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THE EFFECTS OF PLANT COMPETITION ON VEGETATIVE AND
REPRODUCTIVE GROWTH IN SOYBEAN [Glycine max (L.) Merrill]
WITH PARTICULAR REFERENCE TO REPRODUCTIVE ABORTION

A thesis presented in partial fulfilment
of the requirement for the
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ABSTRACT

This thesis reports the results of three complementary studies in which the growth pattern of soybean cultivars Matara (semideterminate) and Amsoy (indeterminate) were compared. The first trial studied the effects of interplant competition on soybean plant growth with particular emphasis on reproductive development. A Nelder's radial spacing design (type 1a) was used which provided plant densities ranging from 5.8 up to 61.2 plants.m⁻². The second study involved a histological and morphological study of glasshouse grown soybean flowers and field grown soybean pod samples to detect possible causes of floral and seed abortion. The third experiment determined the effect of intraplant competition on reproductive development using young leaf removal treatments with glasshouse grown soybeans.

Although interplant competition created by increasing plant density reduced vegetative growth and suppressed reproductive growth such as daily flower production, flowering period and total flower number per plant, it had no significant effect on the rate of reproductive abortion.

The semideterminate Matara showed less vegetative growth during the reproductive phase than Amsoy and produced about half the flowers in a flowering period which was on average 7 days shorter. However, Matara was capable of producing a similar seed yield to Amsoy at all densities. This was because Matara had significantly lower rates of reproductive abortion than Amsoy (average 65 vs 82%, respectively).

Neither problems in pollination nor lack of fertilization was found to be an important cause of flower abortion. It was found that 99 and 95% of the classifiable ovules in normal flowers of Matara and Amsoy, respectively, had been fertilized. Seed abortion within a pod occurred at every stage as a result of the curtailment of subsequent development, and was most frequent in the basal position.

Reproductive abortion in glasshouse grown soybean occurred at all

stages but was more pronounced at the flowering stage (68% for Matara and 71% for Amsoy). Young pod (\leq 2-cm long) abortion was 9% for Matara and 11% for Amsoy, whereas large pod ($>$ 2-cm long) was less than 1% in both cultivars.

Mechanical manipulation to reduce intraplant competition by young leaf removal (YLR) proved that competition between vegetative and reproductive growth certainly existed. In Amsoy YLR diverted assimilate flow into reproductive growth, especially at the R3 growth stage. YLR by 50% starting at growth stage R3 increased flower and pod numbers per plant both by 44% in Amsoy, but did not significantly increase seed yield. However, YLR in Matara, which showed a less plastic pattern of growth, caused detrimental effects, especially with 100% YLR at growth stages R1 and R3 which significantly reduced seed yields. In this experiment, YLR did not change the rate of combined reproductive abortion in either variety.

The consistency of rate of total combined reproductive abortion in both field grown and glasshouse grown soybeans, regardless of large differences in inter- and intraplant competition suggests that reproductive abortion in soybean is under genetic control, possibly through hormone action. A model for explaining assimilate flow in reproductive development as affected by YLR is discussed and emphasizes the likelihood of a role for hormones in this process. Suggestions are made for future work in this area based on the detailed understanding of the reproductive morphology of these two cultivars which has been gained from this study.

SEED APPEARANCE (100 SEEDS) FROM 6 HARVESTING TIMES
(DAYS AFTER PEAK FLOWERING, DAPF),
SHOWING RELATIVE SEED SIZE AND THE SIGNIFICANCE OF SEED ABORTION
OCCURRING AT THE BASAL POSITION OF THREE-SEEDED PODS
IN MATARA SOYBEAN

10 DAPF



40 DAPF



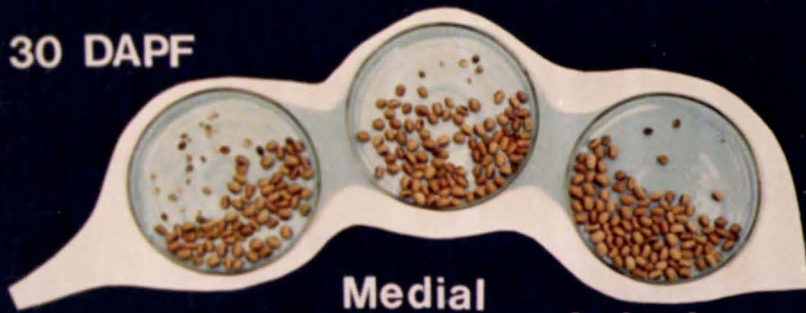
20 DAPF



50 DAPF



30 DAPF



60 DAPF



Basal

Medial

Apical

Basal

Medial

Apical

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CHAPTER 1

GENERAL INTRODUCTION

Soybean is the world's most important oilseed and grain legume crop, having a high content of both protein (ca. 40%) and oil (ca. 20%). It originated in China where first written records date back to 2838 B.C. (Probst and Judd, 1973). Early records also indicate that the soybean was one of the five sacred food-crop seeds along with rice, wheat, barley and millet which were considered essential to the existence of Chinese civilization. Soybeans continue to be an important crop in China and have also now become the prime world source of vegetable oil for human consumption and of protein for animal feed. In recent years, more emphasis has been placed on producing and processing soybeans for high-protein meal as well as for vegetable oil. Soybean protein now outranks all other food proteins in the worldwide nutrition programme (Smith and Circle, 1980). Soybeans contain essential amino acids for animal and human foods, and are a high and available source of calcium, phosphorus and thiamine (vitamin B1) (Martin et al., 1976). In the immediate future, the strong demand for soybean meal and oil is expected to continue and to double by the year 2000 (Hume et al., 1985).

Although the origins of the soybean were in the Orient, production there is now greatly exceeded by that in North America and Brazil. Between 1971 and 1982, world production more than doubled, mainly because of increases in output from the USA and Brazil (Hume et al., 1985). USA production (of which 45% was exported in 1983) is concentrated in the central part of the country, particularly in Illinois and the surrounding Corn Belt states.

In Brazil, rapid expansion of soybeans occurred during the period 1965 to 1975 when hectareage expanded 13-fold with a 28% increase in yield per hectare (Norman, 1978). Potent factors in this rapid expansion were governmental subsidies, the simultaneous development of the processing and marketing infrastructure and a healthy world market for

beans, oil and meal. Brazilian soybeans now have a significant impact on the world market, and Brazil ranks as the second largest producer next to the USA.

In New Zealand, increasing amounts of soybean products have been imported in recent years. In 1984 imports of soybeans and soybean oil were valued at US\$10,509,000, compared with US\$695,000 in 1970 (FAO, 1975; 1986b).

Although experiments with soybeans in New Zealand date back to 1914 (Gerlach et al., 1971), the conclusions from early work did not encourage commercial production. In Northland, stimulated by the Kaipara Co-operative Dairy Company's interest in vegetable oil, soybean trial work by the Ministry of Agriculture and Fisheries Research Division began in 1974 (Haysmith, 1979). However, soybeans are still not a commercially significant crop in New Zealand (Piggot et al., 1980). Agronomically, two problems prevent the general acceptance of the crop for commercial production. Seasonal variation in yield is high and weather conditions during harvest are likely to be unfavourable, particularly where late maturing varieties are sown in anticipation of high yields (McCormick and Anderson, 1981). However, in northern parts of New Zealand, soybeans have been shown to be capable of yielding 2 to 4 t.ha⁻¹ (McCormick, 1974, 1980). Such yields are considered to be relatively high by world standards (see below). Attempts have been made to reduce seasonal yield variation and to improve soybean productivity in New Zealand by varietal screening and crop management. Hopefully in the near future, soybean imports will be decreased as a result of an expansion in local soybean production.

Economically, soybean is one of the most important crops in Thailand and is classified as a crop with high potential for expansion in production (Tosunthora and Rodvinij, 1980). Recently, increases in the domestic and export demand for Thai soybean have occurred as a result of the growth in population, an increase in per capita income and an increase in the use of soybeans in mixed and packaged foods (Sirirugsa, 1984). The domestic demand for soybeans includes that for soybean oil, soybean cake and soybean foods and products such as soya sauce, soybean curd, and soybean milk. The amount and value of Thai soybean exports fluctuates from year to year depending upon the level of production,

prices and government regulations for exports (Sirirugsa, 1984). Currently, however, over 90% of the total production is consumed domestically.

Total soybean production has increased in Thailand over the past two decades. However, this increase is mainly the result of an increase in land area rather than an increase in yield per hectare. The planted area of soybeans has increased by about 7% annually since 1979 (Itharattana, 1984), and occupied an area of 106,320 hectares in the 1985 growing season. The average yield of soybean in Thailand from 1979 to 1986 was about 1.3 t.ha^{-1} , which is lower than that of major soybean producing countries such as USA (2.1 t.ha^{-1}) and Brazil (1.6 t.ha^{-1}) (FAO, 1986a). Nangju et al. (1980) suggested the reasons for poor soybean seed yields in the tropics are that environmental conditions such as the hot, humid climate and short days may not be suitable for soybean which is adapted to a temperate climate and long days. However, at present, soybean research in Thailand is in an active stage and yield potential in experimental stations is much greater than at the farmer level. Therefore, the average yield in Thailand could be increased if varieties and production techniques were improved and were efficiently transferred to the farmers.

Differences in soybean yields between communities and countries are primarily due to differences in crop management (Pendleton and Hartwig, 1973). Factors affecting yield include planting practices, planting pattern, seed quality and treatment, seed inoculation, soil fertility, cropping systems, the tillage system used, water management control, use of growth regulators, topping and defoliation, harvesting and seed storage. To improve soybean seed yield, continued research on plant-environment relationships should be carried out to provide a basis of information for suggesting improved crop management practices.

In the present study, an attempt was made to identify factors affecting soybean seed yield and seed quality by studying the effects of plant competition and crop manipulation on soybean seed production. This work was carried out to identify those aspects of vegetative and reproductive growth which contributed most significantly to seed yield and quality and was followed by a more critical appraisal of the causes of yield variation commonly occurring in this crop.

The study comprises three experiments, which are presented separately in the three following chapters. Each chapter has its own literature review, materials and methods, results and discussion. The first experiment (Chapter 2) considers the effects of plant competition as determined by variations in plant density, on vegetative and reproductive development and seed yield and seed quality in two soybean cultivars which were different in growth habit. In this Chapter, emphasis is placed on reproductive development, and particularly reproductive abortion as an important factor affecting soybean seed yield.

The second study (Chapter 3) investigates the impact of fertilization on floral abortion, and positional effects within the ovary on seed set and subsequent development. The final experiment (Chapter 4) examines the relationships between vegetative and reproductive growth within plants in terms of source-sink relationships, using a young leaf removal system to examine the effects of intra-plant competition on floral and pod abortion.

Chapter 5 discusses the overall results with particular emphasis on factors controlling soybean reproductive abortion. Scope for further study in this area is also suggested.

CHAPTER 2

PLANT COMPETITION UNDER DIFFERENT POPULATION DENSITIES IN SOYBEAN

2.1 INTRODUCTION

Plant population density is known to be one of the most important factors in soybean management. The selection of the optimum plant population to obtain maximum yield in a given environment involves consideration of a number of interacting factors, including planting pattern, planting date, environmental factors, varietal maturity and plant type. These factors have been considered and studied by many workers over the past 50 years (e.g. Wiggans, 1939; Shibles and Weber, 1966; Dougherty, 1969a; 1969b; Enyi, 1973; Lueschen and Hicks, 1977; Dominguez and Hume, 1978; McCormick and Poll, 1979; Safo-Kantanka and Lawson, 1980; Alessi and Power, 1982; Walker and Fioritto, 1984; Reicosky et al., 1985; and Duncan, 1986). However, most of these studies have been conducted to investigate the relationships between plant density, morphology or crop physiology and seed yield. Comparatively little research has involved studies on the effects of plant density on reproductive development.

Each soybean cultivar has an optimum plant density for maximum seed yield (Wiggans, 1939; Wilcox, 1974). Different types of growth habit are also found to respond differently to environmental stresses, especially density stress (Hicks et al., 1969; Dominguez and Hume, 1978; Villalobos-Rodriguez and Shibles, 1985). Significant interactions were found among location, growth habit and plant density in Phaseolus vulgaris, and these factors affected yield (Nienhuis and Singh, 1985). In soybean, Herbert and Litchfield (1982) pointed out that soybean cultivars adapted to the US Midwest show little seed yield response to increased plant density (Weiss, 1949; Lueschen and Hicks, 1977), whereas soybeans adapted to more southern latitudes show depressed seed yields at densities higher than normal (Enyi, 1973; Hoggard et al., 1978). In New Zealand, although many studies have been done on the effects of planting densities on plant growth and seed yield (Dougherty, 1969a; 1969b; Brown et al., 1971;

Tolentino, 1985), very few of them have used a wide range of plant population densities. A study on the effects of plant density on plant growth and yield in a wide range of plant population densities particularly using soybeans with differing growth habits, may therefore be useful for soybean yield improvement and for an understanding of the factors affecting soybean seed yield in New Zealand.

The present experiment was carried out to investigate the plant growth response to competition stress under a wide range of plant population densities in two soybean cultivars, Matara and Amsoy. These two cultivars were chosen because they represent two different types of growth. Matara is a cold tolerant semideterminate cultivar with an average maturity about two days earlier than Maple Arrow and 10-14 days earlier than Amsoy (Anderson, 1987). Yields of Matara have normally been equivalent to Amsoy in warm seasons but in cool seasons it has yielded more. Genetically, Matara is a cross between Amsoy and Portage, the latter being an extremely early and cold tolerant line from Sweden (Anderson, 1987). Amsoy (an indeterminate cultivar, Maturity Group II) is a cross between Adams and Harosoy and is found best adapted to approximately 41° to 42°N latitude (Weber, 1966). Amsoy has been found most acceptable as a commercial and high yielding cultivar in New Zealand (McCormick and Anderson, 1981).

The two main factors involved in plant population are plant density and spatial arrangement. Rogers (1972) emphasized that planting arrangement is especially important in cases where density is altered by changing row width without changing linear spacing. The radial spacing design (type 1a) proposed and developed by Nelder (1962) seems appropriately suitable as a tool for studying the effects of plant population density without the confounding influence of spatial arrangement. This design is based on a grid made by the intersection of concentric circles and with equally spaced circle radii. Although the plant arrangement is not strictly square the deviation from squareness is only slight (maximum 5%) (Nelder, 1962). This property of the design is an advantage because it is known that the highest yield at a given density is obtained when the plant arrangement is square or approximately square (Wiggans, 1939; Donald, 1963; Rogers, 1976; Mack and Varseveld, 1982; Auld *et al.*, 1983) (see also section 2.2.3.1).

The principle objectives of the study considered in this chapter were as follows:

- To study the effect of spacing stress induced by a wide range of plant densities on soybean interplant competition.
- To determine the effect of soybean plant density on crop morphology as related to seed yield.
- To study the effect of plant density on flower production, seed development, seed yield and yield components in soybean.
- To compare the response of two soybean cultivars representing semi-determinate and indeterminate plant types to plant density stress.

2.2 LITERATURE REVIEW

2.2.1 Plant Competition

2.2.1.1 Definition

The term 'competition' has been widely used in various agricultural situations. Donald (1963) defined competition as 'a phenomenon which occurs when two or more organisms seek the measure they require of any particular factor or thing, and when the immediate supply of the particular factor or thing is below the combined demand of the organisms'. This definition is widely accepted among plant ecologists (Hill and Shimamoto, 1973), and can also be applied to intraplant competition.

i) Interplant competition

Interplant competition most commonly occurs as a result of limited supplies of radiant energy (light), nutrients, water, carbon dioxide and to a lesser extent, space (Donald, 1963, Rhodes, 1970, Etherington, 1983). A few active modifications of the environment by secretion of specific toxins (allelopathy) may also be important in some circumstances (Etherington, 1983; Rose et al., 1984).

Competitive ability - the ability of a plant to emerge quickly, to form a canopy rapidly, to exploit the environment efficiently for growth factors and to slow the growth of other competing plants - has been found to differ among cultivars. In soybeans, for instance, competition stress exerted by the spatial arrangement and phenotype of surrounding plants occurs differently among cultivars grown in variety mixtures (variety blends), or in pure stands (Probst, 1945; Hanson et al., 1961; Hinson and Hanson, 1962; Schutz and Brim, 1967; Schutz et al., 1968; Fehr, 1973; Fehr and Rodriguez, 1974). In pure stands, differential cultivar responses to changing plant spacing have been detected (discussed later). Such responses have included differential effects on yield (Probst, 1945; Hicks et al., 1969; Cooper, 1977; Costa et al., 1980); agronomic characteristics such as plant height (Doss and Thurlow, 1974; Lueschen and Hicks, 1977; Dominguez and Hume, 1978), leaf area (Hicks et al., 1969), number of branches (Lehman and Lambert, 1960; Lueschen and Hicks, 1977), number of pods (Lehman and Lambert, 1960; Dominguez and Hume, 1978), and seed filling period and seed weight (Hinson and Hanson, 1962). These characteristics are all influenced by competition stress and have long been recognised as important factors in plant selection in breeding programmes (Hinson and Hanson, 1962).

Plant breeders have become interested in the exploitation of plant structural differences to improve disease avoidance, seed quality, lodging resistance, adaptation to mechanical harvesting and seed yield (Hartung et al., 1980; Adams, 1982; Fuller et al., 1982; Cooper and Waranyuwat, 1985; Nienhuis and Singh, 1985; Foley et al., 1986). Knowledge of plant structural characteristics and yield relationships is therefore considered to be a necessary prerequisite to the design of effective breeding strategies for increasing seed yield. The present review considers the physiological relationships between structural characteristics and yield as a result of morphological adaptation to specific environments, particularly under different degrees of interplant competitive stress.

ii) Intraplant competition

Intraplant competition or internal competition is defined as the competition for limited growth factors between the organs within a plant. Every organ is in competition with every other organ, for instance each leaf is in competition with every other leaf, particularly for water or nutrients and light. The most intense kind of intraplant competition exists between leaves for light (Donald, 1963), basically because light is not redistributed. If a leaf is heavily shaded, it will be unable to maintain itself above compensation point and will die.

Each flower and fruit is also to some degree in competition with the other flowers and fruits on the plant (Addicott, 1982). Competition between vegetative and reproductive organs is recognised as an important phenomenon and, in many instances, can affect the agricultural yield of a crop (Williams and Joseph, 1976).

2.2.1.2 Competition for light

Most plants adapt to changes in radiation regimes through both morphological and physiological changes. The interception of light is so important that it has also been suggested that most other limiting factors ultimately operate through competition for light (Etherington, 1983). Egli (1976) suggested the objective of any crop management system was to intercept as much incident solar radiation for as long as possible, especially during the grain-filling period to maximize production. To accomplish this objective, he proposed that an adjustment of planting date, row spacing and plant population may be required.

As plants grow, light penetration to the central and lower leaves is inhibited by both inter- and intraplant competition. Mutual shading and competition for light is especially evident in soybeans. Johnston *et al.* (1969) studied leaf photosynthesis at three levels of soybean canopies (top, middle and bottom). They found that the rates of apparent photosynthesis of bottom and middle soybean leaves were 13% and 60% of the $20.2 \text{ mg CO}_2 \cdot \text{dm}^{-1} \cdot \text{h}^{-1}$ rate of top leaves under natural

canopy conditions. Light enriched treatment caused an increase in seed yield at the bottom and middle canopy positions by 30% and 20%, respectively. This was due to increasing node numbers, branch numbers, pods per node and seeds per pod.

