of full competition or no competition (Figure 3.4).

Reproductive tillers

The apices of the harvested plants were examined at the first destructive harvest (day 30) and found to be in the reproductive phase of development. Pseudostem elongation began and after 52 days ear emergence was observed. A greater number of reproductive tillers were present in ryegrass plants subjected to shoot competition (0.14 tillers $plant^{-1}$) in contrast to those plants in the remaining treatments (mean of 0.03 tillers $plant^{-1}$) (detransformed data). No reproductive tillers were recorded for plants under full competition. The treatment by time interaction was significant as explained by the observations described.

Figure 3.4: Mean tiller age at death ($\log_{10}$ days) for ryegrass plants subjected to full, root, shoot and no competition. Means within each treatment are significantly different (P<0.01) when not followed by the same letter (df=13). LSD are not shown due to variation in replicates per mean. See Figure 3.2 for further details.



3.3.4 Harvest data

The dry weight of ryegrass sampled at transplanting was recorded (Appendix 5). Although each component of dry weight increased between harvests, the interaction of treatment and time was not significant ($P<0.05$). At the final harvest (day 63) the dry weight of all components (except root dry weight) from plants in the treatments with below ground competition were less than from those with shoot competition or no competition (Table 3.7). The reduced weight of ryegrass plants subjected to below ground competition compared to those without was also present at the day 30 harvest for dead material and the trend was apparent in the remainder. The amount of dead matter per live tiller at the final harvest was greatest in ryegrass plants where above ground competition occurred (2.3 mg $tiller^{-1}$ for full and shoot competition) compared to the lowest value for plants with root competition (2.0 mg $tiller^{-1}$) (see Tables 3.4 and 3.7). At day 63, each tiller was heavier in ryegrass plants subjected to shoot competition than those in the other treatments, the detransformed values were 1611 and 677 mg $tiller^{-1}$ respectively) (see Tables 3.4 and 3.7).

There was no difference in root dry weight between treatments or over time, therefore the following calculations or inferences using the root data should be treated with caution. Roots of ryegrass plants were significantly heavier and longer per tiller in the treatments with below ground competition than those with shoot competition or no competition by the final harvest (see Tables 3.4, 3.8). The initial root : shoot ratio was approximately 1.0 (Appendix 5), but increased in ryegrass plants with below ground competition and decreased in those without (Table 3.8).

Table 3.7: Dry weight ($\log_{10}$ mg) and leaf area ($\log_{10}$ cm^2) of ryegrass plants subjected to full, root, shoot and no competition, from destructive harvests at 30 and 63 days after treatment. Shoot dry weight = leaf + stem + dead. See Table 3.2 for further details.

	Harvest	Competition treatment			
	date	Full	Root	Shoot	None
Shoot	30	3.02 a	3.17 a	3.58 a	3.68 a
	63	3.27 b	3.53 b	4.28 a	4.22 a
Leaf	30	2.76 a	2.87 a	3.33 a	3.41 a
	63	2.86 b	3.18 b	3.84 a	3.90 a
Stem	30	2.46 a	2.75 a	3.08 a	3.25 a
	63	2.73 b	3.06 b	3.94 a	3.79 a
Dead	30	3.03 b	2.21 b	2.56 a	2.53 a
	63	2.75 b	2.79 b	3.40 a	3.41 a
Leaf area	30	1.11 a	1.25 a	1.72 a	1.69 a
	63	1.27 b	1.36 b	2.14 a	2.15 a

Table 3.8: Root dry weight ($\log_{10}$ mg), root length ($\log_{10}$ mm) and root : shoot ratio of ryegrass plants subjected to full, root, shoot and no competition, from destructive harvests at 30 and 63 days after treatment. See Table 3.2 for further details.

	Harvest	Competition treatment			
	date	Full	Root	Shoot	None
Root dry weight	30	3.48 a	3.47 a	3.24 a	3.22 a
	63	3.54 a	3.92 a	3.29 a	3.58 a
Root length	30	3.75 a	3.59 a	3.30 a	3.26 a
	63	3.61 a	3.93 a	3.19 a	3.58 a
Root:shoot ratio	30	1.16 a	1.10 a	0.90 a	0.88 a
	63	1.09 a	1.11 a	0.77 b	0.85 b

3.3.5 Plant size

The interaction between treatment and time was significant ($P<0.0001$) for plant size in ryegrass (Figure 3.5). The size of ryegrass plants subjected to the treatments of root competition and full competition were similar but both were smaller than those with shoot competition or no competition from day 14, although the trend was apparent earlier (Figure 3.5). There was no difference in size between plants in the treatments with shoot competition or no competition throughout the measurement period.

During the experiment there was little change in the frequency distribution of plant size for ryegrass in the treatments subjected to below ground competition (Figure 3.6). Reproductive growth influenced the value of size due to pseudostem elongation for plants in the treatments with shoot competition or no competition from day 42, as shown by outlying observations in the higher classes. The main determinant of size for the plants in these treatments was investigated by multiple regression of size versus plant height and total tiller number. Plant height accounted for 86 and 87 % of the variation in the plants with shoot competition and no competition. Tiller number accounted for 64 and 83 % of the variation in plants subjected to root competition and full competition respectively. Nevertheless,these results should be treated with suitable caution due to the close affiliation of the factors involved.

The relationship between shoot dry weight versus plant height, tiller number and the size of ryegrass plants are shown in Table 3.9, based on data for all the treatments. A substantial proportion of the variation in shoot dry weight was explained by tiller number ($r^2=0.7$), less by plant height but multiplication of these two factors to obtain plant size accounted for more variation ($r^2=0.9$). The relationship of shoot dry weight and size was then tested for each treatment and in a multiple regression model (Table 3.10). Plant height was the best predictor of shoot dry weight for ryegrass plants subjected to below ground competition and tiller number for those plants

Figure 3.5: Plant size (log_{10}) of ryegrass subjected to full, root, shoot and no competition (see Section 3.2.8.1). Means within each measurement date are significantly different (P<0.01) when not followed by the same letter (df=33). LSD = 0.07 days 0-30, 0.08 days 42-63, 0.11 day 83. ◆ full, ▼ root, △ shoot, ○ no competition. See Figure 3.2 for further details.

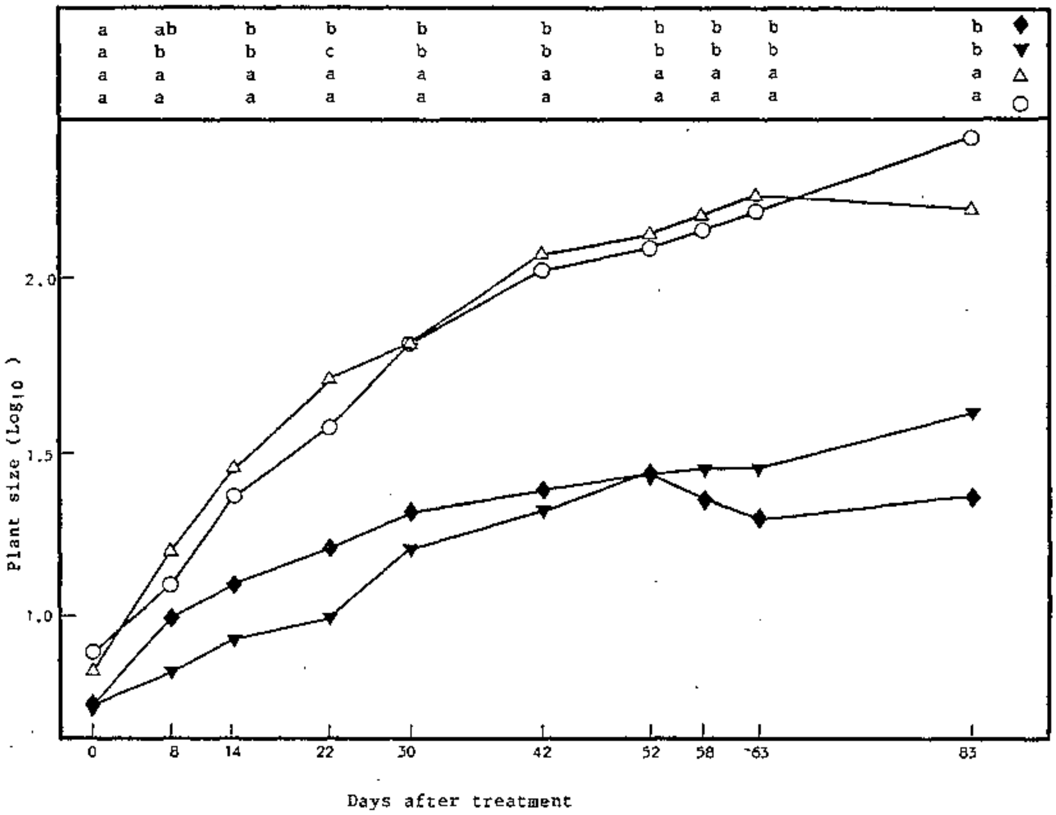


Figure 3.6: Size class frequency distributions for ryegrass subjected to full, root, shoot and no competition (see Section 3.2.8.1). See Figure 3.2 for further details.

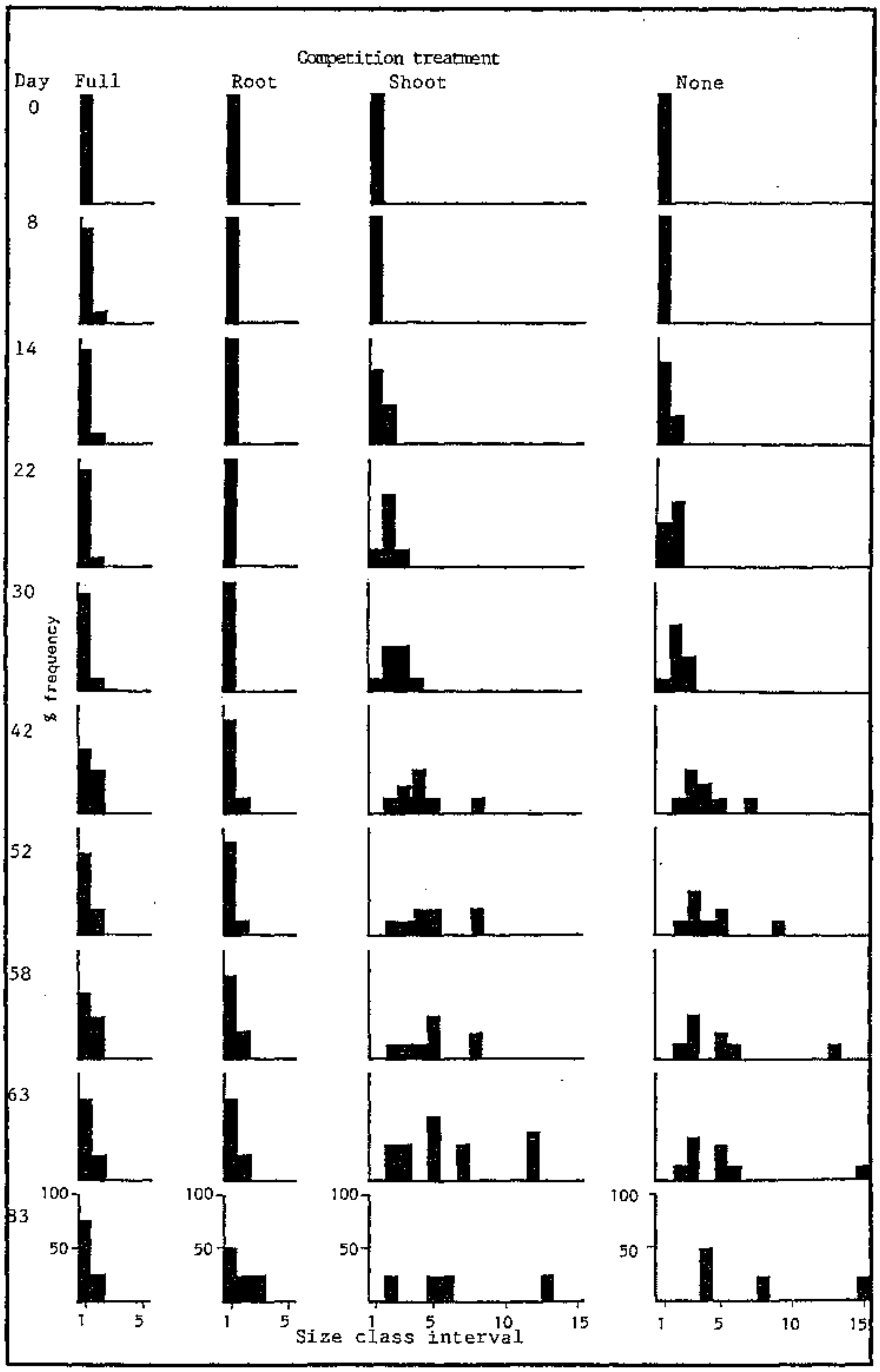


Table 3.9: Regression coefficients (±S.E.) of shoot dry weight against plant height, tiller number and plant size (Y = a + bX, where Y = shoot dry weight and X = plant height, tiller number or plant size). See Table 3.2 for further details.