Penetration of light into the canopy is closely related to plant arrangement and plant population density. Shibles and Weber (1966), working with four populations and four row spacings in soybean, demonstrated that the combination which more nearly approached an equidistant spacing reached 95% light interception first. Safo-Kantanka and Lawson (1980) also demonstrated a slight advantage in yield as plant arrangement approached squareness and commented that this may be due to a much more uniform distribution of light between and within plant canopies as plant arrangement became more uniform.

2.2.1.3 Competition for water

Water stress is one of the important problems in soybean production. The effect of water stress on growth and yield depends both on the degree of stress and on the stage of growth at which stress occurs. Generally, the pre-flowering stage of growth is the most tolerant, whereas the periods of anthesis and pod filling are the most sensitive to water deficits depending on both the severity and duration of stress (Shaw and Laing, 1966; Doss and Thurlow, 1974; Lawn et al., 1977; Sionit and Kramer, 1977; Wien et al., 1979; Laohasiriwong, 1982).

In plant communities, competition for water usually occurs together with other forms of competition - especially nitrogen and light. If competition for water and nitrogen is intensified, and growth is restricted, then competition for light will be less important. On the other hand, if water and nutrients are non-limiting, shading will be a major competitive factor (Donald, 1963).

Studies have been shown that there is an interaction between planting pattern and water use. Generally, plants grown under narrow rows (15-25 cm) seem to use soil water more efficiently than wide-row (76-100 cm) plants (Taylor, 1980; Alessi and Power, 1982; Reicosky et al., 1982; 1985).

2.2.1.4 Competition for nutrients

Based on studies in corn by Lang et al. (1956) and in sweet corn by Chipman and Mackay (1960); Donald (1963) derived a relationship between plant population density and competition for nutrients. As fertility status is improved, so the density required to give maximum yield by annual crops will increase.

Cooper and Jeffers (1984) reported linear yield increases with increasing N fertilizer in a non-nodulated cultivar, Clark rj_1 . A significant yield advantage was obtained at the highest nitrogen rate with a higher plant density, but this was confounded with planting pattern in this study. Leaf nitrogen analysis suggested that the narrower rows used at the higher density may have caused an increase in the plant's ability to exploit available nitrogen at an early stage of development, thus creating an increased nitrogen demand and utilization capacity during subsequent growth.

In nodulated soybean the response to fertilizers is inconsistent (Ohlrogge, 1960). Nutrient stress, especially for nitrogen, will be less pronounced. Buttery (1969a) studied competitive stress by growing soybeans at four plant densities and at two levels of applied fertilizer (with and without N,P,K). He found fertilizer application was associated with slight changes in plant weight and seed yield at all densities. There was no interaction between density and fertilizer. Some researchers, however, consider that the inconsistency of response of soybean seed yield to fertilizer application is due to the redistribution of nutrients from vegetative material to seeds during the seed filling period regardless of the rate of fertilizer application to the soil (e.g. Hanway and Weber, 1971a; 1971b; Egli et al., 1978b).

2.2.1.5 Competition for carbon dioxide

In much crop physiological work, a direct relationship is believed to exist between the leaf photosynthetic rate and economic yield. In soybean, both light intensity and atmospheric CO₂ concentration are

known to limit photosynthesis and dry matter production (Brun and Cooper, 1967; Sakamoto and Shaw, 1967; Johnston et al., 1969; Hardman and Brun, 1971).

CO₂ enrichment has been found to be highly correlated with crop yields in many species (Hardman and Brun, 1971; Krenzer and Moss, 1975; Peet et al., 1977; Sionit et al., 1987). Yield increase by CO₂ enrichment is obviously due to increased photosynthetic activity. However, high CO₂ concentration is also found to affect leaf senescence in soybean. Hardy and Havelka (1975) reported delayed senescence in soybeans, probably because the high CO₂ enabled nodules to fix nitrogen faster, delaying the redistribution processes of nitrogen from the leaves to reproductive parts. A delay in leaf senescence will increase yield in those cases where the length of the fruit growth period would otherwise be limiting (Baker and Enoch, 1983).

Plants grown under environmental stress, such as nitrogen stress, respond differently to plants grown under normal conditions. In non-nodulating soybeans, CO₂ may partially offset the yield effect of nitrogen shortage. In such cases, it will almost certainly be necessary to add more fertilizer nitrogen to crops to take full advantage of the increased CO₂ (Baker and Enoch, 1983).

As crop yields can be increased by CO₂ enrichment, it is clear that the natural atmospheric CO₂ concentration of 300-350 ppm is well below the optimum for photosynthesis. This is especially true in a C₃ crop such as soybean where photorespiration is an important factor limiting carbon fixation. A denser canopy in still air will deplete ambient CO₂ concentrations faster than a less dense one.

2.2.2 Growth and development as affected by plant competition

2.2.2.1 Vegetative growth

Generally, soybean plants grow 90-120 cm in height with the first leaves simple and opposite and all other leaves alternate and trifoliate. Branches (usually 0-6 per plant depending upon planting density) may develop from buds in the lower leaf axils. Soybeans have 19-24 nodes per plant, each possessing the potential for both branching

and floral development (Shibles et al., 1975). The root system consists of lateral roots arising from the upper 10-15 cm section of the primary root. These lateral roots extend outward from the plant nearly horizontally for 40-50 cm and then grow downward to depths as great as 180 cm. Soybean root nodules produced by Rhizobium japonicum are important in nitrogen fixation which, of course, affects the density-fertilizer response of soybean stands as already discussed (section 2.2.1.4).

i) Morphological characteristics

Some morphological characteristics such as plant height, node number, internode length and branch number are changed by interplant competition. Among these characteristics, plant height is the first characteristic affected by plant population density (Doss and Thurlow, 1974; Wilcox, 1974; Wallace, 1986). After the first month of growth, the height of higher density plants tends to increase faster than that of low density plants, basically because of increased internodal length (Doss and Thurlow, 1974).

However, in cultivars that are susceptible to lodging, plant height may not be affected by plant population density (Hoggard et al., 1978; Lueschen and Hicks, 1977). Increased lodging as plant population density increases appears to be associated with decreased stem diameter rather than changes in height per se.

In soybean, the number of nodes per plant (Buttery, 1969a; Enyi, 1973), the number of nodes with pods (Enyi, 1973) and the number of branches per plant (Hinson and Hanson, 1962; Weber et al., 1966; Buttery, 1969a; Enyi, 1973; Costa et al., 1980) normally decrease with increases in plant population density.

ii) Leaf development and crop growth

Plant population arrangement combinations which favour the rapid attainment of a high LAI can lead to maximum dry matter production. High population density plants take less time to reach maximum light interception than low population density plants (Shibles and Weber, 1965 and 1966). Under very high population conditions, soybeans tend to be taller and produce smaller leaflets and longer petioles than plants grown at lower population densities. Shibles and Weber (1966) suggested that these structures of high density plants show a less dense canopy and can better intercept solar radiation.

However, in soybean, maximum seed yield has been shown to be attained at LAI values less than the LAI for maximum dry matter production (Weber et al., 1966). There are two stages of energy conversion by plants (Weber, 1968); i.e. the capture and transformation of light energy into sugar intermediates (photosynthesis); and the conversion of these sugars into plant parts and products (growth and differentiation). Yield limitation in plants with maximum LAI may be on the latter process, with vegetative growth competing with reproductive growth for photoassimilate.

The typical pattern of LAI development in a field crop may be divided into three phases - leaf expansion, mature canopy and leaf senescence (Fisher, 1984). Leaf expansion is a result of the rate of leaf formation and the rate of expansion of leaves already formed, which is greatly affected by temperature, nutrition and soil moisture. High planting density obviously increases LAI in the early growth stages and usually has some influence on peak LAI. Leaf senescence is often associated with redistribution of nutrients formerly assimilated in leaves into developing fruits and seeds. Any environmental factor that stimulates early flowering will also accelerate leaf senescence. Water stress, low light intensity and inadequate mineral nutrition are all reported to hasten leaf senescence (Fisher, 1984).

Dry matter production in soybean is highly correlated with LAI. Shibles and Weber (1965) revealed that rate of dry matter production increased with increasing leaf area development of the plant community and approached a maximum asymptotically. For some crops an 'optimum LAI' exists such that the rate of dry matter production is at a maximum at a particular LAI and is less at LAI values below or above this value (Donald, 1963). For those crops which have attained an optimum LAI, lower leaves are apparently net sinks and require photosynthates for maintenance by translocation from active upper leaves. However, soybeans do not attain an optimum LAI (Weber et al., 1966; Buttery, 1969b), since dry matter production increases as LAI increases to a maximum of about 5.0 but does not decrease at greater LAI values.

2.2.2.2 Soybean growth habit

Two types of growth habit are common in soybeans, the indeterminate type and the determinate type. Indeterminate cultivars generally begin to flower when plants have reached less than half the final plant height whereas determinate cultivars have often reached nearly full height before flowering begins. There are two genetic types which control determinacy in soybean, dt_1 recessive and Dt_2 dominant to indeterminateness. According to Bernard (1972) 'the primary effect of both dt_1 and Dt_2 is to hasten the termination of apical stem growth, which decreases both plant height and number of nodes, but dt_1 has a much greater effect'. The common form of the determinate stem type is controlled by dt_1 a recessive gene that abruptly terminates stem growth at the time of flowering. Shibles et al. (1975) described indeterminates as having the largest leaflets and longest petioles in mid-plant with gradations in size toward each end of the stem, whereas, in determinate plants, leaflet size and petiole length are not smaller at the top of the plant. Since upper leaves of determinate types are large, their canopies possess poorer light distribution characteristics than indeterminate types. After flowering begins, indeterminate plants continue stem growth and leaf production for a long period of time, whereas the stem growth of determinate plants terminates either before flowering or shortly thereafter (Foley et al., 1986). One important

characteristic of determinate types is that the stem and branches possess a terminal raceme with a cluster of pods.

Egli and Leggett (1973) studied dry matter accumulation patterns in determinate (an experimental strain, D66-5566) and indeterminate (Kent) soybeans and reported that at initial flowering D66-5566 had reached 84% of its maximum height, compared with 64% for Kent. At this point the stem dry weight of D66-5566 was 67% of the maximum compared with only 30% for Kent. This result points out that although stem elongation of the determinate type was nearly complete when flowering began, the dry weight continued to increase.

Determinate and indeterminate soybean cultivars have been found to respond differently to water stress. Villalobos-Rodriguez and Shibles (1985) reported that indeterminate cultivars were better able to recover from water stress than determinate ones, as indicated by their greater seed yield after recovery from stress treatment. This may be because of the longer vegetative growth potential during the flowering period in indeterminate cultivars which allows them to escape the stress by vegetative re-growth when water stress is removed.

Plants which are classified as semideterminate types, have a dominant gene Dt_2 which continues stem growth after flowering is initiated, but they terminate stem growth sooner than indeterminate types (Bernard, 1972). Results from comparisons between near-isogenic lines of semi-determinate and indeterminate types generally show that the stem growth termination type has no effect on seed yield (Green et al., 1977; Chang et al., 1982). Semi-determinate cultivars do have advantages in terms of earlier maturity, and being shorter in height may have lesser lodging than indeterminate cultivars under conditions of luxuriant growth (Green et al., 1977; Chang et al., 1982). In terms of response of soybean to planting pattern and plant population density, Green et al. (1977) reported no significant interaction between row spacing (30 and 100 cm) and growth habit of semi-determinate and indeterminate cultivars, but determinate cultivars may require different production practices (Hicks et al., 1969; Villalobos-Rodriguez and Shibles, 1985).

Fehr et al. (1985) studied yield loss following defoliation (removing fully developed leaves) and found that semi-determinate genotypes were more susceptible to 100% defoliation at growth stage R2 (full bloom) and R5 (beginning of seed formation) than indeterminates with a similar genetic background. This suggests that stem growth termination of a cultivar may be a factor to consider when assessing the impact of defoliation from hail, insects, or other factors.

2.2.2.3 Reproductive growth

i) Flowering and reproductive abortion

Flower production and reproductive abortion are reported to be affected by genetic and environmental conditions. Van Schaik and Probst (1958a) showed the results from a 2-year study with 4 parental soybean varieties and their 6 crosses (F_1 and F_2). Flower production varied from 5 to 33 from node to node and flower shedding percentages ranged from 32 to 83 from line to line. They found that there was a considerable environmental influence. In their following studies (Van Schaik and Probst, 1958b), both temperature and photoperiod were implicated, the percentage of flower and pod shedding being increased by both high temperature and long photoperiod.

Vrataric (1986) found in a 3-year study of 8 soybean varieties that the number of flowers per plant varied with sowing date, variety and year and there were interactions among these factors. Low rainfall and high temperature were the main factors suppressing flower production. Sionit and Kramer (1977) reported that water stress during flower induction and flowering caused soybean plants to produce fewer flowers, pods and seeds than controls as a direct result of a shortened flowering period and increased flower abortion. Stress during early pod formation however, resulted in the greatest reduction in the number of pods and seeds at harvest.

Low humidity is also reported to cause reproductive abortion in soybean. Woodward and Begg (1976) found that soybean yields decreased when grown in low humidity conditions as a result of

a reduction in pod number and seed number. The reduction in pod number was related to flower abortion rather than pod abortion. However, they suggested that abortion was possibly a consequence of reduced photoassimilate supply, probably through the reduction in stem and shoot dry weight.

Hardman (1970) reported that soybean flowering behavior was affected by planting date. The differences in both temperature and light intensity at each planting time were suggested to influence the level of flower abortion.

Relatively little research has been conducted to investigate the effect of plant population density on flower production and reproductive abortion in soybean. Buttery (1969a) studied soybeans grown at 4 plant population densities (4, 8, 16 and 32 plants.m⁻²) with and without fertilizer (N,P,K). He reported that flowers were first observed 42 days after planting and pods were seen 56 days after planting. Flower numbers reached a peak around 71 days after planting, before declining gradually. Pod numbers reached their highest numbers around 85 days after planting, declining slightly thereafter in both years. Both flower and pod numbers were very much influenced by density. Fertilizer had little effect on flower numbers but increased pod numbers in both years. Reproductive abortion significantly increased as plant density increased ranging from 41.4% to 49.8% in 1965 and from 27.3% to 50.8% in 1966. In this study, he suggested that the values used for total flowers produced were almost certainly underestimated, since some flowers may have been formed and abscised between sampling periods.

Dominguez and Hume (1978) observed flower and pod formation every 7 days after flowering began in a first-year study (1975) and every 4 days in a second-year study (1976). They found that flower numbers decreased as plant density increased and four different cultivars performed in the same manner. Averages of four cultivars, in terms of total flower numbers per plant ranged from 24 to 43 in 1975 and 32 to 51 in 1976 when plant densities were decreased from 120 to 40 plants.m⁻².

Total abortion of flowers however, was found to increase with increasing plant density ranging from 48% to 57% in 1975 and 29% to 51% in 1976. They noted that the greatest percentage of total abortion occurred during the flowering period and pointed out that the abortion process exerted considerable control over the number of pods available for the plant to fill in the later stages of seed development. No reason is given in either paper for varying abortion rates from year to year.

In lupin, Herbert and Hill (1978) reported that in dense populations, plants produced fewer inflorescence orders, and had a shorter flowering period.

ii) Pod and seed development

Typically, there are three stages in normal seed development, i.e. development of the embryo, accumulation of food reserves and ripening (Thomson, 1979). In the first stage, cell division occurs rapidly until the embryo is almost fully formed. The moisture content throughout is about 80%. When the seed starts rapid accumulation of dry matter, seed moisture content declines progressively during seed development, reaching approximately 60% or less as the seed approaches maximum dry weight (i.e. physiological maturity) (Andrews, 1966; Obendorf et al., 1980). Any increase in the size of the embryo during the second stage is due to enlargement of the cells formed in the first stage, rather than to further cell division. At the end of this stage, the seed is structurally complete. Thereafter, there is little or no increase in the material content and dry weight remains constant, although seed moisture content continues to decrease to somewhere between 10 and 20%.

In soybean, the developing pod normally reaches its maximum length and width before linear seed growth (Fraser et al., 1982). Maximum dry weight (so called physiological maturity) has been related to visual indicators of seed suitability for efficient harvest. Of 11 parameters observed by Crookston and Hill (1978), the parameter most consistently coinciding with

physiological maturity was the initial shrinking of the seed (separation from pod wall). Another positive indication of physiological maturity was the complete loss of green colour from pods (Gbikpi and Crookston, 1981). TeKrony et al. (1979) suggested that the change of soybean seed coat colour to yellow indicates physiological maturity and showed that when the seed coat turned yellow, seed respiration rate declined rapidly, seed moisture content dropped below 60% and the transport of ^{14}C -labelled assimilates into the seed ceased.

High seed yield is thought to be associated with the rate and duration of accumulation of dry matter in the seed and, consequently, factors influencing either the rate or duration of food reserve accumulation may have a direct influence on seed yield. Egli and Leggett (1973) reported a positive relationship between the duration of the seed filling period and seed yields. Nelson (1986) also demonstrated the same effect and suggested that the use of the R4 or R5 growth stages (described by Fehr and Caviness, 1977; see also Appendix 10) as estimates of the beginning of seed fill and R7 as the termination of dry matter accumulation is reasonable. In contrast to the duration of dry matter accumulation in seed, studies show that seed growth rate has no effect on seed yield. Egli (1975) found that four genotypes which were different in seed growth rate (ranging from 3.38 to 8.32 $\text{mg}\cdot\text{seed}^{-1}\cdot\text{day}^{-1}$) were not different in seed yield. Meckel et al. (1984) investigated the effect of moisture stress on the growth of individual seeds. They found that although stress treatment reduced yield and vegetative growth, the rate of seed growth ($\text{mg}\cdot\text{seed}^{-1}\cdot\text{day}^{-1}$) was not affected. However, the seed filling period (estimated as days from growth stage R5 to R7) was shortened by severe water stress. From these studies, therefore, it may be noted that seed growth rate is consistent and not affected by environmental stresses, whereas duration of seed dry matter accumulation is more sensitive to environmental stresses and is closely related to seed yield.

iii) Seed quality at final harvest

High yield and high seed quality are the primary goals of seedsmen. In contrast to yield, little work has been directed towards determining the effect of environmental stress on seed quality.

The capacity for germination of soybean seed is developed before seed reaches maximum dry weight (Burris, 1973; Obendorf et al., 1980). Obendorf et al. (1980) reported that the capacity for germination of air-dried field grown seeds increased as harvest date was extended from 34 to 46 days after flowering. Full germinability was attained at about 46 days after flowering, while seed dry weight reached a maximum about 50 days after flowering. Moreover, Andrews (1966) found that seed from increasingly later flowers attained specific levels of germinability within increasingly shorter periods of time, or in other words, late produced flowers in soybean were found to develop faster in terms of germinability.

In general terms, plants have evolved a remarkable capacity to adjust seed production to the resources available. Commercially, the few seed produced under marginal conditions may be as good as seed produced under more favorable conditions in terms of quality. The typical response of plants to environmental stresses such as low soil fertility and/or chronic moisture stress is reduction in the quantity of seed produced rather than in their quality (Delouche, 1980). The results by Juntakool (1983) who studied the effect of irrigation and plant spacing on seed development in Siratro, determined at 5, 10, 20, 30 and 40 days after peak flowering support this. Her results clearly showed that neither variable differentially affected seed germination capacity and moisture content. However, in soybean, seed size is not always conserved (Burris, 1973 : see section 2.2.3.1) and there are a few reports indicating that environmental conditions affect seed quality, which may affect parameters such as seed storability.