Terms included in regression	Plant height	Tiller number	Plant size
r^2	0.5	0.7	0.9
Constant (a)	2.867***	2.441***	2.142***
S.E.	0.172	0.140	0.107
Coefficient (bX)	1.269***	1.329***	0.918***
S.E.	0.224	0.152	0.065

*** = P<0.0001.

Table 3.10: a) Regression coefficients (±S.E.) of shoot dry weight against plant size (Y = a + bX, where Y = shoot dry weight and X = plant size) and b) multiple regression of shoot dry weight against plant height and tiller number for ryegrass plants subjected to full, root, shoot and no competition. See Table 3.2 for further details.

Terms included	Competition treatment			
in regression	Full	Root	Shoot	None
a)				
r^2	0.8	0.8	0.9	0.8
Constant (a)	2.401***	1.752**	1.964**	1.432*
S.E.	0.148	0.329	0.349	0.558
Coefficient (bX)	0.642**	1.264**	0.974**	1.335**
S.E.	0.120	0.258	0.170	0.294
b)				
Plant height	**	*	ns	-
Tiller number	-	ns	**	**

\- = significance level not reached for entry into the model.
*** = P<0.0001.
** = P<0.01.
* = P<0.05.

with shoot or no competition (Table 3.10).

3.3.6 **Shading**

In clipped and unclipped areas, 81 and 24 % of full sunlight penetrated to the base of the pasture respectively. An estimate of shading was obviously relevant only to ryegrass plants in the treatments with above ground competition,

the results from a quadratic regression of PPFD versus time (days after treatment) showed that the r^2=0.7 for these treatments and <0.1 for those with root competition or no competition.

The relationship between tiller number, plant size or shoot dry weight against PPFD or shading index was examined by regression for data from each treatment but was poor (generally <40 % of the variation was accounted for by these factors). Plant height (dependent variable) was incorporated in a multiple regression model where the independent variables were PPFD or shading index and time, with the inclusion of all possible interactions (linear and quadratic) of these factors. The height of ryegrass plants subjected to the treatment of full competition was influenced more by shading than time in contrast to those with shoot competition where time accounted for all of the variation (P<0.01) (Table 3.11).

Table 3.11: Variance accounted for by multiple regression of plant height against a) shading index and b) PPFD for ryegrass plants subjected to full and shoot competition (see Section 3.2.6.1). Overall r^2 includes terms to P<0.15.

Terms included in regression	Competition treatment Full	Shoot
Overall r^2	0.7	0.9
a) Time	<0.1**	0.8***
Time (time²)	-	<0.1***
Shading index	0.6***	-
Overall r^2	0.7	0.9
b) Time	0.5***	0.8***
Time (time²)	-	<0.1***
PPFD	0.1***	-

- = significance level not reached for entry into the model
*** = P<0.0001
** = P<0.01

3.4 DISCUSSION

3.4.1 Introduction

Below ground competition occurred before above ground competition when ryegrass seedlings were transplanted into a hill country pasture (see Figure 3.5). On a number of measurements, below ground competition was found to be more severe than above ground competition (Figures 3.3, 3.5, 3.6, Tables 3.4, 3.5, 3.6, 3.7) nevertheless plant growth and development was affected by both (Figure 3.2, Tables 3.2, 3.3). The discussion will form two main sections based on these findings followed by a critique of the method used in the experiment reported in this thesis compared with those of other workers and, finally a comment on the practical application of this work in the field.

The objective of the experiment was to study competition from established paspalum plants on ryegrass seedlings. Paspalum did not commence vigorous growth until mid November, this was later than expected, possibly because the weather was cooler than the long term average in August and September (Table 3.1). Percival (1977) found paspalum growth occurred between October and December depending on the region. Therefore, competition from the resident vegetation against the transplanted seedlings came mainly from ryegrass and other species in the pasture, but not from paspalum. Thom *et al*. (1986b) demonstrated the severe competition from resident *Poa* spp. was equal to that from paspalum in a study on ryegrass transplanted into a Waikato dairy pasture and Rhodes (1968a) found that H1 ryegrass (*L. perenne* x *L. multiflorum*) growth was reduced from competition with established plants of the same species.

3.4.2 The relative influence of above and below ground competition

The severe effect of below ground competition on the growth of ryegrass seedlings transplanted into a hill country pasture was demonstrated from the experiment described in this chapter.

Competition below the ground was clearly shown to occur before that above the ground (Figure 3.5, see Section 3.3.5) and apparently for the first time in the field. These results, therefore, provide an answer to the relevant objective from Chapter 1. Milthorpe (1961) concluded from the work of several other researchers that root competition began before shoot competition in an establishing association of plant species, as did Weiner (1986). The method Weiner (1986) used may have invalidated his results (see Section 2.6.2).

The size of ryegrass plants was clearly divided into two categories, plants subjected to: i) below ground competition and ii) shoot competition or no competition (Figure 3.5), and this trend was also exhibited by many other factors, for example, the number of tillers, size class frequency distribution, leaf area, shoot dry weight, and root : shoot ratio (see Figures 3.3, 3.6, Tables 3.6, 3.8, 3.10, 3.11). Throughout the experiment fewer tillers were present on ryegrass plants subjected to below ground competition than those with shoot competition or no competition (Figure 3.3, Tables 3.4, 3.6). In green panic, the number of tillers per plant were similarly affected by competition from the native vegetation (Cook and Ratcliff, 1984). An analogy may be drawn with the suppressed species of a mixture; less tillers were extant in plants subjected to below ground competition compared to those with shoot competition or no competition (Donald, 1958; Rhodes, 1968c; Remison and Snaydon, 1980b). Yet, it must be remembered that research previous to that by Cook and others was criticised for the use of poor techniques (see Section 2.6.2). In the competition experiment described in this chapter and in those by Rhodes (1968c) and Remison and Snaydon (1980b) there were fewer tillers per plant under shading (Table 3.4) although this contrasts with the results from other experiments (Donald, 1958; Cook and Ratcliff, 1984). Artificial shading of plants, relative to unshaded conditions, was shown to result in fewer tillers per plant by Mitchell (1953), Mitchell and Coles (1955) and Ludlow *et al.* (1974). The rate of tillering was less under shading in the experiment reported in this chapter (Table 3.5) in agreement with Ludlow (1978) but was, unfortunately, not measured in other competition experiments.

Confirmation of the detrimental effect of below ground competition on plant growth was demonstrated by the harvest data. Total shoot dry weight (and components) of ryegrass in the treatments with below ground competition were lower than those without at day 63 (Table 3.7). These findings were in agreement with those of Donald (1958), Remison and Snaydon (1980b), but with Rhodes (1968c) for tall fescue only. Moreover, the severe stress imposed by the treatment of full competition was shown because ryegrass plants were similar in height but weighed less (Figure 3.2, Tables 3.2, 3.3, 3.7) than those without competition due to reduced shoot growth as a result of below ground competition. An analogous situation occurred for plants growing under density stress (Harper, 1977). The leaf area of ryegrass subjected to shoot competition and no competition was greater than those plants with root competition or full competition (Table 3.7), furthermore, this demonstrated the inconsistent pattern of growth between plants in the treatments with above ground competition. Accurate measurement of root growth in a field trial is inherently difficult, and may account for the lack of significant differences in root dry weight between treatments (Table 3.8). Consequently shoot measurements were mainly used to determine the effects of below ground competition on plant growth. Nevertheless, root : shoot ratio increased in plants with below ground competition (final harvest only) probably due to the longer roots of ryegrass in this treatment (Table 3.8). An increase in root : shoot ratio was also found for several species grown under conditions of low nutrient supply (Hart _et al_., 1981; Chapin _et al_., 1982; Caradus, 1983; Mouat, 1983a).

Tiller height largely determined the size of ryegrass plants in the treatments with below ground competition presumably because few tillers per plant were present (Figure 3.3, Table 3.4), whereas the number of tillers largely determined plant size for ryegrass subjected to shoot competition or no competition (Table 3.10). When data from all the treatments was pooled, in the experiment described in this chapter (Table 3.9), and in that by Bellotti (1984), most of the variation in shoot dry weight was accounted for by tiller number: 70 and 76 % respectively. In a similar fashion, plant height accounted for 80 % of the variation in shoot dry weight in the study by Cook and Ratcliff (1984). The size of ryegrass plants was a better predictor of shoot dry weight than either tiller number or plant height by 20 and 40 % respectively (Table 3.9), but smaller differences were observed (1 and 22 % respectively) in the study by Bellotti (1984).

As individual plants compete for space a pattern of dominance and suppression is established, where large plants become larger and exert influence over their neighbours while smaller plants may die if subjected to further competition or environmental stress (de Wit, 1960; Harris and Sedcole, 1974). For example, as stress increased, Bellotti (1984) demonstrated that the seedling size frequency distribution became skewed towards smaller individuals. The severe stress associated with below ground competition was exhibited by the skewed distribution of ryegrass plants in those treatments compared to the more normal distribution of ryegrass subjected to shoot competition or no competition (Figure 3.6). In addition, the size class frequency histogram clearly showed that plants with below ground competition were small and did not increase markedly in size over time (see Figure 3.5, Table 3.7). Bellotti (1984) obtained similar results in treatments that exerted a high level of stress on the establishing seedlings where the population consisted of a large proportion of small seedlings, hence a highly skewed distribution. The frequency distribution of shoot dry weight in the annual vine (Ipomoea tricolor Cav.) (Weiner, 1986) was consistent with the results obtained from the study described in this chapter. The prediction of shoot dry weight from plant size (Table 3.10) overcame problems of statistical accuracy associated with the variability shown by plants subjected to full competition (see Sections 3.2.8.1, 3.3.3.1). Similarly, Weiner (1986) reported that the greatest variation in plant size occurred with full competition.

Plant height was greatest for ryegrass in the treatment with shoot competition (Figure 3.2, Tables 3.2, 3.3). Many comparable studies have not measured plant height, but after 56 days green panic plants subjected to shoot competition were taller than those in the other treatments (Cook and Ratcliff, 1984) similarly for ryegrass tillers (pre grazing) surrounded by unclipped compared to clipped herbage (Thom et al., 1986c). The increase in height of plants subjected to shoot competition was consistent with plant response to shading (Ludlow, 1978). The influence of shading (above ground competition) on the height of ryegrass plants (Table 3.2) was only significant in the presence of below ground competition (Table 3.11). In contrast, the growth of plants subjected to shoot competition was entirely dependent on time factors, and hence apparently unaffected by shading. Donald (1963) considered solar radiation to be the major factor that limited plant growth, since competition for light (inter and intra plant shading) occurred irrespective of the soil nutrient or water status. He further speculated that with the increased use of fertilisers and irrigation, light would become the sole limiting factor to production. The modification of growth by inter plant shading was shown from the results presented in this chapter, from which it was assumed that below ground factors were of the same status in the treatments of shoot competition and no competition. Shoot weight was determined by tiller number in ryegrass subjected to shoot and no competition (Table 3.11) but the shaded plants, that is shoot competition, had fewer tillers and reduced relative tillering rate in contrast to unshaded plants (Tables 3.4, 3.5).

The experiment described in this chapter was not designed to identify the limiting factor for which below ground competition occurred, but it was unlikely to be for water due to the wet conditions in August and September 1986 (Table 3.1) therefore, it was postulated that below ground competition was for nutrients. The experiment was conducted on tracks where, for hill country, a high level of soil nutrients (mainly nitrogen) would be expected (Chapman and Macfarlane, 1985), perhaps verified by the lack of clover in the pasture, and where a similar amount of shading occurred as under fertilised conditions in a native pasture (cf. Section 3.3.6 and Cook and Ratcliff, 1984). The soil analysis (Appendix 3) indicated that soil at the site was deficient in phosphate and to a lesser extent sulphur. Reduced allocation of biomass to the shoot system under conditions of low phosphate availability was reported by Chapin (1980) and a similar response was shown by the ryegrass plants subjected to below ground competition, as these were smaller and lighter, with less tillers, lower relative tillering rate and higher root : shoot compared to those without below ground competition (Figure 3.5, Tables 3.7, 3.4, 3.5, 3.8). Cook and Ratcliff (1984) hypothesised that if competition for nutrients was the major factor limiting seedling growth, then it should be possible to increase the growth of plants in the treatments with root competition to equal those without competition through applications of fertiliser (provided that sufficient supplies of light and water are available) and this was demonstrated (Cook, 1985). Harper (1977) questioned whether the apparent importance of root competition simply reflected the fertility level at which measurements were made, hence if soil fertility was increased then shoot competition would become more important than root competition. Donald (1963) (see previous paragraph) stated that competition for light would occur independently of the soil nutrient status. Following an application of a high rate of nitrogen fertiliser, Snaydon and Howe (1986) found that the effect of root competition was partially alleviated but that of shoot competition was not increased.