Environmental factors during seed development and seed maturation such as soil water, nutrients and temperature, can all influence soybean seed quality (Delouche, 1980), particularly during the postmaturation-preharvest period. Green et al. (1965) found that soybean plants from early planting dates which matured during hot, dry weather produced seed of reduced quality. Seed from later dates of planting which reached maturity after the hot, dry weather conditions had ended, were high in quality.

Few studies have determined the effects of plant population density on soybean seed development and seed quality. In soybean, Burris (1973) reported that the patterns of seed development in terms of seed dry weight at 2 planting densities (75x3.75 cm vs 75x7.5 cm) were the same, but low densities showed a decrease in seed weight in Amsoy of more than 1 g. 100 seeds⁻¹. He reported a significant reduction in germination percentage in seeds grown from low plant density, but did not give the data. Presented values for average germination over the two densities are between 96 and 98% for four different cultivars, suggesting that differences are small.

Hinson and Hanson (1962) studied plant competition in 4 soybean cultivars grown under 5 plant densities (spacings from 5.1x96.5 to 81.3x96.5 cm). Seed quality was evaluated by rating seed appearance and they reported that spacing treatments per se apparently had no direct effect on seed quality, and that competition did not influence seed quality. Percentage of protein and oil were also determined in their study. Considering the average of all four cultivars, percent protein increased and percent oil decreased as plant densities increased. However, one of the four cultivars was conspicuously stable in both percent protein and percent oil over all spacings, therefore general statements did not apply to all genotypes.

Dornbos and Mullen (1985) also found in soybean seed that protein percentage increased while oil percentage decreased

significantly with increased drought stress. Protein content in seeds from the bottom half of the main axis and from branches of drought stressed plants was higher than in seeds from the top half of the main axis. Seeds from branches contained a higher oil content than seeds from the main stem. They also determined the quality of seeds using germination tests, seedling axis dry weight and conductivity measurements. The results revealed that both viability and seed vigour decreased as drought stress intensity increased. Seed germination was reduced by a small but significant amount, dependent upon position on the plant. Germination percentages of seed from the top half of the main axis and from branches did not decrease with moderate drought stress, then decreased slightly from 98 to 95% germination with severe drought stress. Seed from the bottom half exhibited slightly poorer quality in the control plants, and germination percentage decreased more rapidly to 89% with severe drought stress. Further studies by Smiciklas *et al.* (1987) have found that drought stress during the R5 stage reduced the concentration of calcium in the seed. This reduction was associated with reduced germination and increased seed leakage. The relationship between calcium and membrane integrity is well documented (e.g. Sutcliffe and Baker, 1974).

2.2.3 Economic yield as affected by plant competition

Soybeans not only require large amounts of nitrogen for seed production but are also one of the lowest producers of seed biomass per unit of photosynthate (Sinclair and de Wit, 1975). Therefore, yield improvement with high seed protein is important, but may be difficult.

2.2.3.1 Yield and yield components

Soybean yield components traditionally comprise the number of plants per unit area, pods per plant, seeds per pod and individual seed weight. When a range of genotypes or environments is investigated regardless of the number of plants per unit area, the number of pods per plant is the component most closely correlated with yield (e.g. Pandey and Torrie, 1973; Dominguez and Hume, 1978; Herbert and

Litchfield, 1982; Board, 1985). Dominguez and Hume (1978) reported that increasing plant densities reduced both initial and final pod numbers per plant. A larger reduction was observed when the density increased from 40 to 80 plants.m⁻² than when the density increased from 80 to 120 plants.m⁻². Differential responses in pod increase may occur because of the formation of more pods on branches, greater numbers of pods per node, more nodes bearing pods, or due to combinations of some or all of these factors (Hume et al., 1985).

Number of seeds per pod and individual seed weight are also influenced both by environment and genotype, but most genotypes tend to have a characteristic seed weight range from 120-280 mg.seed⁻¹ (Shibles et al., 1975). There have been inconsistent results from plant density studies in terms of seeds per pod and seed weight. For example, Dominguez and Hume (1978) found that the production of more pods per plant in low densities was accompanied by fewer seeds per pod rather than the reduction in average seed size, whereas Burris (1973) found that low density plants produced smaller seeds, because the increased pod numbers caused an additional demand on available photosynthate and the increased branching which occurred on plants grown at the lower population density reduced the amount of photosynthate going to any one pod and thus reduced seed size.

Safo-Kantanka and Lawson (1980) studied the effect of row spacing and planting pattern in 2 short-season soybean cultivars. Although they found no significant yield differences in different planting patterns, they reported that the number of pods per plant and seed size both increased significantly as plant arrangement approached square planting.

Other studies have supported this finding. Wiggans (1939), following a 4-year spacing study with 'Cayaga' soybeans, concluded that as the arrangement of plants in a given area approaches a uniform distribution, the yield increases. Donovan et al. (1963) evaluated the performance of 'Mandarin' soybeans in five row widths ranging from 18 to 90 cm and at spacings of 2.5, 5, and 7.5 cm within the row. Maximum yield was obtained from the combination of narrowest row width and widest plant spacing within the row.

One reason why the square planting pattern yields more seeds per unit area than a row planting pattern within the same plant density has been suggested by Duncan (1986). For any selected dense planting rate, row planting will cause the plants in each row to be closer together than in the square pattern. As a result, the within-row plants will shade each other more during early growth and because each plant intercepts less light than in the less crowded square plants, each row plant will weigh less. Greater vegetative weight of the square plants during the seed initiation period ultimately results in higher seed yield. This postulate can be supported by the redistribution of assimilates from vegetative parts to the seed during its development.

Within a square planting pattern, soybean yield increases with plant density, reaches a maximum and then plateaus. Wilcox (1974) used the radial design (type 1a) of Nelder (1962) and three different cultivars to give plant densities of 2.5 to 58.0 plants.m⁻². He reported that seed yields of the three cultivars differed in their response to plant density. Maximum seed yields for C1477 and L15 occurred at 28.1 plants.m⁻² and for C1421 at 45.6 plants.m⁻². Tolentino (1985) also used an identical radial design to determine the effect of plant density on seed yield in the soybean var. Matara. At densities ranging from 2.0 to 84.0 plants.m⁻², the maximum seed yield per unit area was found at 30 plants.m⁻². Densities greater than 30 plants.m⁻² produced no increase in seed yield. Duncan (1986) suggested that the increase in seed yield per unit area in a square planting pattern may be due both to the increase in light intercepted and to an increase in the efficiency with which light is used, but the two effects are confounded.

2.2.3.2 The spatial distribution of seed yield within plants

Vertical distribution patterns of seed yield and yield components have been used to document the contribution of various strata of the soybean plant to total yield. Determination of the relationships between seed yield distribution and cultural practices may be helpful in analysing those factors that influence yield.

Some factors such as genotype, plant density and irrigation have been reported to influence the distribution of seed yield (Dominguez and

Hume, 1978; Herbert and Litchfield, 1982; Ramseur et al., 1984; Wallace, 1986). Dominguez and Hume (1978) reported that in determinate soybeans, the top third of the plant contributed more yield than the bottom third, whereas in indeterminate genotypes the bottom third of the plants generally contributed more yield than the top. Increasing plant density reduced the proportion of seed from the bottom part of the plant. This effect was more marked in earlier than in later maturing genotypes. They noted that the reduction in the bottom contribution to final yield in early genotypes at high densities may be beneficial in lowering harvesting losses.

In determinate cultivars, Ramseur et al. (1984) found that seed number, pod number and yield were maximized in the lower half of the nodes. The upper six nodes of a total of 24, contributed the least to yield in all treatments. The larger contribution to yield came from lower nodes because of the large proportion of yield borne on branches produced from lower nodes. In this study, narrow row spacings decreased yield because of a greater reduction in the contribution of yield at lower nodes. Wallace (1986) also found that changes in row width affected seed yield in the lower part of the plants in the same way, but no significant differences in seed yield per unit area were found.

In an indeterminate soybean, Herbert and Litchfield (1982) reported seed yield increased with narrower rows and higher plant densities. Yield increased by 20% (averaged from 2 years) when plant density was increased from 21 to 68 plants.m⁻² and remained approximately constant up to 113 plants.m⁻². The number of pods per plant and per node were the yield components most affected by increasing either row width or plant density. The number of seeds per pod and seed size however, both showed only minor responses to changes in row width, plant density and node position on the plant. Nodes 5 to 9 carried the greatest percentage of seed yield (36 to 67%) in all treatments except for plants in the low density where branches contributed most of the yield at the lowest main axis nodes. Branches formed on plants grown at low densities produced 30 to 40% of the seed yield, while at medium and high densities they contributed only 5 to 16%.

2.2.4 Concluding remarks

From this literature review, it is clear that there is not enough information on the effects of plant population density on reproductive development in soybean, especially flowering response, reproductive abortion, seed development and seed quality. An effective radial spacing design (type 1a) which provides a wide range of plant densities may be very useful to the study of all of these plant responses. The limitation of this design may be that under certain circumstances relatively few numbers of plants are available per sample, but this problem may be overcome by the use of curve fitting techniques. Although a few authors (e.g. Buttery, 1969b) have used curve fitting techniques on data obtained in rectangular planting density experiments, no one appears to have used this approach in published literature on soybean density studies in a radial spacing design. The use of curve fitting techniques is further discussed in section 2.3.4.1 of the materials and methods.

2.3 MATERIALS AND METHODS

2.3.1 Experimental site

The field experiment was established on land sited adjacent to the Seed Technology Centre, Massey University, Palmerston North (40° 21'S), on a Tokomaru silt loam soil. Details of soil analysis are given in Appendix 1.

2.3.2 Soil preparation and seed treatment

The land used in this study was cultivated out of a perennial ryegrass and white clover pasture. The land was prepared as follows:

- | | |
|---|-----------------|
| - Ploughed | 22 October 1985 |
| - Applied 2.5 t.ha ⁻¹ of finely ground lime | 30 October 1985 |
| - Harrowed | 31 October 1985 |

- Broadcasted fertilizer
(20:10:10:5% S) at 250 kg.ha⁻¹ 14 November 1985
- Harrowed 14 November 1985
- Incorporated Treflan (trifluralin,
400 g.litre⁻¹ as an emulsifiable
concentrate) 3 litres of product
per hectare 15 November 1985

Seeds of Amsoy and Matara soybeans were inoculated with Rhizobium japonicum before planting.

2.3.3 Planting and crop management

Seeds of Amsoy and Matara soybeans were sown on 15 November 1985 using the systematic design type 1a of Nelder (1962). This design provided the nearest to a square arrangement and created twenty plant population densities ranging from 4.2 to 83.9 plants.m⁻² as shown in Table 2.1. Further details of this design are presented in Appendix 3.

Each variety was planted in 4 separate semicircles (4 replicates) (Plate 2.1). Each replicate contained 41 radii (to meet the sample requirement, see Fig.2.1) and 20 concentric arcs, each representing one plant density. The intersection of the radii and the arcs was indicated using a marked rod. Three to four seeds were sown at each marked position. After the first radius was planted the marked rod was rotated by 4.5 degrees (i.e. it was moved 47.6 cm around the circumference of the outer arc) and seeds were sown along the second radius. The procedure was repeated through 180°. The remaining 180° was planted with the other variety (see Plate. 2.2).

Some surplus seeds of both varieties were sown outside the circles to provide spare seedlings of the same age for later transplanting into positions where seedlings failed to emerge .

One week after planting, Thimet 20G (200 g.kg⁻¹ phorate as pellets) was applied at a rate of 1 kg.ha⁻¹ to control chewing insects and aphids and slug pellets (Mesurol, 20 g.kg⁻¹ (2%) methiocarb as a bait) were broadcast at about 100 baits.m⁻².

Table 2.1 Plant population densities used in the field experiment

| Arc Number (from innermost) | Plant Density (plants.m ⁻²) |
|--------------------------------|--|
| 1 | 83.9 |
| 2 | 71.6 |
| 3* | 61.2 |
| 4 | 52.3 |
| 5 | 44.7 |
| 6* | 38.2 |
| 7 | 32.6 |
| 8 | 27.8 |
| 9* | 23.8 |
| 10 | 20.3 |
| 11 | 17.4 |
| 12* | 14.8 |
| 13 | 12.7 |
| 14 | 10.8 |
| 15* | 9.2 |
| 16 | 7.9 |
| 17 | 6.7 |
| 18* | 5.8 |
| 19 | 4.9 |
| 20 | 4.2 |

* identifies the six selected plant densities used for reproductive studies

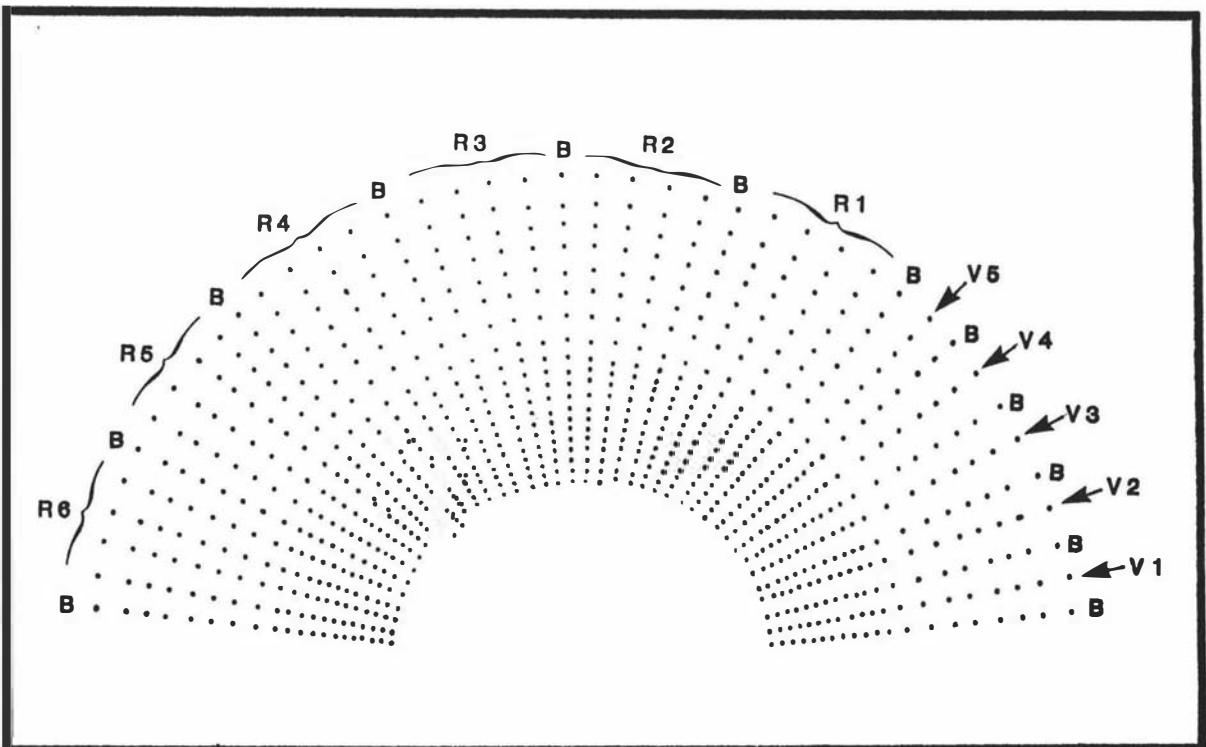


Fig. 2.1 Diagram showing sample utilisation in each semicircle

B = Border radii

V1-V5 = Vegetative measurements

R1-R6 = Reproductive measurements



Plate 2.1 Field grown Matara and Amsoy soybeans in a radial spacing design (type 1a): An overview of the whole experiment at 55 days after planting



Plate 2.2 a) Soybean seedlings in a radial design (type 1a) with 20 density levels at 3 weeks after planting; b) Matará and Amsóy soybeans at 55 days after planting

Three weeks after planting, seedlings were thinned to one plant per position and missing positions were filled by transplanting seedlings from the adjacent nursery area.

Tenoran (chloroxuron, 500 g.kg⁻¹ wettable powder) was applied at 3 kg of product per hectare in 300 litres of water at the first true leaf stage to control broadleaf weeds. Hand weeding was done once at 30 to 40 days after planting.

2.3.4 Data collection

2.3.4.1 Vegetative study

Pearce (1983) has suggested that curve fitting is an appropriate statistical tool to express the relationship between plant growth and plant density in a systematic radial design. Based on this suggestion, the vegetative parameters of this study were planned to accommodate the use of curve fitting techniques.

To utilize plant samples efficiently, the number of replicates for data collection should be carefully considered. In some previous studies using the radial spacing design, researchers have chosen to use a large number of replicates from each density and have collected plants from only selected densities along the radii (e.g. Tolentino, 1985). Instead of sampling only some densities (arcs), it was thought to be more efficient to collect plants from every density except the innermost and outermost border arcs, reduce the number of replicates in each density and employ multiple regression analysis to determine the nature of the relationship between vegetative growth and plant density. This idea was also based on the recommendation of Radford (1967) concerning growth analysis. He stated that 'it is no longer necessary to take large samples at relatively infrequent time intervals in order to obtain accurate results. It will be appreciated that, for the curve fitting needed in this approach, it is preferable to have frequent smaller samples'. Clawson *et al.* (1986) employed growth analysis techniques to quantify and compare growth of 2 soybean varieties by

following Radford's recommendation. They reported a similar form of each curve obtained for 10 growth analysis parameters (e.g. crop growth rate, net assimilation rate) to other previous studies that used more samples but less often such as Buttery (1970), Koller et al. (1970), Buttery and Buzzell (1972, 1974). In most cases, Clawson et al., (1986) obtained higher R^2 values.

In the present study, one plant was sampled at each sampling time from arcs 2 to 18 (Table 2.1). Plants from each replicate (i.e. 1x4 plants from each variety) were collected at 30, 50, 70, 80 and 90 days after emergence (DAE) for Matara and 30, 50, 70 and 90 DAE for Amsoy (see Fig. 2.1). These plants were cut at ground level and were used to determine the following characteristics per plant.

- a. Node number and internode length
- b. Branch number
- c. Leaf number
- d. Total leaf area
- e. Branch leaf area
- f. Shoot dry weight
- g. Total leaf dry weight
- h. Branch leaf dry weight

The following definitions of terms were used in this study;

- i) Node = nodes on main stem that bore at least one visible leaf
- ii) Branch = shoots from the main stem which bore at least one visible leaf
- iii) Leaf = trifoliate leaf which was more than half unfolded

Leaf area was measured using a LI3100 Li-Cor meter (Li-Cor Inc., Nebraska, USA). Tissue dry weights were determined after drying in an air oven at 80°C for 3 days.

Plant height (from ground level to the highest canopy level) was measured at 30, 50, 70 and 80 days after emergence (DAE) for Matara, and at 30, 50, 70, and 90 DAE for Amsoy. Five and ten plants per

replicate were measured for Matara and Amsoy respectively. Light interception measurement was done at ground level, mid point between plants of the same density at 32, 48 and 62 DAE for Matara and at 30, 42 and 56 DAE for Amsoy, using a Li-185 solarimeter (Li-Cor, Inc., Nebraska, USA) with a quantum sensor. Percent light interception was calculated from the ratio of light intercepted (light energy in $\mu\text{E}\cdot\text{m}^{-2}\cdot\text{sec}^{-1}$ at the top of the canopy minus light energy measured at ground level) to light intensity at canopy level.

Several equations were tested to determine the mathematical models which best described the observed changes in vegetative growth characteristics relative to plant density. These equations were examined to ascertain which gave the best 'least squares' fit to the observed data. The criteria used were R^2 values, visual examination of curve in relation to the plotted data and, finally, residuals were plotted to ensure they showed random and not systematic variation around the calculated curve.

The equation chosen in this experiment were quadratic exponentials. Details are given in Appendix 4. Predicted values from these equations at plant densities 61.2, 38.2, 23.8, 14.8, 9.2 and 5.8 plants m^{-2} were used to plot changes against time and are discussed along with reproductive data.

2.3.4.2 Growth analysis

Crop growth rate (CGR) is defined as the increase of plant material per unit of time (Radford, 1967) and normally is expressed on the basis of unit area of crop (e.g. $\text{g}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$). Net assimilation rate (NAR) is the increase of plant material per unit of assimilatory material per unit of time [$\text{g}\cdot\text{m}^{-2}(\text{leaf})\cdot\text{day}^{-1}$]. Donald (1963) indicated that the limitation of the concept of NAR as applied to agriculture is that plants do not grow as isolated individuals, but as communities of individuals under strong competitive stress. CGR which is a function of NAR and LAI, therefore may be a more meaningful measure of plant performance in population density studies.

Leaf area index (LAI) and crop growth rate (CGR) were calculated from the predicted values obtained from the equation. LAI was calculated

from leaf area per plant ($\text{m}^2.\text{plant}^{-1}$) multiplied by the number of plants per square metre. CGR involves the calculation of various mean rates from changes in plant weight per unit area of ground (W_2 and W_1) observed at two sampling periods (t_2 and t_1) (Radford, 1967; Buttery, 1969b), as follows :

$$\text{CGR} = (W_2 - W_1) / (t_2 - t_1)$$

unit = $\text{g}.\text{m}^{-2}\text{land area}.\text{day}^{-1}$

2.3.4.3 Reproductive study

Six selected plant densities; 61.2, 38.2, 23.8, 14.8, 9.2 and 5.8 $\text{plants}.\text{m}^{-2}$ were used for reproductive development, yield and yield component studies.

i) Flowering pattern

Five plants per replicate for Matara and ten plants per replicate for Amsoy were marked by mapping and used for counting the number of flowers per plant at 3-day intervals throughout the flowering period. This interval was more frequent than the intervals used by Buttery (1969a) and Dominguez and Hume (1978). Previous observation on flower production in both varieties was done in the glasshouse before the field study to assess the time sequence and extent of changes in colour and freshness of petals from the first day of flower appearance. Flowers counted in the field study were those which were fresh and had unshrunk petal edges. These were flowers comparable to those observed on the first day of corolla appearance in the glasshouse. By this means, only those flowers that appeared on the counting day were included, allowing daily flower production per plant to be determined.

The date of peak flowering for each plant density was noted and used for later seed development studies. Total flower production per plant and flowering period were also determined. Total flower production was determined by calculating the cumulative flower number from the daily rate of flower production curves.

ii) Seed development study

Plant samples (4 plants per replicate) were collected at 10 day intervals following the day that peak flowering occurred in each plant density as shown in Table 2.2.

The following characteristics were determined:

- Number of pods (≥ 2 cm) per plant
- Number of seeds per pod
- 100-seed fresh weight (gm)
- 100-seed dry weight (gm)
- Seed moisture content (%)
- Air-dried seed germination (%)

Fresh seeds were obtained by hand removal from pods and were used to determine seed fresh and dry weights and seed moisture content by oven drying at 103°C for 17 hours. Air-dried seeds with approximately 12% moisture content were obtained from pods which were slowly air dried in the glasshouse for about 2 weeks after detaching from the plants. Germination tests were conducted at 25°C, 100% RH using 50 seeds per replicate in the 'between paper' method. Seedlings were evaluated following the prescriptions in the ISTA Rules for Seed Testing (ISTA, 1985).

iii) Yield and yield components at final harvest

Matara was harvested 60 DAPF, Amsoy plants matured later and harvesting was delayed until 75 DAPF. A split block design was used to analyse the data at the final harvest with variety as the main plot and density as the subplot.

Yield, both on a per plant basis and per unit area was evaluated at 10% seed moisture content which was derived from the weight of dry seed using the following formula

$$W_2 = (100 W_1)/90$$

where W_1 = Seed dry weight (g)
 W_2 = Seed weight at 10% moisture content

Table 2.2 Relationship between 'days after emergence' (DAE) and 'days after peak flowering' (DAPF) and sampling times for reproductive growth study

| Plant densities | Days after emergence until Peak flowering | Sampling times for Matara (DAPF) | | | | | |
|-----------------|---|----------------------------------|----|----|----|----|----|
| | | 1 | 2 | 3 | 4 | 5 | 6 |
| 61.2 | 47 | 10 | 20 | 30 | 40 | 50 | 60 |
| 38.2 | 47 | 10 | 20 | 30 | 40 | 50 | 60 |
| 23.8 | 47 | 8 | 18 | 28 | 38 | 48 | 58 |
| 14.8 | 44 | 10 | 21 | 31 | 41 | 51 | 61 |
| 9.2 | 44 | 10 | 24 | 34 | 44 | 54 | 64 |
| 5.8 | 44 | 14 | 24 | 34 | 44 | 54 | 64 |

| Plant densities | Days after emergence until Peak flowering | Sampling times for Amsoy (DAPF) | | | | | |
|-----------------|---|---------------------------------|------|------|------|------|------|
| | | 1 | 2 | 3 | 4 | 5 | 6 |
| 61.2 | 50 | 10 | 20 | 30 | 40 | 57 | 75 |
| 38.2 | 53 | 10 | 20 | 30 | 40 | 57 | 75 |
| 23.8 | 50 | 10.5 | 20.5 | 30.5 | 40.5 | 57.5 | 75.5 |
| 14.8 | 47 | 10.5 | 20.5 | 30.5 | 40.5 | 57.5 | 75.5 |
| 9.2 | 50 | 10 | 20 | 30 | 40 | 57 | 75 |
| 5.8 | 53 | 10 | 20 | 30 | 40 | 57 | 75 |

For partitioning seed yield, plants were divided into three parts based on plant height at final harvest (top, middle and bottom). Seed yield from each arc was divided into main stem seed yield and branch seed yield. Seed yield was partitioned within plants into 5 and 6 parts for Matara and Amsoy, respectively, as shown in Table 2.3.

iv) Seed quality at final harvest

Seed moisture content and air-dried seed germination at final harvest were also analysed in a split-block design.

Table 2.3 Description of plant partitions for Matara and Amsoy soybean

| Plant Part | Matara | Plant Part | Amsoy |
|------------|---|------------|------------------------------------|
| 1 | Seed yield from branches (top) | 1 | Seed yield from branches (top) |
| 2 | Seed yield from main stem (top) | 2 | Seed yield from main stem (top) |
| 3 | Seed yield from branches (middle) | 3 | Seed yield from branches (middle) |
| 4 | Seed yield from main stem (middle) | 4 | Seed yield from main stem (middle) |
| 5 | Seed yield from main stem and branches (bottom) | 5 | Seed yield from main stem (bottom) |
| | | 6 | Seed yield from branches (bottom) |

2.4 RESULTS

2.4.1 Plant growth and development

Observations on plant growth and development in the radial spacing trial clearly showed the effects of plant density. Plant growth from the circumference ($4.9 \text{ plants.m}^{-2}$) towards the centre ($71.6 \text{ plants.m}^{-2}$) was well described by the quadratic exponential model (Appendix 5). Six selected densities; i.e. 61.2, 38.2, 23.8, 14.8, 9.2 and $5.8 \text{ plants.m}^{-2}$, were taken from predicted values to present in this thesis.

2.4.1.1 Vegetative growth

i) Plant height

Figs. 2.2a and 2.3a show the relationship between plant height and time for plants grown at different densities. In both varieties, plant competition was still low at 30 days after emergence (DAE), but showed clearly when plants were measured from 50 DAE onwards, with plant height increasing with density. At the final measurement of maximum plant height (80 DAE for Matara and 90 DAE for Amsoy), Matara was 7 to 10 cm shorter than Amsoy depending upon plant density. At this stage in both cultivars, plant height was clearly shown to be dependent on density up to $38.2 \text{ plants.m}^{-2}$. Plant heights at $38.2 \text{ plants.m}^{-2}$ and $61.2 \text{ plants.m}^{-2}$ were similar.

A different response was observed between the two varieties. Matara was more sensitive than Amsoy. Increasing plant density from 5.8 to $61.2 \text{ plants.m}^{-2}$ resulted in a plant height increase at maturity of 53% in Matara compared to only 37% in Amsoy at the final measurement (80 DAE for Matara and 90 DAE for Amsoy).

ii) Node number

Plant density had a large effect on main stem node numbers per plant. Increasing plant density approximately 10-fold (from

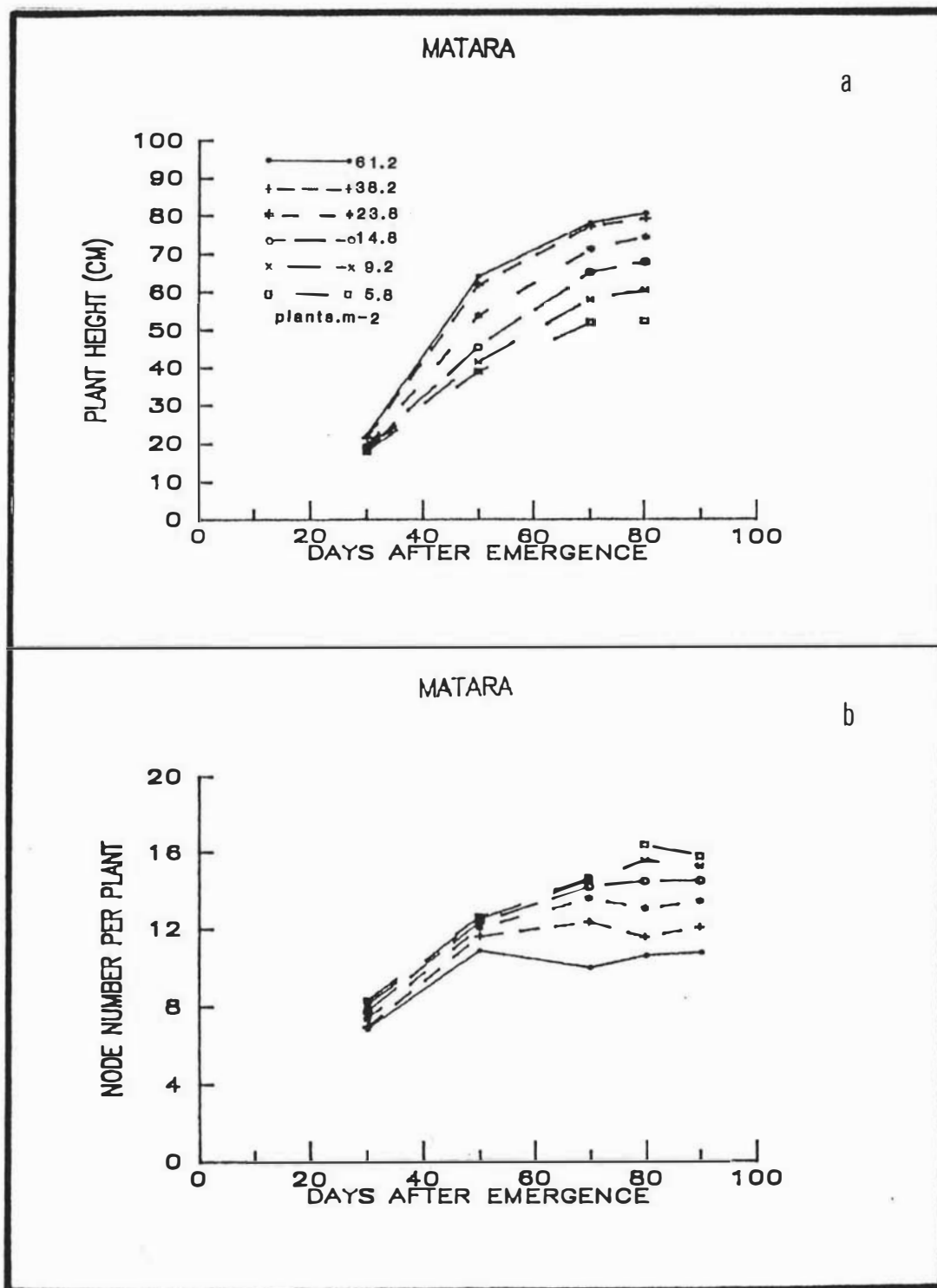


Fig. 2.2 Effect of plant density on plant height (a) and node number per plant (b) in Matara soybean

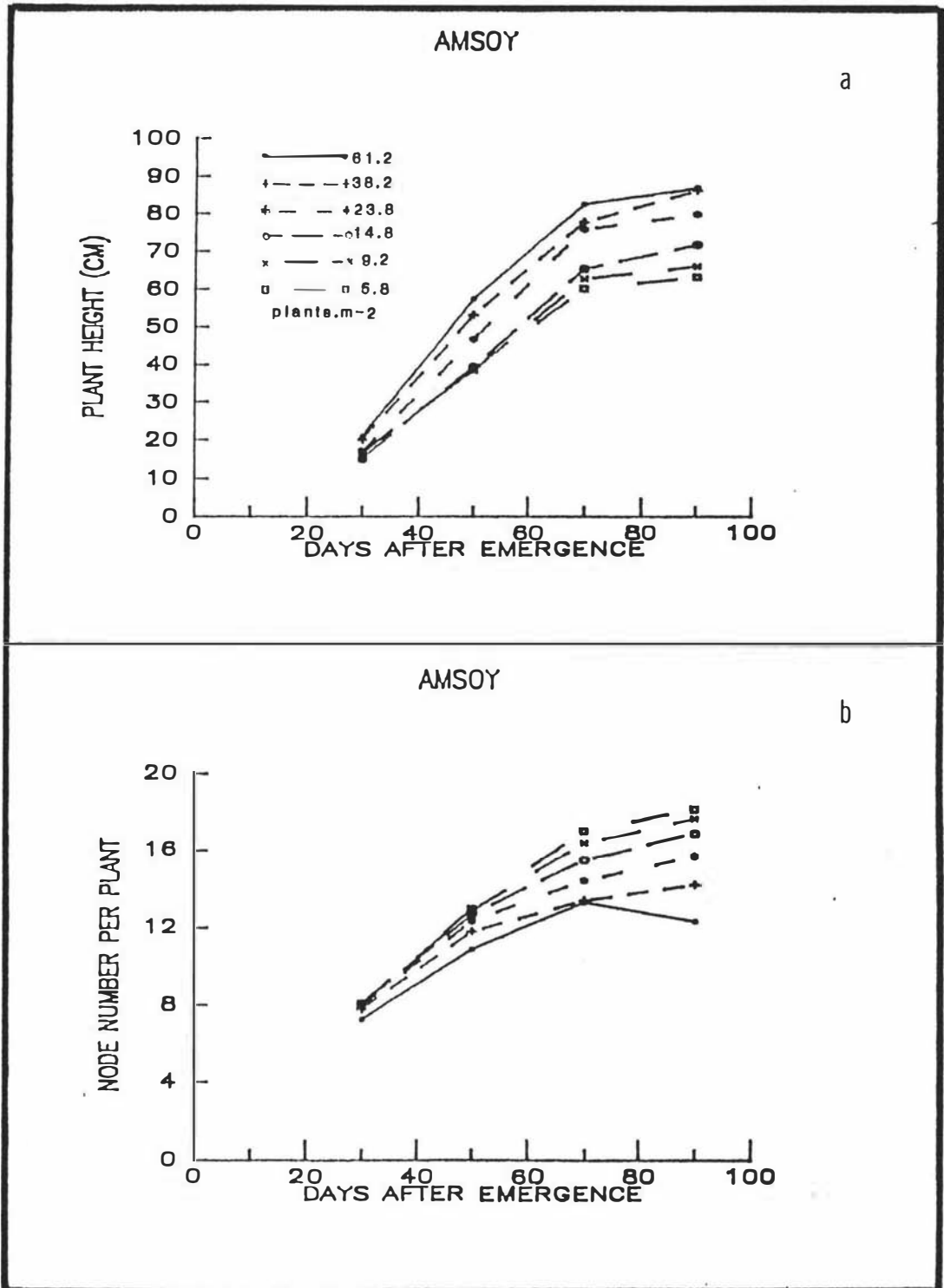


Fig. 2.3 Effect of plant density on plant height (a) and node number per plant (b) in Amsoy soybean

5.8 to 61.2 plants.m⁻²) reduced node numbers at final harvest by 5 nodes in Matara and 6 nodes in Amsoy (Figs. 2.2b and 2.3b).

In both varieties and all plant densities, there were 7 or 8 main stem nodes per plant at 30 DAE, and then numbers increased with time. Generally, in high density plants, node production was slowed down earlier than in low density plants. At 61.2 plants.m⁻², interplant competition was observed through inhibited node production at 50 DAE for Matara, compared with 70 DAE in Amsoy. At low densities, node numbers approached their maximum which was 16 for Matara and 18 for Amsoy.

iii) Internodal elongation

Figs. 2.4 and 2.5 show the effect of plant density on internodal elongation at different stages of growth. Three selected densities, i.e. 61.2, 23.8 and 5.8 plants.m⁻¹ are presented. It is clear that as plants grew, the elongation of internodes at the top of the plants (young stem internodes) was largely affected by plant density. In the lowest density (5.8 plants.m⁻¹), plants continued to produce more nodes without any significant increase in internode length, whereas in high competitive stress conditions (61.2 plants.m⁻¹), plants produced fewer nodes but increased their height through internodal elongation. The period which was most sensitive to competition was between 30-50 DAE in Matara and 30-70 DAE in Amsoy.

iv) Leaf area per plant

Total leaf area increased rapidly in all plant density treatments up to at least 50 DAE (Figs. 2.6a and 2.7a). In high density plantings of Matara, this increase in leaf area per plant subsequently slowed down and stopped before decreasing rapidly after 70-80 DAE because of leaf drop and leaf senescence. At 90 DAE, leaf area was less than 500 cm².plant⁻¹ in the three highest density plantings compared with 2,800 cm² at the lowest plant density.

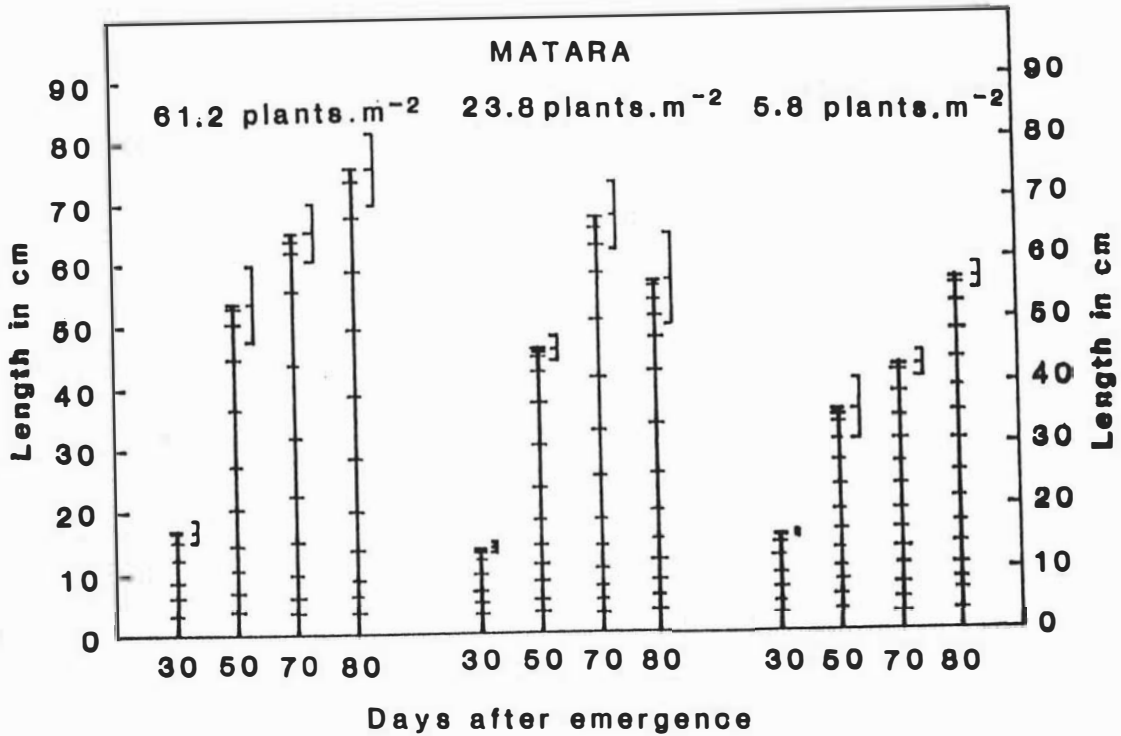


Fig. 2.4 Effect of plant density on internodal elongation in Matara soybean. Mean values were averaged from 4 plants and vertical bars represent \pm SE of the single means for total plant height.