In this chapter, the experiment described demonstrated that above ground competition affected plant growth in both the presence and absence of below ground competition, where plants in the latter treatment were presumably in a situation of higher nutrient availability than the former. Above ground competition did not markedly affect the growth of plants subjected to shoot competition compared to those in the treatment with no competition. Therefore, in reply to Harper's query (Harper, 1977), it appears that below ground competition has a greater influence on plant growth than above ground competition irrespective of the soil fertility level and this is in agreement with the conclusion drawn by Snaydon and Howe (1986).

3.4.3 Effect of competition on development

Comparison of plant development purely on the basis of time does not incorporate the effect of an experimental treatment on ontogeny, but an alternative index (for example, total dry weight) may be used (Hunt, 1982). In the experiment reported in this chapter (where emphasis was placed on non destructive measurements) information obtained from the fitted functions of plant height and tiller number (Figures 3.2, 3.3) was reworked to equate development on a plant based index (Table 3.12). At a specified number of tillers, ryegrass plants subjected to competition (both shoot and root) were identical in height but were taller than ryegrass under treatments where no competition occurred (Table 3.12). A greater number of reproductive tillers were present when ryegrass was subjected to shoot competition than for those in the other treatments (see Section 3.3.3.3). The similarity in height of plants in the treatments with shoot and root competition may therefore have been due to pseudostem elongation prior to ear emergence, however, the severe effect of below ground competition resulted in the latter plants taking four times as long to reach the same height as those in the shoot competition treatment. The increase in plant height associated with above ground competition when plants were compared on a temporal basis (Figure 3.2, Table 3.2) was also apparent when ryegrass plants were compared at the same tiller number. The plants that were affected by shoot competition were 33 % taller than those with no competition (Table 3.12). Weiner and Thomas (1986) found plants experiencing competition developed in the same way as those that were not competing, only more slowly and this was similar to ryegrass plants subjected to below ground competition in the experiment described in this chapter (Figures 3.2, 3.3, Tables 3.2, 3.4, 3.5, 3.12). Floral development was suppressed in ryegrass plants with full competition (see Section 3.3.3.3), presumably a reflection of the severe stress imposed by the treatment, similar to blue canary

Table 3.12: Comparison of ontogeny in ryegrass plants subjected to root, shoot and no competition by relating plant height (log_{10} cm) and time (days) to tiller number (log_{10}) calculated from the fitted functions (see Figures 3.1 and 3.2).

Tiller number		Competition treatment Root	Shoot	None
0.70	Plant height	0.4	0.4	0.3
	Time	27	6	3
0.75	Plant height	0.5	0.5	0.3
	Time	34	8	6
0.80	Plant height	0.5	0.5	0.4
	Time	41	10	9
0.85	Plant height	-	0.5	0.4
	Time	-	12	12

grass (Phalaris coerulescens Desf.) grown under conditions of severe competition (Rhodes, 1968b).

3.4.4 Critique of the methods used in the experiment

Problems associated with the technique of separating above and below ground competition between plants were evaluated in the literature review, consequently only those pertinent to the methods described in this thesis will be discussed. Clipping the above ground herbage and the use of root tubes inevitably introduces some degree of artificiality into an experiment.

There was no obvious deleterious effect of root tubes on plant growth, for example, ryegrass plants in the treatments with tubes (shoot competition and no competition) were larger and heavier (Figure 3.5, Table 3.7) than those grown without root tubes. The technique may limit the duration of experiments and species used as a result of the restricted root distribution in tubes (Cook and Ratcliff, 1984; Cook, 1985) where the volume of soil per tube was 1193 and 1963 cm^3. No mention was made by Snaydon and Howe (1986) of restricted root growth although the volume of soil per tube was 982 cm^3 and similar to that from the experiment described in this thesis (954 cm^3). Ryegrass plants in the treatment with no competition continued to grow throughout the experiment (see Tables 3.2, 3.4) perhaps because temperate grasses have a smaller basal diameter than tropical species (Cook and Ratcliff, 1984). Moreover, the age of tillers at death (Figure 3.4) increased throughout the experiment for plants grown without competition, that is, unusual patterns of death did not occur.

Clipping of herbage surrounding the transplanted seedlings may affect the root growth of the herbage plants, and hence root competition. Growth of roots is thought to cease following defoliation, albeit temporarily (Evans, 1973; Harris, 1978). Little research has been undertaken to quantify the effects of defoliation on root growth, nevertheless, results obtained have shown considerable variation (Evans, 1973). That clipping of the vegetation surrounding the transplanted seedling did not reduce root competition was demonstrated by the similar pattern of plant growth in the treatments with root competition and full competition (for example, Figure 3.5). If it is assumed that the majority of root activity occurred in the top 2.5 cm soil (Jackman and Mouat, 1972) and defoliation caused cessation of root growth (Harris, 1978) then, following the weekly clipping, new root growth would occur in this region of the soil and thus below ground competition would continue. On the other hand, the experiment was not designed to define the precise cause of below ground competition, perhaps, for example, competition for nutrients decreased ryegrass growth when plants were subjected to full competition but allelopathic chemicals secreted from the dead roots of the clipped vegetation decreased growth of ryegrass subjected to root competition.

All research projects have constraints, for the experiments described in this thesis chiefly the amount of time available on site per visit. In hindsight, the within treatment variation could have been reduced if a greater number of plants had been used, although the magnitude of the variation may have been due to the severity of some of the treatments imposed (Weiner, 1986). Also, more destructive harvests would allow better correlations with the non destructive measurements. On the whole, a more detailed determination of plant growth was provided by leaf measurements in response to external stress than tiller number or plant height, for example, Bellotti (1984) although not always (Rhodes, 1968a, 1968b). Perhaps too little emphasis was placed on leaf measurements during the experiment reported in this chapter. Further information must be obtained about root growth in relation to these studies, perhaps with the use of dyes and radioactive tracers.