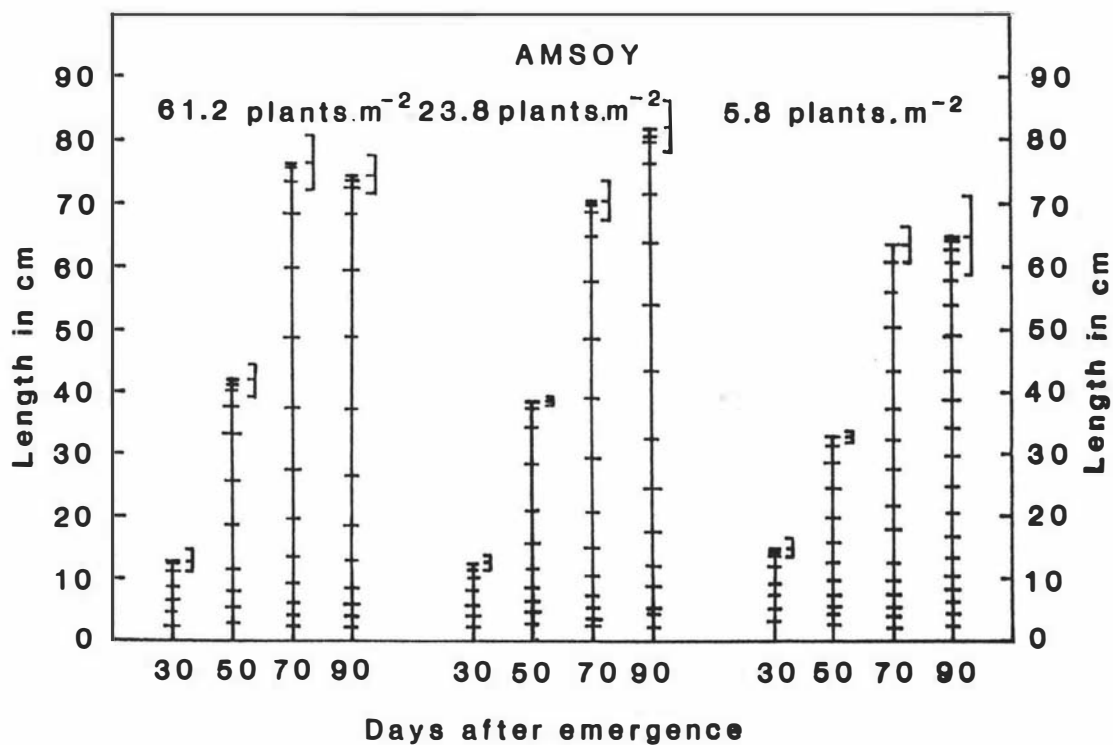


Fig. 2.5 Effect of plant density on internodal elongation in Amsoy soybean. Mean values were averaged from 4 plants and vertical bars represent \pm SE of the single means for total plant height.

In Amsoy, plants grown at high densities retained their leaf area for a longer time compared to the same densities in Matara and still had a leaf area of more than $1,000 \text{ cm}^2 \cdot \text{plant}^{-1}$ at 90 DAE. In all densities, leaf area continued to increase linearly to a maximum leaf area at 70 DAE before decreasing slightly by 90 DAE. Maximum leaf area of $5150 \text{ cm}^2 \cdot \text{plant}^{-1}$ for Amsoy was found at 70 DAE at the lowest density.

v) Dry weight accumulation

The effect of plant density on above ground shoot dry weight is depicted in Figs. 2.6b and 2.7b. No competitive effect was found at 30 DAE, although competition due to plant density effects became apparent from 50 DAE onwards. In Matara, maximum shoot dry weight was found at 70 DAE in high densities (61.2 and $38.2 \text{ plants} \cdot \text{m}^{-2}$) but was not reached until 80 DAE when plant density was decreased. In Amsoy, maximum shoot dry weight occurred at 70 DAE irrespective of plant density.

vi) Branch number

The number of branches as affected by plant density is shown in Fig. 2.8. As plant density decreased, branch numbers in both varieties increased, but Amsoy was more responsive than Matara. There was not much difference between the two cultivars when plant density exceeded $38 \text{ plants} \cdot \text{m}^{-2}$, but there was a big difference at the lowest density. Amsoy plants produced twice as many branches as Matara plants at $5.8 \text{ plants} \cdot \text{m}^{-2}$ (10 vs 5).

Branch leaf area per plant measured in both cultivars showed a similar trend to total leaf area per plant (data not shown). The highest branch leaf area in the lowest density planting in Matara was $1,970 \text{ cm}^2 \cdot \text{plant}^{-1}$, recorded at 80 DAE compared to $3,820 \text{ cm}^2 \cdot \text{plant}^{-1}$ in Amsoy. At the highest plant density, branch leaf area was less than $300 \text{ cm}^2 \cdot \text{plant}^{-1}$ in both cultivars.

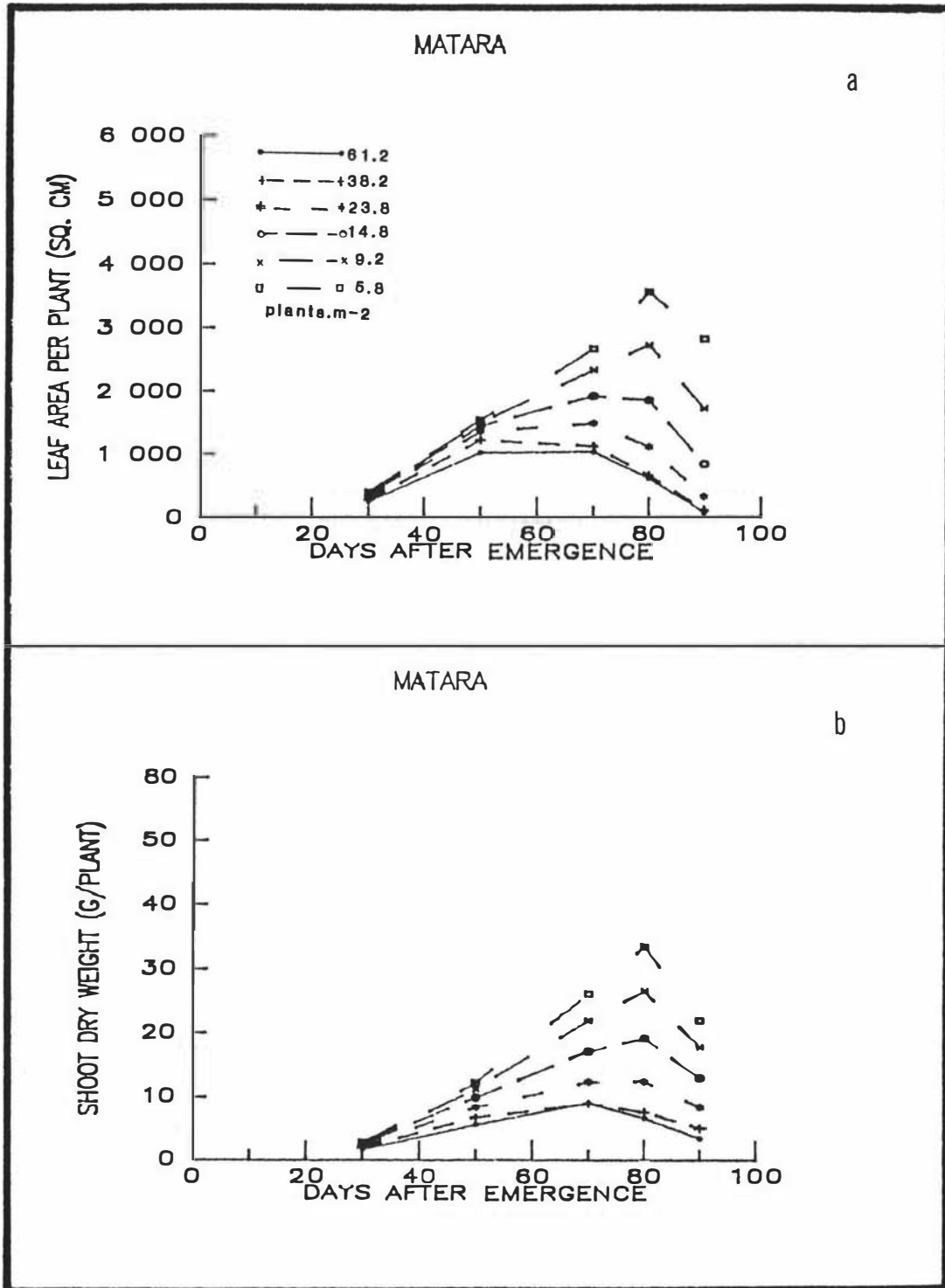


Fig. 2.6 Effect of plant density on leaf area (a) and above ground shoot dry weight (b) per plant of Matara soybean

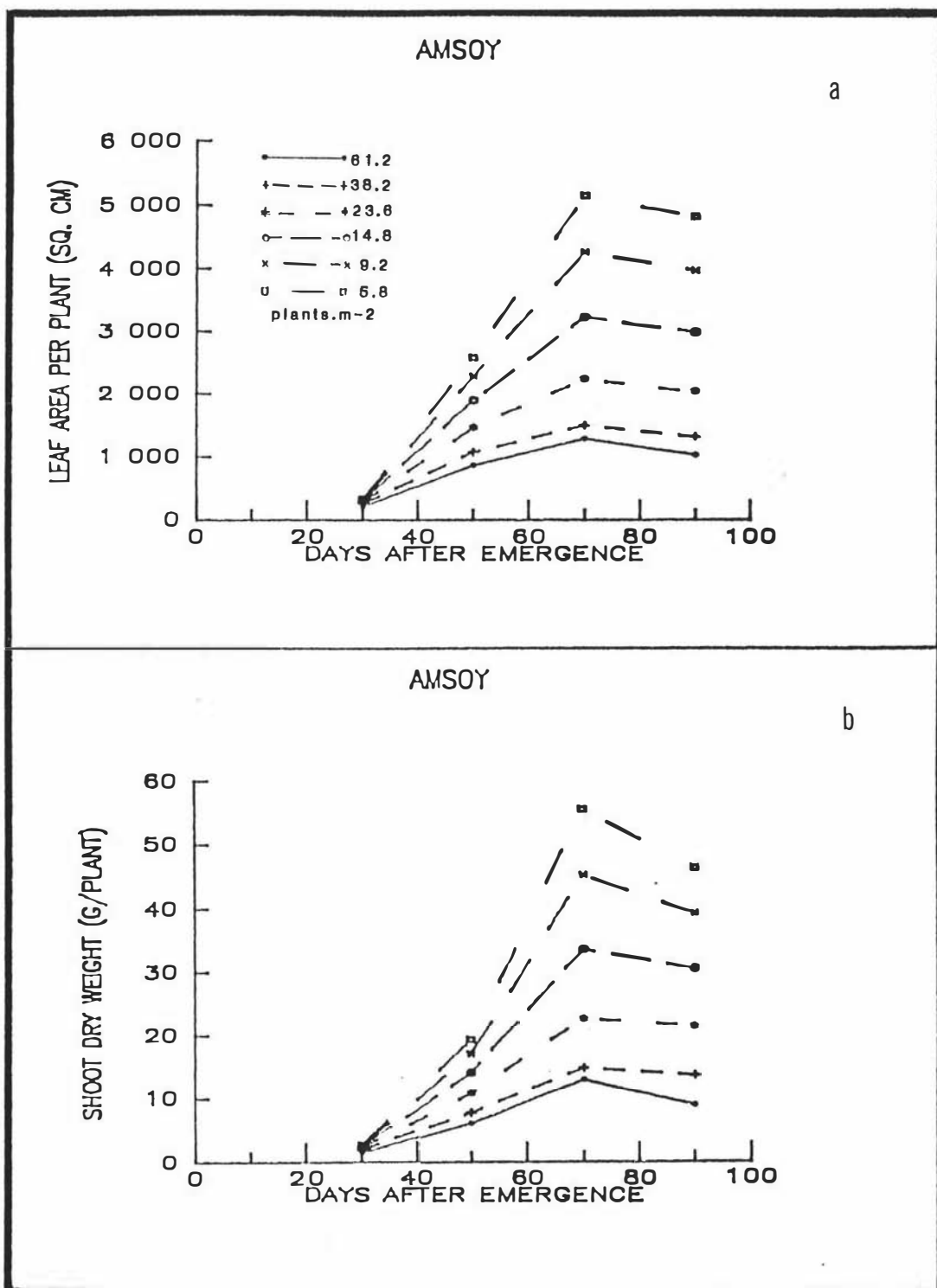


Fig. 2.7 Effect of plant density on leaf area (a) and above ground shoot dry weight (b) per plant of Amsoy soybean

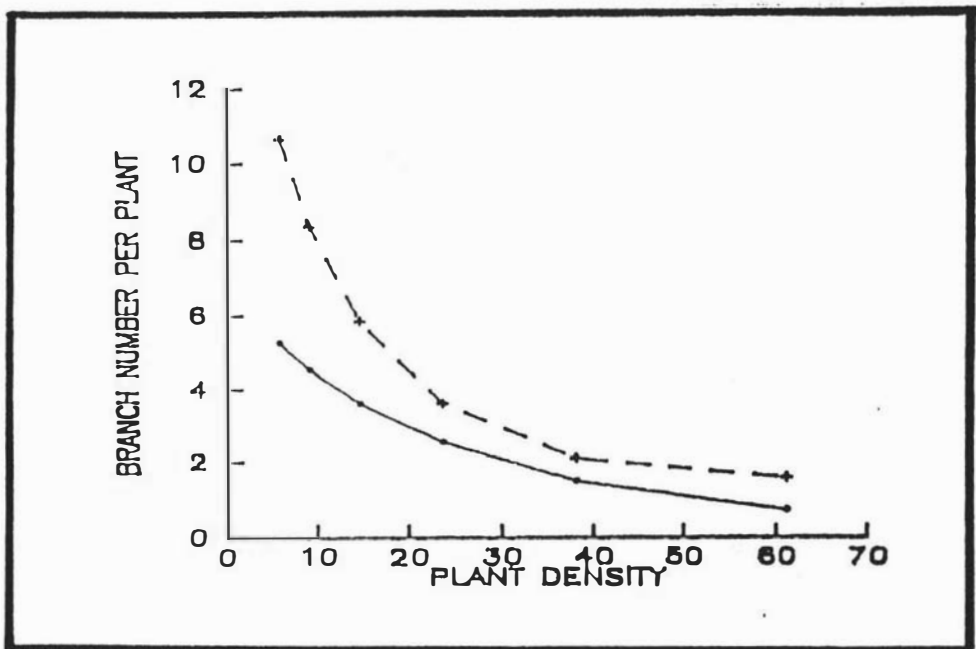


Fig. 2.8 Effect of plant density on branch number per plant at maturity in Matara (—●—) and Amsoy (+ - - +) soybeans

vii) Crop growth

Besides individual plant performance, overall crop performance is also important since the ultimate goal in crop management is to maximize seed yield per unit area. Interplant competition in a plant community can be precisely expressed by the measurement of crop growth per unit of land area. In this section, crop growth rate (CGR) and leaf area index (LAI) are considered.

The calculation of crop growth rate (CGR) - the increase in dry matter per unit of land area - for the entire sampling period is shown in Figs. 2.9a and 2.10a. Generally, CGR increased with time to maximum rates at midseason and then declined quite rapidly. During the early stage of growth (15 DAE), Matara and Amsoy had CGRs, ranging from 0.5 to 3.5 $\text{g.m}^{-2}.\text{day}^{-1}$ for Matara and from 0.5 to 2.9 $\text{g.m}^{-2}.\text{day}^{-1}$ for Amsoy, depending upon plant density. By 40 DAE, CGRs ranged from 3 to 12 $\text{g.m}^{-2}.\text{day}^{-1}$ for Matara and 5 to 14 $\text{g.m}^{-2}.\text{day}^{-1}$ for Amsoy. In Matara, CGRs of plants grown at 61.2, 38.2 and 23.8 plants.m^{-2} subsequently declined, whereas the increase in CGRs of plants grown at 14.8, 9.2 and 5.8 plants.m^{-2} continued until 60 DAE and then decreased rapidly after 75 DAE. In Amsoy, CGRs still increased actively after 40 DAE until 60 DAE when Amsoy had a CGR approximately twice that of Matara. Subsequently, however, CGRs of Amsoy plants declined rapidly irrespective of planting density.

The graphs of CGR clearly show the effects of interplant competition. During the early to mid period of plant growth (15 to 60 DAE), the CGR in dense communities increased at a higher rate than in sparsely spaced communities. This higher rate was attributed to the greater number of plants per unit area. Plants grown under high competitive stress in a dense community reached maturity earlier (65-70 DAE), as shown by the sharp decrease in CGR which reached zero earlier.

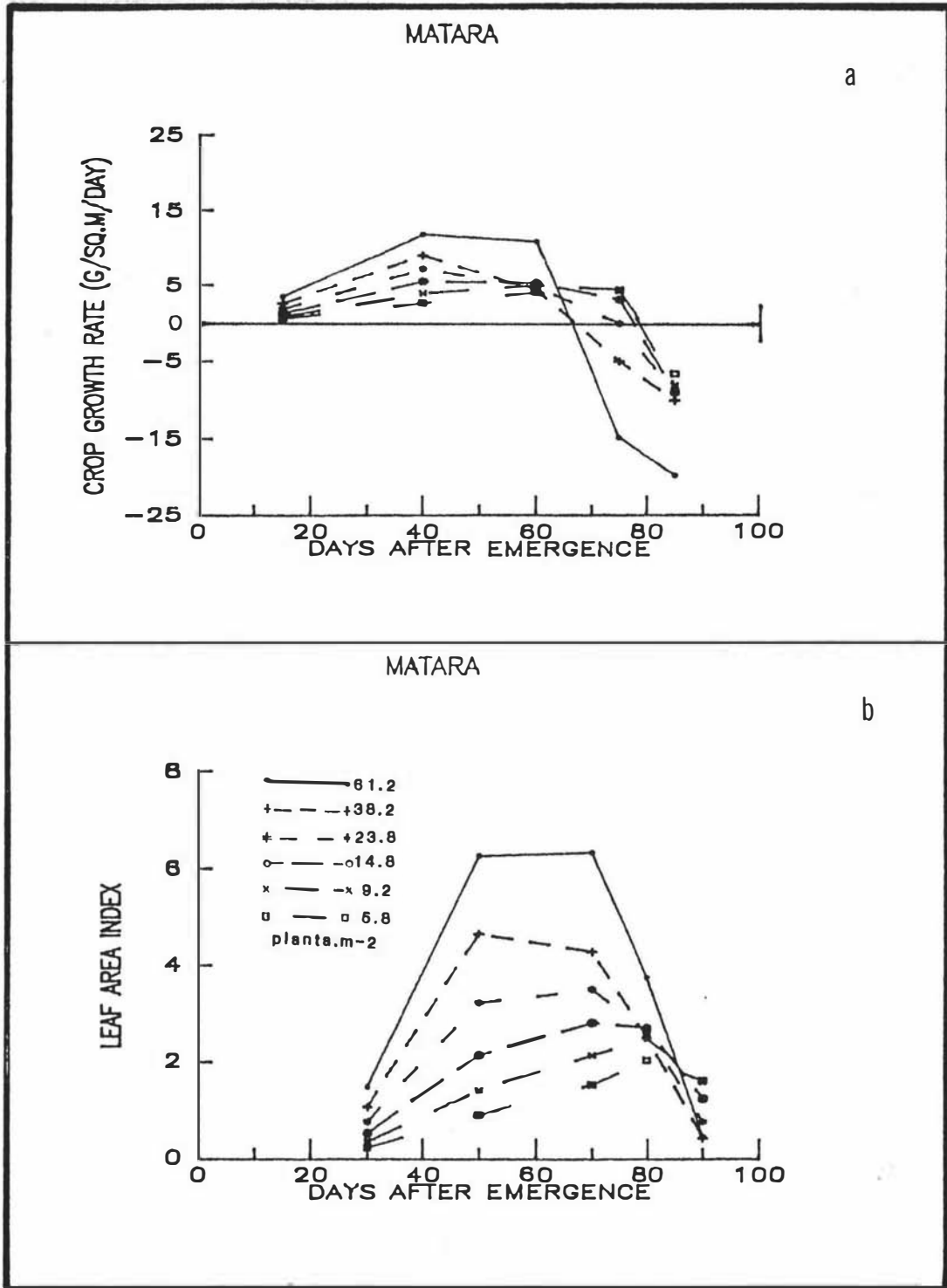


Fig. 2.9 Effect of plant density on crop growth rate (CGR) (a) and leaf area index (LAI) (b) in Matara soybean

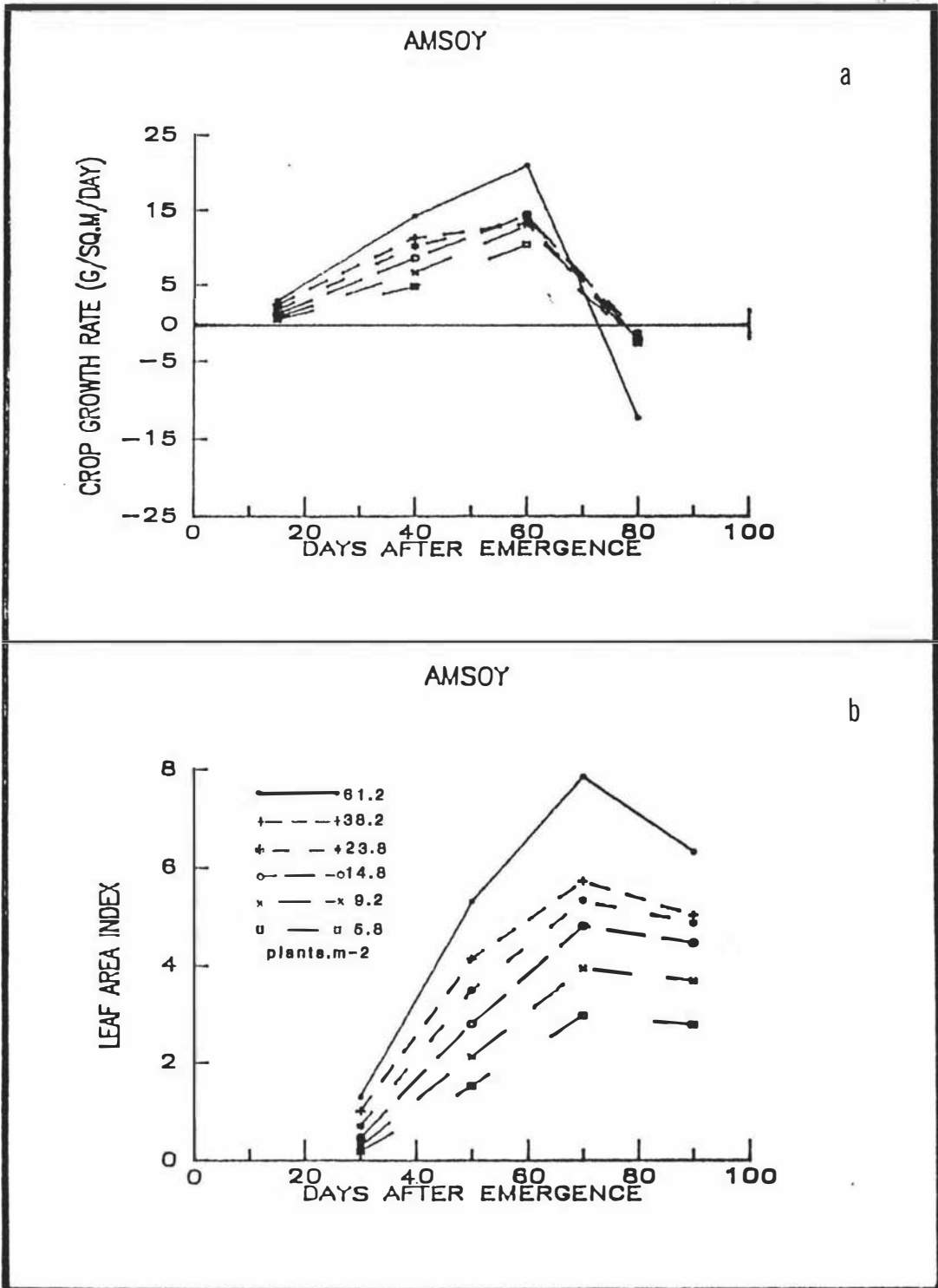


Fig. 2.10 Effect of plant density on crop growth rate (CGR) (a) and leaf area index (LAI) (b) in Amsoy soybean

LAI is frequently regarded as an indicator of the intensity of competition for light experienced by individual plants within a community. As shown in Figs. 2.9b and 2.10b, LAI increased with time and attained maximum values between 50 and 80 DAE for Matara and at 70 DAE for Amsoy. Peak LAI ranged from approximately 2 to 6 for Matara and 3 to 8 for Amsoy when plant density was increased from 5.8 to 61.2 plants.m⁻².

In Matara, maximum LAI was reached earlier in high than low plant densities. Initially (30-70 DAE) plants grown at high densities had a higher LAI than plants grown at low densities. However, by 80 DAE, while the LAI of low density plants had reached a maximum, the LAI of high density plants decreased rapidly, ultimately reaching lower levels than low density plants by 90 DAE.

In Amsoy, LAI reached a maximum at about 70 DAE in all densities. The subsequent decline in LAI was, however, faster in high densities than low densities, although this effect was not as marked as in Matara.

In this study, high correlations were found for both cultivars between CGR and mean LAI at corresponding sampling times before plant senescence (i.e. 80 DAE). Correlation coefficients were 0.800** for Matara and 0.959** for Amsoy.

2.4.1.2 Reproductive growth

i) Daily flower production

In both cultivars flowering began 29-30 DAE. Plants grown at different densities followed a similar flowering pattern although the duration of flowering varied, with low density plants continuing to flower 8-11 days longer than high density plants.

The responses in flower production per day in Matara and Amsoy soybeans as affected by plant density are shown in Figs. 2.11

and 2.12, respectively. The patterns of flowering of these 2 varieties were similar, but Amsoy reached a higher flowering peak than Matara. In Matara, flower production increased slowly during the early period at high densities (61.2 and 38.2 plants.m⁻²), but at low densities the number of flowers increased sharply and reached a maximum 15 days after first flowering. High density plants reached maximum daily flower production 18 days after first flowering and had only one prominent peak. At 9.2 and 5.8 plants.m⁻², the plants produced 2 flowering peaks which were 12 days apart. Amsoy plants grown at 14.8, 9.2 and 5.8 plants.m⁻² showed one flowering peak followed by a sudden but relatively short second increase in daily flower numbers 8 to 10 days later. No second flowering peak was observed at higher densities. Maximum flower production ranged from 3.4 to 12.9 flowers.plant⁻¹.day⁻¹ for Matara and from 8.0 to 23.3 flowers.plant⁻¹.day⁻¹ for Amsoy, flower numbers increasing as plant density decreased.

ii) Flowering period and flower number per plant

Table 2.4 shows the mean values of total flowering period, flower numbers per plant and percentage of reproductive abortion as influenced by plant density.

Although Amsoy had a significantly longer flowering period (7 days) and produced about twice as many flowers as Matara (296 vs 143, mean values over all densities), both varieties showed a similar increase in both flowering period and flower number as plant density decreased. There was no interaction between variety x density in both parameters.

As plant density decreased from 61.2 to 5.8 plants.m⁻², the flowering period increased by 8.2 days in Matara and 11.0 days in Amsoy. This was accompanied by a 7-fold increase in flower numbers per plant in Matara (36 to 264) and a 4-fold increase (115 to 497) in Amsoy.

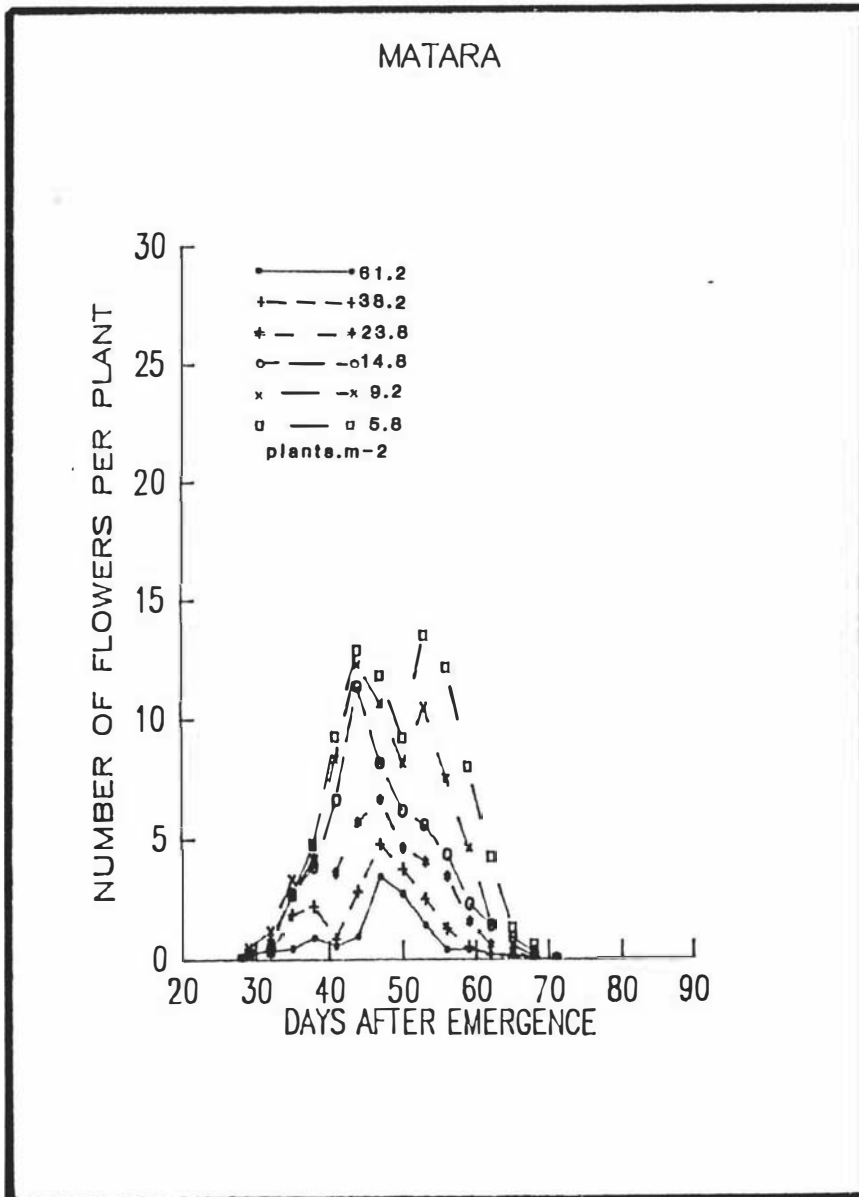


Fig. 2.11 Effect of plant density on daily flower numbers per plant in Matara soybean

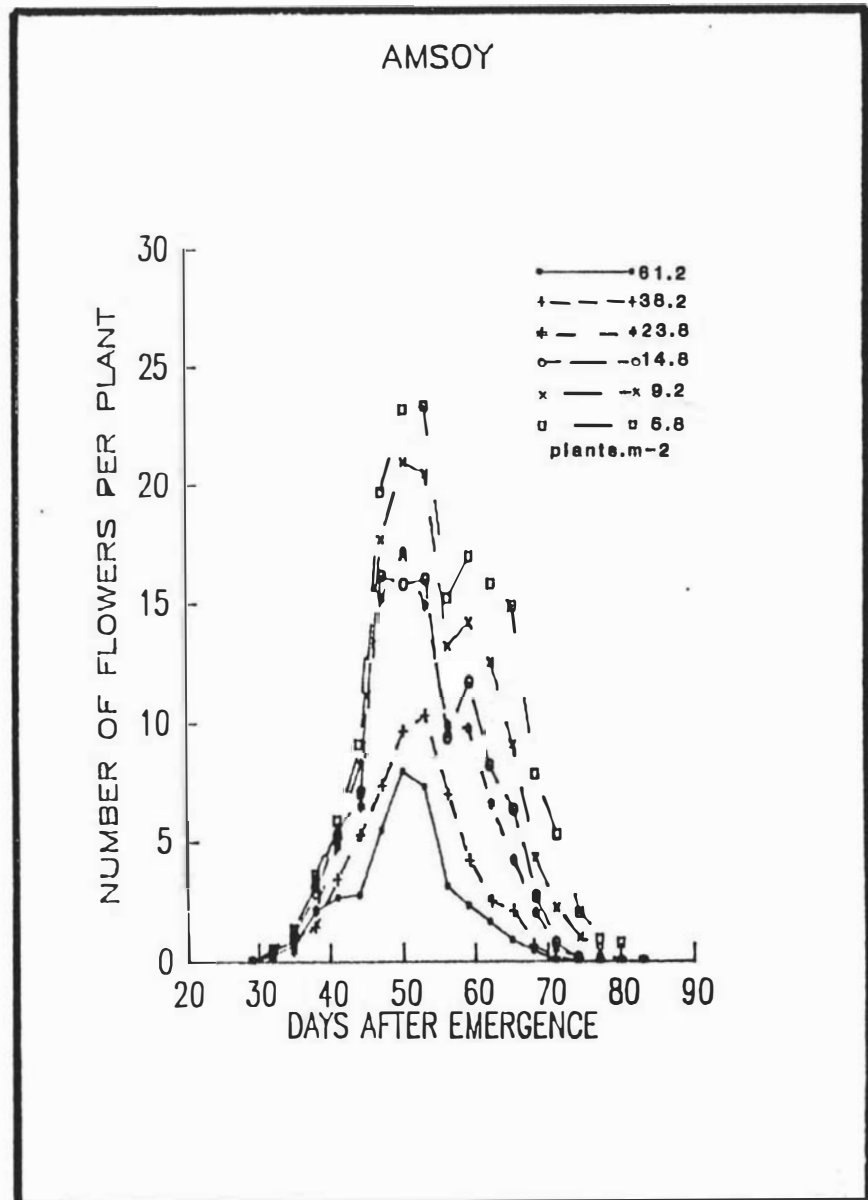


Fig. 2.12 Effect of plant density on daily flower numbers per plant in Amsoy soybean

iii) Reproductive abortion

The percentage of reproductive abortion was calculated from the ratio of the number of reproductive structures that failed to develop into mature pods at final harvest and total flower numbers per plant.

The percentage of reproductive abortion as influenced by plant density is shown in Table 2.4. Increasing plant density about 10 times from 5.8 to 61.2 plants.m⁻² did not significantly alter the percentages of reproductive abortion. However, there was a significant difference between cultivars. Matara had a lower percentage of reproductive abortion (average 65.2%) than Amsoy (average 81.8%).

iv) Pod and seed development

Three plant densities were chosen to depict the effect of plant density on pod and seed development based on days after peak flowering (DAPF), i.e. 61.2, 23.8 and 5.8 plants.m⁻². DAPF as related to DAE has been shown previously in Table 2.2.

As shown in Figs. 2.13 to 2.18, the effect of density stress was more pronounced in relation to pod development than seed development. In most cases, both varieties showed the same trend. Differences were found only in rates of seed growth and in the period of seed fill which were slightly slower and shorter in Amsoy.

Pod development

Figs. 2.13a and 2.14a show the development of pods per plant at the 3 selected plant densities. At the highest density (61.2 plants.m⁻²), pod numbers per plant reached a maximum at 10 days after peak flowering (DAPF) for Matara and a few days later for Amsoy. At the medium density (23.8 plants.m⁻²), both cultivars reached maximum pod numbers per plant at 20 DAPF. Pod

numbers per plant at these two plant densities subsequently remained relatively constant until harvest. At the low density ($5.8 \text{ plants.m}^{-2}$), low competitive stress conditions allowed plants to develop more pods to a maximum at 40-44 DAPF.

Changes in seed numbers per pod

Figs. 2.13b and 2.14b show the number of seeds per pod at different times after peak flowering. Seed numbers per pod in Matara were relatively constant throughout the developmental period and were slightly greater than in Amsoy. There was a tendency in Matara for plants at the highest plant density to produce fewer seeds per pod than at medium and low densities. In Amsoy, all densities showed similar seed numbers per pod, but there was a tendency for seeds per pod to decrease with time from about 2.7 at 10 DAPF to about 2.4 at 75 DAPF.

Seed fresh weight

Seed fresh weight increased with time and reached a maximum at about 40 DAPF for Matara and about 40 to 55 DAPF for Amsoy, before gradually decreasing (Figs. 2.15a and 2.16a). In Matara, maximum seed fresh weight ranged from 38 to 43 g.100 seeds^{-1} and there was a tendency for seeds from high density plants to lose weight earlier than low density plants. In Amsoy, maximum seed fresh weight in the lowest density plants tended to be higher than in the other two densities, but decreased to the same value at 75 DAPF.