Future experiments to study above and below ground competition in the field should perhaps be of longer duration than those by Cook and Ratcliff (1984), Cook (1985) and the experiment described in this thesis, therefore similar to that of Snaydon and Howe (1986). To prevent root volume inside the tube from limiting growth a perforated tube could be constructed and overlaid with a material that permits free movement of water, nutrients and perhaps allelopathic chemicals (if present) but still prevents competition between roots for space. An interesting topic for further investigation would be the effect of competition on regrowth following defoliation of the transplanted seedling.

3.4.5 Practical applications

"Surprisingly little is known about roots in pastoral systems and this component is seldom considered in management decisions" (Davidson, 1978). The severe effect of below ground competition restricted the growth of ryegrass seedlings transplanted into hill country and it was postulated that competition occurred for nutrients (probably phosphate). Addition of fertiliser would be necessary to overcome the deficit commonly found in many hill country pastures, as in other situations, for example, tropical grasslands (Cook, 1985). Aerial oversowing has been used in steep hill country as a method to increase pasture productivity by introduction of grasses, such as cocksfoot, yorkshire fog, and legumes. Management procedures designed to reduce competition from the existing vegetation and allow oversown species to establish must be capable of minimising root competition. Cook and Ratcliff (1984) demonstrated, and results from the experiment reported in this chapter suggested, that procedures such as hard grazing would convey little benefit to establishing grass seedlings in the absence of other practices to control competition, or unless severe enough to reduce root competition. Severe grazing of pastures before renovation was recommended by Thom et al. (1985) to eliminate shoot competition, but they did not consider the role of root competition. Blanket application of a broad spectrum herbicide was shown to be an effective means to control both root and shoot competition by Cook (1985) and Thom et al. (1986c), although band application of herbicide and fertiliser would reduce costs (Thom et al. (1986a) it would be impracticable on steep terrain.

Unfortunately, due to the current economic situation, pasture improvement in hill country is unlikely to be undertaken. Under severe financial constraints where even topdressing is considered uneconomic, grazing management should be used to reduce the effects of above and below ground competition. Strategic transfer of nutrients from dung and urine via the grazing animal is also possible. On the other hand, the current trends of farming in New Zealand may lead to increased use of specialist pastures on selected areas of hill country. Renovation of pasture should incorporate preparation methods to reduce competition from the existing vegetation. The use of herbicides (preferably to achieve total kill) either pre or post oversowing and hard grazing is recommended (Macfarlane, 1987). Fertiliser should be applied to increase the soil nutrient status, and therefore help to alleviate the effects of below ground competition.

Chapter 4 SURVIVAL EXPERIMENT

A study to determine the effect of environmental factors on the rate of survival of ryegrass seedlings transplanted into a hill country pasture.

4.1 INTRODUCTION

The survival and growth of plants in a pasture will be affected by a combination of environmental and management conditions, in addition to competition from the surrounding herbage , the latter aspect has already been discussed (see Sections 2.4, 2.5). Numerous experiments have been undertaken to determine the relationship between plant growth and environmental factors, for example, Norris (1985) and similar relationships would presumably influence seedling survival.

Water availability was regarded as the principle component of stress during establishment of transplanted seedlings. A situation of extreme water shortage caused early senesence, wilting and premature plant death (Christie, 1982). An experiment by Norris (1982) investigated the effect of imposed drought and irrigation treatments on grass growth during spring and summer, from which it was shown that reduced water supply decreased grass growth rate, leaf extension rate and the number of tillers per plant. When water stress was alleviated by irrigation, Norris (1985) found that the growth of grass was positively correlated with temperature and, to a lesser degree, solar radiation.

Plant size has been shown to be an important determinant of survival. The greater survival rate of large compared to small plants during summer was demonstrated by Hoen (1968) in all five trials on perennial grass species. From these results, it was assumed that the larger plants were better able to explore the soil for moisture than smaller ones due to the proportionately larger root system. Howe and Snaydon (1986) proposed that differences in initial plant size between seedlings (grown from seed) and ramets (transplanted at the two tiller stage) accounted for the greater survival of the ramets, and hence greater competitive ability of these plants. The transplanting of seedlings (ramets) rather than seeds into an established pasture therefore appeared a suitable technique to determine the relationship between environmental factors and survival of young ryegrass plants.

4.2 MATERIALS AND METHODS

4.2.1 Site description

Meteorological data was collected (see Section 3.2.7). Soil samples for moisture analysis were taken from each block on every planting and harvest date, for details of the analysis procedure see Section 3.2.7. The nutrient status of the soil was determined (Appendix 3, see Section 3.2.1).

4.2.2 Experimental procedure

A randomised complete block design was used with four blocks and six treatments per block. Two blocks were placed on tracks and two on slopes. The experimental layout is shown in Appendix 1. Each plot (1.60 by 0.70 m) contained ten evenly spaced plants. The transplanting procedure was carried out as described previously (see Section 3.2.3) except that the plastic tubes used were of two lengths (10 and 20 cm), therefore the holes were dug to the appropriate depth. Six treatments were imposed as a result of two planting dates, two harvest dates and two tube lengths. The combination of these were as follows:

Treatment	Planting date	Harvest date	Tube length	Age of plants at harvest
1	August	October	10 cm	2 months
2	August	October	20 cm	2 months
3	August	November	10 cm	3 months
4	August	November	20 cm	3 months
5	September	November	10 cm	2 months
6	September	November	20 cm	2 months

At the August planting (19 and 20) each ryegrass seedling had 3-4 leaves, by the planting on 16 September, 2-3 tillers were present per plant. Prior to the second planting, seedlings were trimmed to a height of 6 cm as part of the standard procedure to facilitate survival of larger plants (Christie, 1982).

4.2.3 **Measurements**

4.2.3.1 Non destructive sampling

A 'survival score' ranging from 0-5 was evaluated according to the quantity of dead material per plant where 0 and 5 denoted 100 and 0 % death respectively. The score was recorded for the marked plants on three occassions (16 September, 8 October and 11 November).

4.2.3.2 Destructive sampling

The above ground portion of each replicate ryegrass plant was cut and transported to the laboratory in a plastic bag. After each harvest the shoot was partitioned into leaf, stem and dead material, the number of tillers was recorded and leaf area per plant measured (see Section 3.2.6.2). Similar measurements were taken for plants on each of the planting dates. All yield components were dried in a forced draught oven for 48 hours at 80 °C.

4.2.4 Statistical analysis

Standard statistical procedures were carried out, including a $\log_{10}$ transformation (see Section 3.2.8). Planned F tests were used as these offered a more precise procedure for mean separation than the LSD or Duncan's new multiple range test. As many independent questions could be asked as there were degrees of freedom for treatments. The independent comparisons were orthogonal - a desirable characteristic, as the comparisons led to clear cut probability statements (Little and Hills, 1978). Data from the survival score was analysed as a split plot in time (see Section 3.2.8).

4.3 RESULTS

4.3.1 Site classification

Climatic data during the experimental period was shown previously (Table 3.1, Section 3.3.1). The moisture content of the soil (mean for all blocks) was 31, 33, 31 and 21 % for the samples taken in August, September, October and November respectively. The nutrient status of the soil at the beginning and end of the experiment was quantified (Appendix 3). The nutrient status of the soil was adequate for plant growth, except phosphate, but generally that on the tracks was higher than on the slopes. Unusually high values were recorded for potassium and phosphorus on slopes at the end of the experiment, possibly due to poor sampling.

4.3.2 Survival score and harvest data

Differences in the survival of ryegrass plants (obtained from the survival score) were not observed between treatments but only between blocks. A smaller number of plants survived in block four than the other three blocks (4.58 and 4.97 respectively) and a similar pattern of variation was obtained with data from the destructive harvests. Ryegrass plants in block four had fewer tillers and reduced shoot weight compared to those plants in the other blocks (3.7 and 5.2 tillers respectively and 783 and 1312 mg respectively; detransformed data). The variation in growth of ryegrass plants between the slopes and tracks did not entirely account for the observed effect because only one block was different.

There were differences between treatments in shoot dry weight and leaf area when analysed further using the method of orthogonal contrasts. The procedure indicated (cf. Tables 4.1, 4.2) that shoot dry weight and leaf area of ryegrass plants harvested in November were greater than for those harvested in October, also planting in August reduced leaf area of ryegrass compared to those transplanted one month later.

Table 4.1: Orthogonal contrasts of leaf area, shoot dry weight and tiller number of ryegrass transplanted into a hill country pasture in 1986, from data based on all destructive harvests.

Contrast	Leaf area	Shoot dry weight	Tiller number
10 vs 20 cm tube length	ns	ns	ns
August vs September planting	***	ns	ns
October vs November harvest	***	**	ns
2 vs 3 month growth period	*	ns	ns
Tube length vs growth period	ns	ns	ns

*** = $P<0.0001$
** = $P<0.01$
* = $P<0.05$

Table 4.2: Leaf area ($\log_{10}$ cm ^{2}) and shoot dry weight ($\log_{10}$ mg) of ryegrass plants (see Section 4.2.2). See Table 4.1 for further details.

Treatment	Leaf area	Shoot dry weight
1	0.99	2.84
2	0.99	3.03
3	1.27	3.13
4	1.22	3.12
5	1.34	3.16
6	1.27	3.14

Plant growth was not affected by tube length, hence there was no difference for the contrast tube length versus plant age at harvest. The number of tillers per ryegrass plant remained unchanged by any treatment.

4.4 DISCUSSION

A similar score for survival of ryegrass plants transplanted into a hill country pasture was recorded between treatments (see Section 4.3.2) and plant survival was unexpectedly high. The objective, to determine the survival rate of transplanted seedlings in relation to environmental factors (see Chapter 1), was not appropriate for the atypical environmental conditions experienced by ryegrass transplanted during late winter / spring 1986 (Table 3.1) and the rate of survival was not determined. The association of environmental factors and plant survival was not studied in great detail due to the lack of a significant difference in survival score between treatments. Nevertheless, seedling survival was probably related to rainfall and consequently the soil moisture status. The results of ryegrass survival and plant growth will be discussed in relation to environmental factors, the transplanting technique and finally to the experiment reported in Chapter 3 of this thesis.

The hill country around Wanganui was quoted in Section 2.2 as an example of land that tended to become dry in late spring and summer (Thomson, 1983; Chapman and Macfarlane, 1985). Rainfall during August and September 1986 was higher than the long term average (Table 3.1) and may account for the high survival score of transplanted seedlings (see Section 4.3.2) because water stress was the environmental factor most likely to cause seedling death (Christie, 1982; Norris, 1982, 1985). In addition, the moisture content of the soil was similar for the first three months of the experiment (see Section 4.3.1) although a quantitative estimate of the relationship between soil moisture and plant available water was not made. In summer when the soil moisture content was reduced compared to that in spring, high losses of ryegrass seedlings transplanted into a dairy pasture (range 33-44 %), were calculated from data presented by Thom _et al_. (1986b, 1986c) but losses were much lower during spring (range 1-9 %) (Thom _et al_., 1986b, 1986c) and similar to the 2 % loss reported from the experiment in this chapter. Howe and Snaydon (1986) found that seedling mortality was also greatest during the summer months but unfortunately the seasonal distribution of ramet survival was not given. The experiment described in this chapter was not designed to assess the survival of ryegrass plants over summer so that a direct comparison with the seasonality of deaths from the studies by Thom et al. (1986b, 1986c) and Howe and Snaydon (1986), although interesting, could not be made.

Leaf area was greater for ryegrass transplanted in September than August and plants were also heavier when harvested in November than October (cf. Tables 4.1, 4.2). Norris (1985) showed that in spring, dry matter production was restricted and leaf area reduced in grasses by both low soil surface temperatures and low levels of solar radiation. The relationship described by Norris (1985) applied to spring when moisture did not limit plant growth, but in summer the association between temperature and leaf extension was masked by the effect of drought. Therefore, the growth of ryegrass from the first transplanting (August) and first harvest (October) may have been restricted by temperature and perhaps solar radiation, in accordance with the results from Norris (1985), as soil moisture was not limiting during this period (Table 3.1,see Section 4.3.1). The number of tillers was similar between treatments (Table 4.1) in contrast to Norris (1982) where the number was reduced by water deficit, these results also indicate that moisture stress was probably not a limiting factor during the experiment reported in this chapter. The suitability of the transplanting technique was clearly demonstrated by the high survival of seedlings from transplanting to the first measurement date, this was: 100, 99.5 and 98 % in hill country (results from the experiment reported in this chapter) and in dairy pastures by Thom et al. (1986b, 1986c) respectively. The results from some experiments indicated that plant growth may be restricted by the volume of soil per tube (see Section 3.4.4), but it apparently did not affect the growth of ryegrass in the experiment reported in this or the previous chapter (see Figure 3.5, Table 4.1), although the two studies were not directly equatable.