Seed dry weight

Seed dry weight increased with time in the same manner as seed fresh weight but reached a maximum slightly later than seed fresh weight (Figs. 2.15b and 2.16b). In Matara, an early maturing cultivar, seed dry weight in high density plants reached a maximum 8 to 14 days (based on days after peak

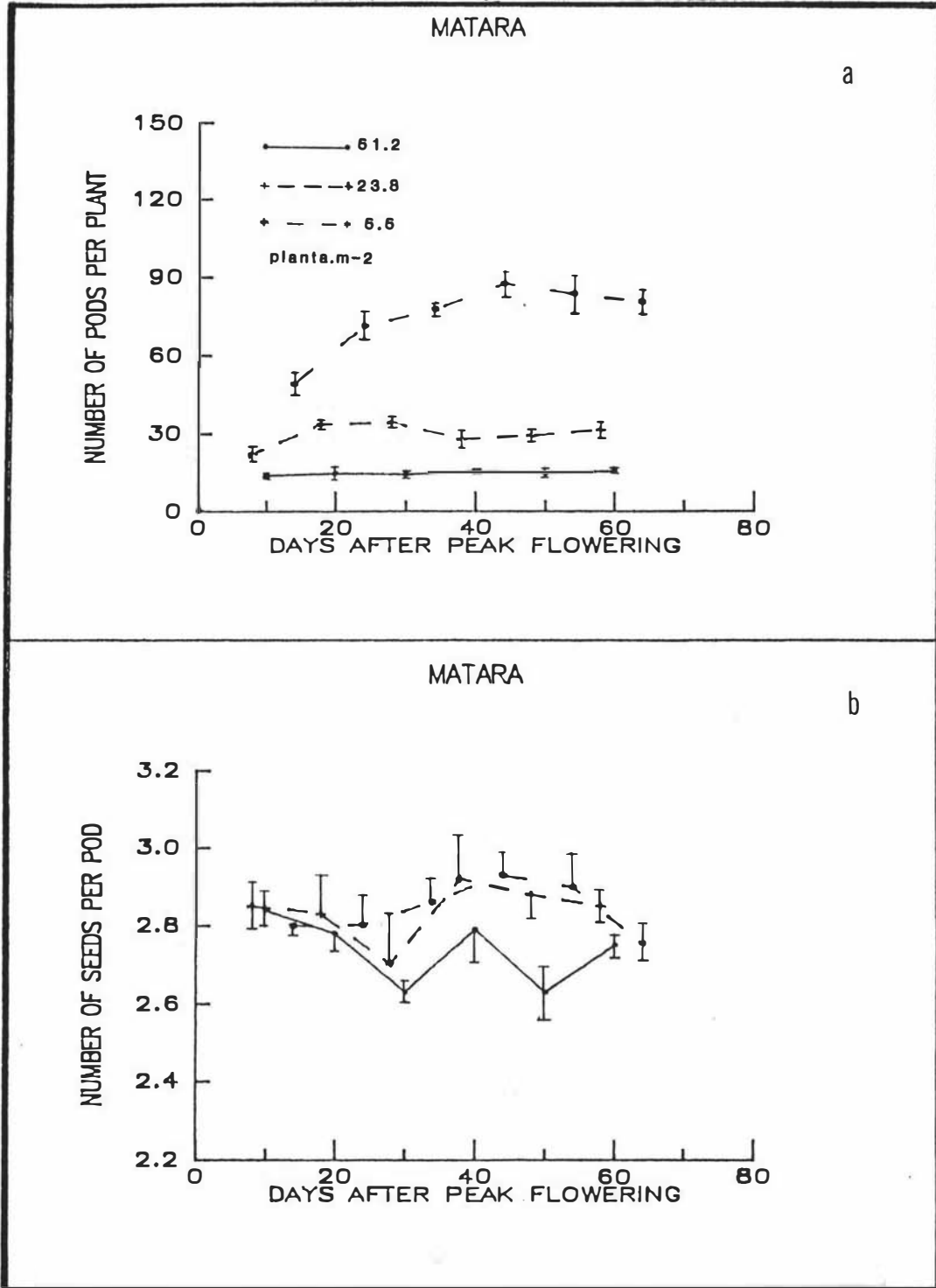


Fig. 2.13 Changes in pod numbers per plant (a) and seed numbers per pod (b) with time at 3 different plant densities (61.2, 23.8 and 5.8 plants.m⁻²) in Matara soybean. Vertical bars represent SE of the means.

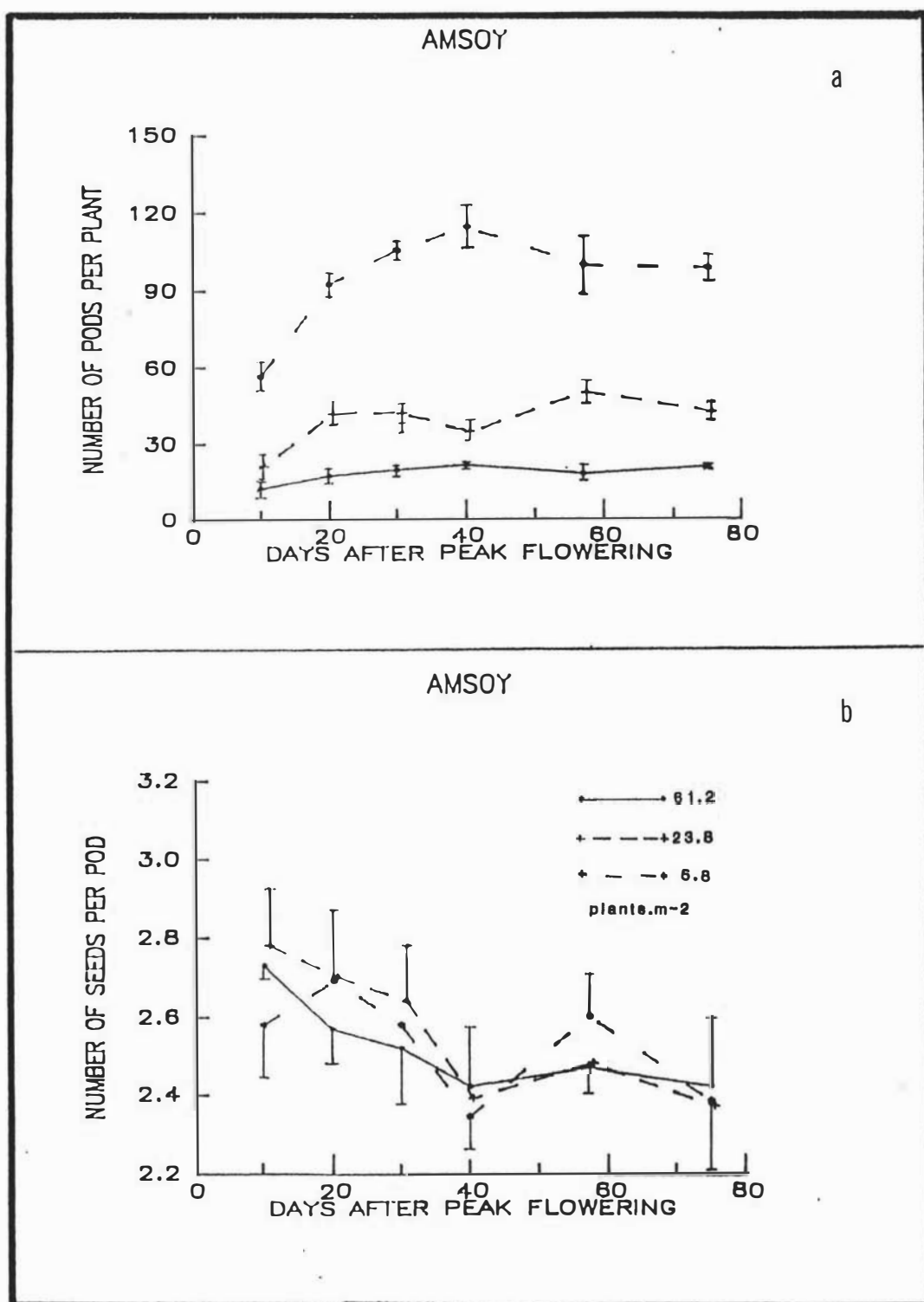


Fig. 2.14 Changes in pod numbers per plant (a) and seed numbers per pod (b) with time at 3 different plant densities (61.2, 23.8 and 5.8 plants.m⁻²) in Amsoy soybean. Vertical bars represent SE of the means.

flowering) earlier than medium and low density plants, respectively. Seed growth rates during stage II (accumulation of food reserves) of seed development were similar (about $5 \text{ mg.seed}^{-1}.\text{day}^{-1}$).

In Amsoy, seed growth rate was slower, reaching a maximum 3 to 17 days later than Matara depending upon plant density. Seed growth rates during stage II of seed development were similar irrespective of plant density (about $4 \text{ mg.seed}^{-1}.\text{day}^{-1}$).

Seed moisture content

Seed moisture content decreased slowly from approximately 80% at 10 DAPF and reached about 60% at 40 DAPF. Subsequently seed dehydration occurred at a faster rate (Figs. 2.17a and 2.18a). In Matara, seed moisture content in low density plants decreased at a slower rate compared to seed moisture content of plants in the other two densities during 40-64 DAPF. The rate of dehydration was relatively slower in Amsoy than in Matara. Seed moisture content finally decreased to approximately 20% at about 60 DAPF in Matara and at about 75 DAPF in Amsoy. At final harvest, it was clear that the dehydration process in seeds tended to occur faster in high plant densities than in low plant densities (Table 2.5).

Seed germination

The germination capacity of air-dried seed (Figs. 2.17b and 2.18b) increased rapidly and reached a maximum between 30 and 40 DAPF in both varieties. Matara seeds had a higher germination capacity than Amsoy at 10 DAPF. Plant density had no effect on seed germination level during the early stages of seed development. However, after 40 DAPF there was a suggestion that seeds produced from high density plants of both varieties had a lower germination capacity than seeds produced from lower density plants, a tendency which was also evident at final harvest (Table 2.5). Plants grown at $5.8 \text{ plants.m}^{-2}$ produced seeds with the highest germination capacity (96.8%,

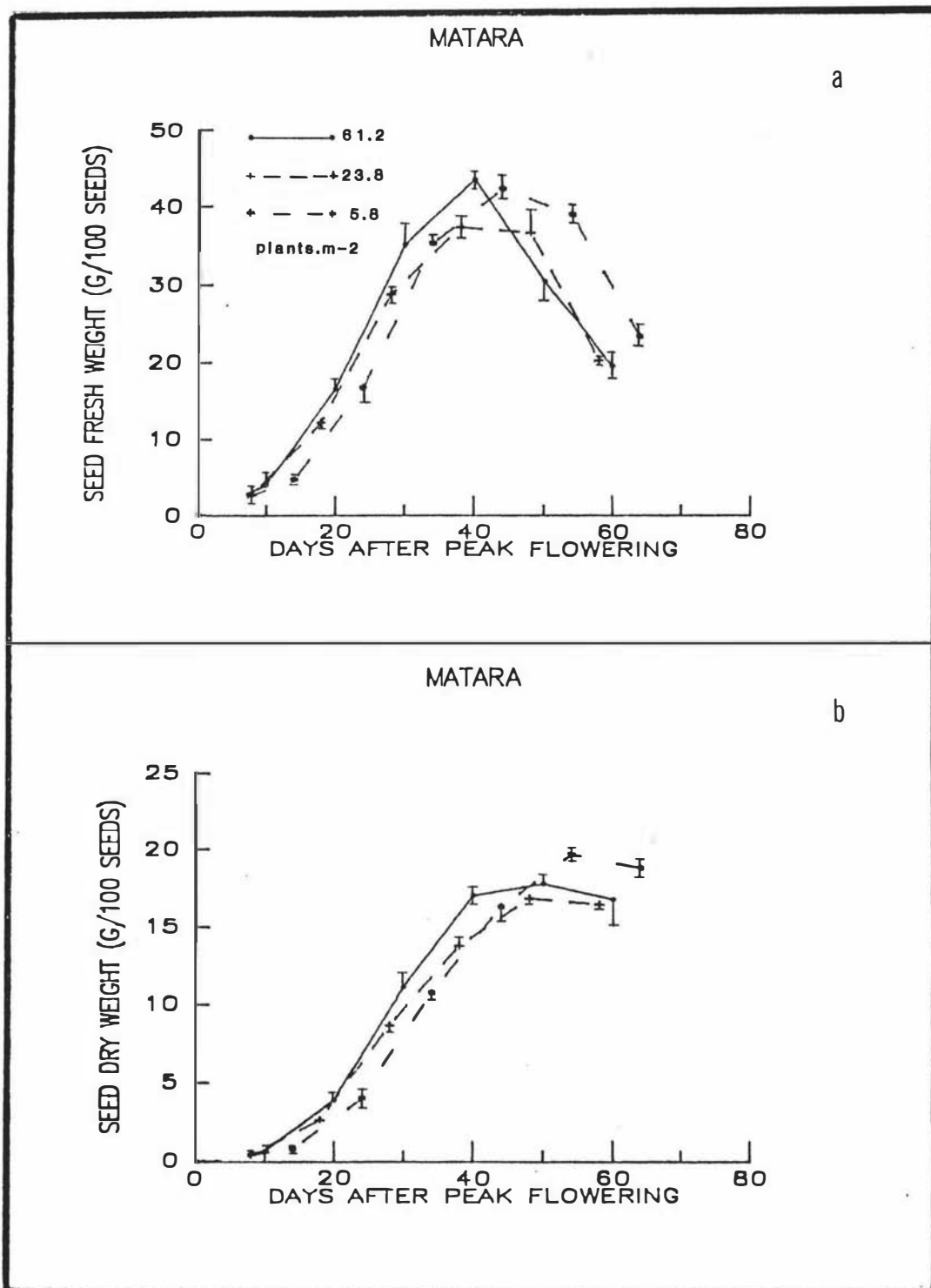


Fig. 2.15 Changes in seed fresh weight (a) and seed dry weight (b) with time at 3 different plant densities (61.2, 23.8 and 5.8 plants.m⁻²) in Matará soybean. Vertical bars represent SE of the means.

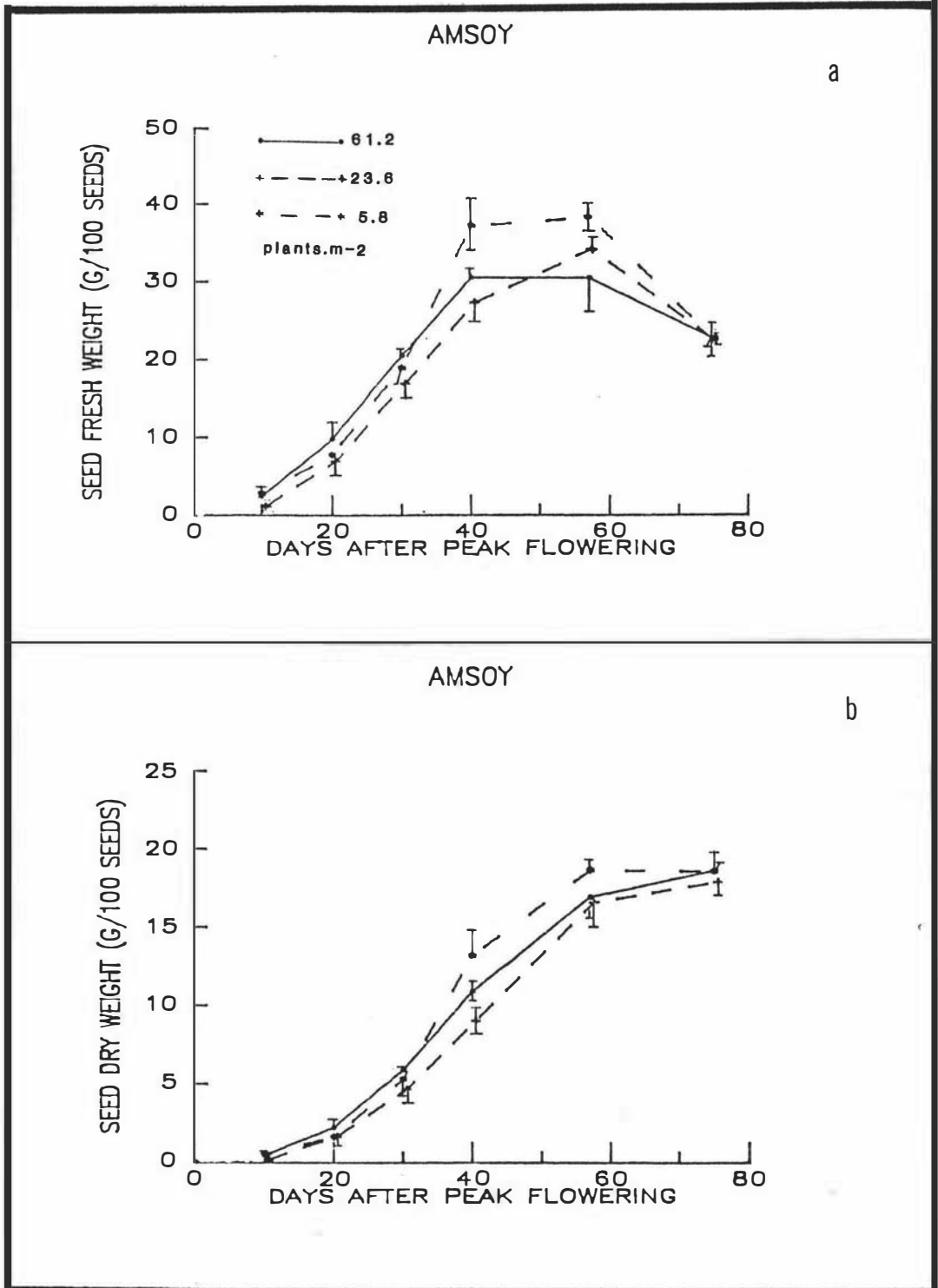


Fig. 2.16 Changes in seed fresh weight (a) and seed dry weight (b) with time at 3 different plant densities (61.2, 23.8 and 5.8 plants.m⁻²) in Amsoy soybean. Vertical bars represent SE of the means.

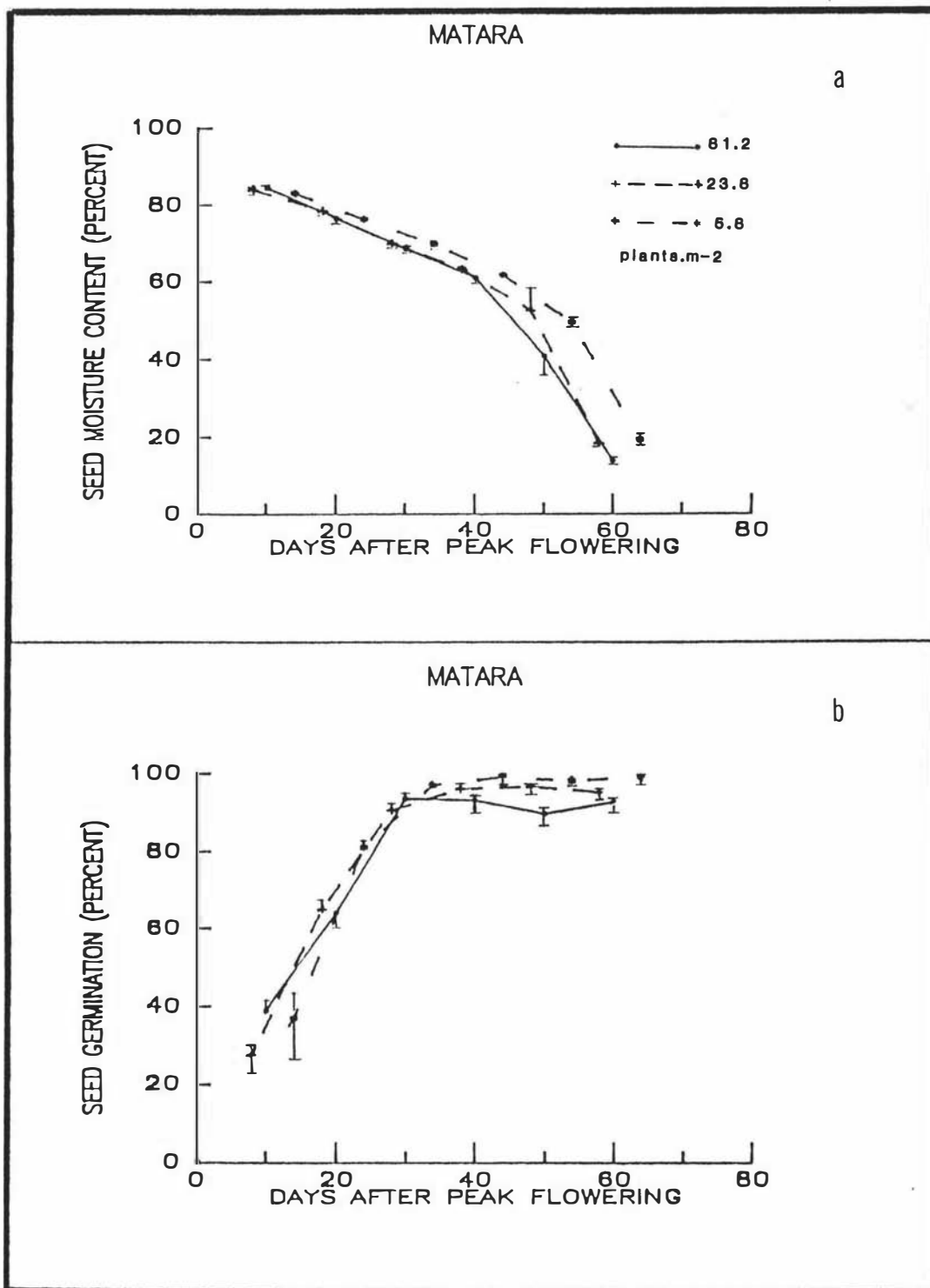


Fig. 2.17 Changes in seed moisture content (a) and air-dried seed germination (b) with time at 3 different plant densities (61.2, 23.8 and 5.8 plants.m⁻²) in Matara. Vertical bars represent SE of the means. Data presented for seed germination are back-transformed values after analysis using arc-sin $\sqrt{\quad}$ transformations.