The differences recorded between blocks (see Section 4.3.2) could not be categorically identified, but a visual assessment of herbage growth on the tracks was made at each harvest on the relative basis of low, medium or high (translated into 'herbage index' values of 1, 2 or 3). The herbage index for the two blocks situated on the tracks was 2.0 and 2.8 (block three in October and November) and 3.0 (both months in block four) respectively, in contrast to blocks one and two (slopes) where herbage index was never greater than 1.0. The severe effects of below ground competition on plant growth were clearly demonstrated in a related experiment (see Chapter 3, for example, Figure 3.5), especially for ryegrass subjected to full competition, presumably the poor growth of ryegrass transplanted into block four was the result of a similar degree of competition.

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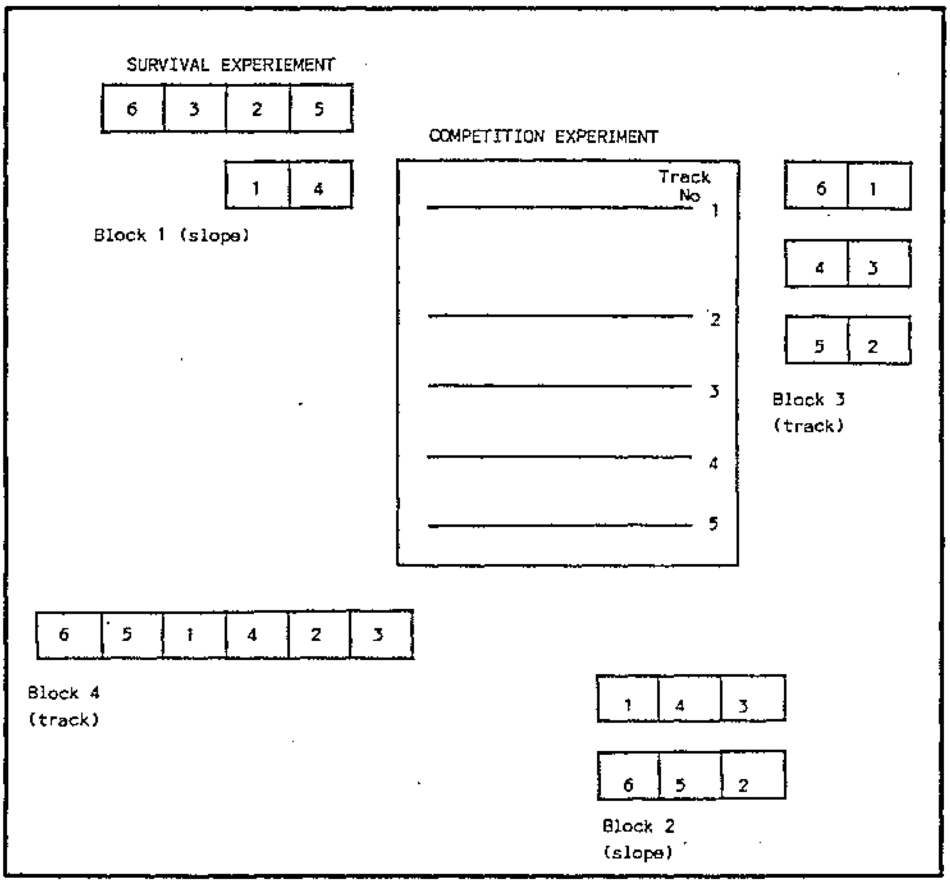
Appendix 1: Plan of experimental site at Wanganui (not drawn to scale).



Appendix 2: Covariance analysis of leaf area, plant height and shoot dry weight for ryegrass plants from all treatments using track as the covariate (see Section 3.2.8.1).

Terms included in regression	df	Covariance analysis F value	Probability > F value (%)
Leaf area:			
Treatment	3	22.94	0.01
Track	1	2.00	18.50
Plant height:			
Treatment	3	13.37	0.01
Track	1	1.26	27.22
Shoot dry weight:			
Treatment	3	13.78	0.05
Track	1	0.13	72.08

Appendix 3: Nutrient analysis of soil samples collected from the experimental sites at Wanganui (see Sections 3.2.1 and 4.2.1). Values are expressed as Olsen P for phosphorus (P), ppm for sulphur (S) and meq $100g^{-1}$ soil for potassium (K), calcium (Ca) and magnesium (Mg). (mean ± S.E.).

			Nutrient analysis					
Experiment	Date	Site	pH	P	S	K	Ca	Mg
Competition	Aug		5.8±0.1	16±4	17±2	14±3	8±1	58±2
(Chapter 3)	Dec		5.8±0.1	16±1	20±1	17±1	7±0	59±1
Survival	Aug	slope	5.6±0.1	13±2	19±0	11±1	8±0	58±3
(Chapter 4)	Aug	track	5.7±0.1	28±9	20±7	20±6	10±0	60±0
	Dec	slope	6.3±0.3	72±3	34±4	40±0	11±1	60±0
	Dec	track	5.7±0.2	27±3	34±11	21±6	10±0	60±0

Appendix 4: Regression coefficients (±S.E.) of new tillers against time ($Y = a + bX + cX^2$, where Y = new tillers and X = days) and multiple regression against 'weather variables' or both for ryegrass plants from all treatments (see Section 3.3.3.2).

Terms included in regression	Time	Weather variables	Time and weather variables
r^2	0.36	0.30	0.37
Time			
Constant (a)	0.249		0.192
Coefficient (bX)	0.022 ***		0.019 ***
S.E.	0.002		0.003
Coefficient (CX^2)	-0.0002***		-0.0001***
S.E.	0.00003		0.00003
Weather variables			
Constant		-1.097	
Rain day^{-1}		0.071***	-
S.E.		0.012	-
20cm soil temp.		0.078***	-
S.E.		0.008	-
Windrun		0.002***	-
S.E.		0.0004	-
Minimum temp.			0.015 *
S.E.			0.006

\- = significance level not reached for entry into the model
*** = P<0.0001
* = P<0.05

Appendix 5: Dry weight (mg), leaf area (cm^{-2}) and root : shoot ratio(log_{10}) (mean ± S.E.) of ryegrass at transplanting in September 1986.
Shoot dry weight = leaf + stem.

	Dry weight
Shoot	265.5+80.0
Leaf	146.8+43.1
Stem	118.7+42.3
Root	328.7+119.4
Leaf area	1.9+0.8
Root:shoot ratio	1.03