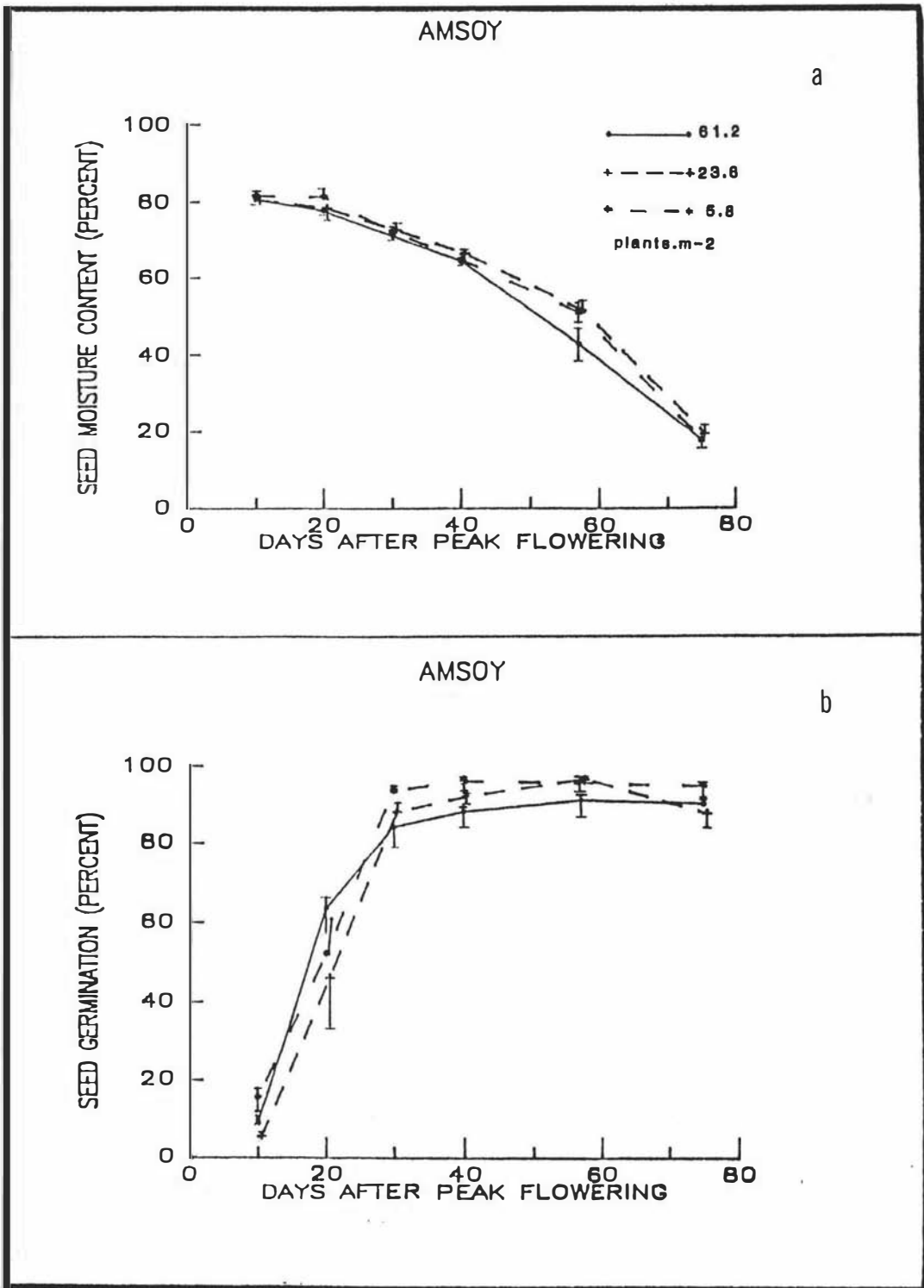


Fig. 2.18 Changes in seed moisture content (a) and air-dried seed germination (b) with time at 3 different plant densities (61.2, 23.8 and 5.8 plants.m⁻²) in Amsoy. Vertical bars represent SE of the means. Data presented for seed germination are back-transformed values after analysis using arc-sin $\sqrt{\quad}$ transformations.

averaged over the two cultivars) whereas plants grown at 61.2 plants.m⁻² produced seeds with the lowest germination percentage (91.3%). There was no variety x density interaction.

The average percentage of seed germination in Matara was significantly higher than in Amsoy (95.7 and 90.7% respectively). Cracked seed coats were constantly found in Amsoy whereas Matara plants produced very few or no cracked seeds.

2.4.2 Economic yield

In this section, the effects of plant density and variety are considered under 2 headings, viz. (i) yield and yield components and (ii) partitioning of seed yield between different parts of the plant.

2.4.2.1 Yield and yield components

Seed yield per plant (Table 2.6) increased with decreasing plant density below 38.2 plants.m⁻², but differences in seed yield per plant at the two highest densities (38.2 vs 61.2 plants.m⁻²) were not statistically significant. Similar responses were found in both varieties. There were no significant differences in yield and yield components between Matara and Amsoy.

Seed yield per unit area increased with plant density showing the importance of plant numbers per unit area (Table 2.6). Maximum seed yield was found at the two highest plant densities (38.2 and 61.2 plants.m⁻²) in both cultivars. Again, there were no differences between the two cultivars.

Table 2.5 Effect of plant density on final seed quality of Matara and Amsoy soybean

| plants.m ⁻² | Seed Moisture Content(%) | | | Air-dried seed germination(%) | | |
|------------------------|--------------------------|---------------------------|---------|-------------------------------|--------------------------|----------|
| | Matara | Amsoy | Mean | Matara | Amsoy | Mean |
| 61.2 | 13.9 | 17.6 | 15.8 c* | 92.5 | 90.0 | 91.25 c |
| 38.2 | 14.8 | 17.6 | 16.2 c | 95.0 | 89.5 | 92.25 bc |
| 23.8 | 18.4 | 19.3 | 18.9 ab | 95.0 | 87.5 | 91.25 c |
| 14.8 | 20.0 | 20.1 | 20.0 a | 95.0 | 90.5 | 92.75 bc |
| 9.2 | 16.5 | 18.0 | 17.2 bc | 97.5 | 92.0 | 94.75 ab |
| 5.8 | 19.3 | 17.8 | 18.5 ab | 99.0 | 94.5 | 96.75 a |
| mean | A 17.1 | A 18.4* | | A 95.7 | B 90.7 | |
| | CV _{var} 17.1 % | CV _{dens} 11.1 % | | CV _{var} 7.0 % | CV _{dens} 7.5 % | |

* Values followed by the same lower case letter in each column and values preceded by the same capital letter in each row of each parameter are not significantly different at probability .05 by Duncan New Multiple Range Test. Analysis of variance for germination percentage was done on arc-sin transformed data.

Table 2.6 Effect of plant density on final seed yield of Matara and Amsoy soybeans

| plants.m ⁻² | Seed Yield (g.plant ⁻¹) | | | Yield g.m ⁻² | | | |
|------------------------|-------------------------------------|---------------------------|--------|--------------------------|---------------------------|-------|----|
| | Matara | Amsoy | Mean | Matara | Amsoy | Mean | |
| 61.2 | 7.3 | 10.3 | 8.8 e* | 445.9 | 632.0 | 538.9 | a |
| 38.2 | 10.2 | 15.3 | 12.8 e | 390.0 | 582.9 | 486.5 | a |
| 23.8 | 14.7 | 20.0 | 17.3 d | 348.9 | 474.6 | 411.8 | b |
| 14.8 | 23.8 | 25.3 | 24.6 c | 352.8 | 375.2 | 364.0 | bc |
| 9.2 | 35.9 | 37.2 | 36.6 b | 331.7 | 343.7 | 337.7 | c |
| 5.8 | 41.6 | 48.5 | 45.0 a | 239.2 | 279.1 | 259.1 | d |
| mean | A 22.3 | A 26.1* | | A 351.4 | A 447.9 | | |
| | CV _{var} 21.6 % | CV _{dens} 16.3 % | | CV _{var} 21.1 % | CV _{dens} 16.3 % | | |

* Values followed by the same lower case letter in each column and values preceded by the same capital letter in each row of each parameter are not significantly different at probability .05 by Duncan New Multiple Range Test.

Of the seed yield components, pod numbers showed the greatest influence in determining seed yield per plant. Increasing plant density from 5.8 to 61.2 plants.m⁻², resulted in a reduction in pod numbers per plant of approximately 80% in both cultivars (Table 2.7). Average figures from 6 plant densities in Matara and Amsoy were 45.9 and 53.8, respectively which were not statistically different.

Seed numbers per pod were also not significantly different either between cultivars or across plant density treatments (Table 2.7). Seed weight showed an inconsistent but minor effect when plant density was altered.

2.4.2.2 Partitioning of seed yield

Three plant densities (61.2, 23.8 and 5.8 plants.m⁻²) were selected to show the effects of plant density on the partitioning of seed yield among different plant parts. The results are shown in Table 2.8. Plants were divided into 3 parts; top, middle and bottom based on plant height and in each stratum pods from branches and main stem were also separated (see also Plate 2.3).

The distribution of seed yield within the plant was closely related to the degree of interplant competition imposed on it by plant density. The percentage of seed yield from the top portion of individual plants was decreased as plant density decreased. As plant density decreased, branches became increasingly important sites as contributors to seed yield. This effect is readily seen in Amsoy and was also found in the middle portion of Matara plants. At the lowest plant density (5.8 plants.m⁻²), the middle portion of plants made the greatest contribution to seed yield in Matara compared with the basal portion in Amsoy. At the medium density (23.8 plants.m⁻²), there was no significant difference in seed yield between the middle and the bottom region of the plants in both varieties. At the highest density (61.2 plants.m⁻²), the main stem contributed more seed yield than branches. Top and middle regions on the main stem were likely to be most important in Matara while middle and basal portions of the plant were major yield contributors in Amsoy.

Table 2.7 Effect of plant density on pod numbers per plant, seed numbers per pod and seed weight (g.100 seeds⁻¹) of Matara and Amsoy soybean

| plants.m ⁻² | Pods per plant | | | | | | | |
|------------------------|--------------------------|---------------------------|------|--|--------------------------|--------------------------|-------|----|
| | Matara | Amsoy | Mean | | | | | |
| 61.2 | 15.8 | 20.9 | 18.3 | f* | | | | |
| 32.2 | 23.2 | 30.6 | 26.9 | e | | | | |
| 23.8 | 31.4 | 41.9 | 36.6 | d | | | | |
| 14.8 | 51.4 | 54.1 | 52.8 | c | | | | |
| 9.2 | 72.9 | 77.6 | 75.3 | b | | | | |
| 5.8 | 80.8 | 97.9 | 89.3 | a | | | | |
| mean | A 45.9 | A 53.8* | | | | | | |
| | CV _{var} 14.8 % | CV _{dens} 12.3 % | | | | | | |
| | Seeds per pod | | | Seed weight (g.100 seeds ⁻¹) | | | | |
| | Matara | Amsoy | Mean | Matara | Amsoy | Mean | | |
| 61.2 | 2.75 | 2.42 | 2.59 | a | 16.74 | 18.59 | 17.67 | ab |
| 38.2 | 2.86 | 2.43 | 2.65 | a | 15.41 | 18.41 | 16.91 | ab |
| 23.8 | 2.85 | 2.37 | 2.61 | a | 16.42 | 17.86 | 17.14 | ab |
| 14.8 | 2.81 | 2.44 | 2.63 | a | 16.40 | 17.30 | 16.85 | b |
| 9.2 | 2.78 | 2.42 | 2.60 | a | 17.73 | 17.84 | 17.78 | ab |
| 5.8 | 2.76 | 2.39 | 2.57 | a | 18.74 | 18.52 | 18.63 | a |
| mean | A 2.80 | A 2.41 | | | A 16.91 | A 18.09 | | |
| | CV _{var} 8.2 % | CV _{dens} 3.0 % | | | CV _{var} 11.4 % | CV _{dens} 8.8 % | | |

* Values followed by the same lower case letter in each column and values preceded by the same capital letter in each row of each parameter are not significantly different at probability .05 by Duncan New Multiple Range Test.

Table 2.8 Seed yield (g.plant part⁻¹) from 5 different plant parts for Matarara and 6 different plant parts for Amsoy from 3 plant densities (61.2, 23.8 and 5.8 plants.m⁻²) (SE is given in parenthesis)

| Strata | Matarara | | | | Amsoy | | | |
|-----------------------------|-------------------------|------------------|------------------|------|-----------------|------------------|-------|------|
| | Main Stem | Branches | Total | % | Main Stem | Branches | Total | % |
| 61.2 plants.m ⁻² | | | | | | | | |
| Top | 2.51 (+0.24) | 0.0 | 2.51 | 32.6 | 1.72 (+0.37) | 0.0 | 1.72 | 17.8 |
| Middle | 2.26 (+0.24) | 0.33 (+0.09) | 2.59 | 33.7 | 2.50 (+0.51) | 1.13 (+0.41) | 3.63 | 37.7 |
| Bottom | Not analysed separately | | 2.59 (+0.44) | 33.7 | 2.33 (+0.52) | 1.96 (+0.61) | 4.29 | 44.5 |
| | | | | | | | | |
| 23.8 plants.m ⁻² | | | | | | | | |
| Top | 3.55 (+0.17) | 0.64 (+0.14) | 4.19 | 27.3 | 2.04 (+0.20) | 0.84 (+0.13) | 2.88 | 15.5 |
| Middle | 3.12 (+0.30) | 2.15 (+0.20) | 5.27 | 34.3 | 3.87 (+0.97) | 4.28 (+0.56) | 8.15 | 43.7 |
| Bottom | Not analysed separately | | 5.90 (+0.93) | 38.4 | 3.27 (+0.68) | 4.34 (+0.92) | 7.61 | 40.8 |
| | | | | | | | | |
| 5.8 plants.m ⁻² | | | | | | | | |
| Top | 5.90 (+0.85) | 4.66 (+0.96) | 10.56 | 24.3 | 2.10 (+0.41) | 3.51 (+0.71) | 5.61 | 12.1 |
| Middle | 6.95 (+0.18) | 11.14 (+0.37) | 18.09 | 41.6 | 6.14 (+0.40) | 12.03 (+2.22) | 18.17 | 39.1 |
| Bottom | Not analysed separately | | 14.88 (+1.45) | 34.2 | 6.66 (+0.90) | 16.06 (+1.64) | 22.72 | 48.8 |



Plate 2.3 Above ground plant forms at final harvest of Matara soybean grown at different plant densities

2.5 DISCUSSION

2.5.1 Radial spacing design in plant density study

The results from this study show that the radial spacing design (type 1a) is very useful for studying the effects of a wide range of densities on plant growth and development in soybean. Comparing the results of Buttery (1969b) with the results of the present study, the radial design (type 1a) proved reliable in that it demonstrated the same pattern of plant growth responses to density (see also section 2.5.2). Buttery used a soybean variety (Harosoy 63) which is a parental line of Amsoy and is in the same maturity group (Amsoy originated as an F₇ plant selection from the cross 'Adams' x 'Harosoy'). Moreover, he conducted his work at Harrow, Ontario, Canada where the latitude (42° 02') is in about the same range as New Zealand. As might be expected, mean values differ, but results from both experiments in terms of plant dry weight (shoot dry weight), leaf area per plant, CGR and LAI are comparable between Harosoy 63 and Amsoy at the same density and the same time (Figs. 1A, 1B, 6A and 7 in Buttery, 1969b compared, respectively, with Figs. 2.7b, 2.7a, 2.10a and 2.10b in the present study). These similarities between a rectangular planting and this radial planting show the appropriateness of the Nelder 1a design in plant density studies. Curve fitting techniques can be successfully used to overcome sample shortages in the radial as previously discussed (2.3.4).

2.5.2 Factors influencing vegetative plant growth and development

The present study has clearly shown that in soybeans, plant growth and development are substantially affected by plant competition. Generally, these observations on changes in plant morphological characteristics as influenced by plant density indicate similar effects to those reported previously, particularly in relation to plant height (Hinson and Hanson, 1962; Weber et al., 1966; Doss and Thurlow, 1974; Wilcox, 1974); node number (Weber et al. 1966, Buttery, 1969a; Enyi, 1973); branch number (Hinson and Hanson, 1962; Weber et al., 1966; Buttery, 1969a; Enyi, 1973; Costa et al., 1980); and maturity date (Hinson and Hanson, 1962). In the present study, interplant

competition created by wide variations in plant density was generally found to be minimal up to 30 DAE (Figs. 2.2-2.7). The competitive effect, however, became more extreme as plants grew bigger. By 50 DAE, the growth of high density plants was obviously depressed, especially in Matara. The high competitive stress occurring in these crowded Matara plants started to inhibit node production and leaf growth (Figs. 2.2b, and 2.6a). However, total shoot dry weight accumulation (Fig. 2.6b) was inhibited in these high density conditions rather later, since it reached its maximum at 70 DAE. In low density plants, all these parameters reached their maximum at 80 DAE. Data from Buttery (1969b) have also shown that plants grown at high densities reach maximum growth earlier than plants grown at low densities. In Amsoy, maximum growth occurred at 70 DAE irrespective of plant densities (Figs. 2.3b, 2.7a and 2.7b). Because no data were collected at 80 DAE in Amsoy, it is difficult to conclude whether high density responses in this cultivar follow a similar pattern to Matara.

Throughout the experiment described, stringent efforts were made to maximise soil fertility, nodulation, weed control, insect and disease protection to maintain maximum plant growth throughout the growing season. Under such conditions Donald (1963) has suggested that of all the factors influencing competition in crops, light becomes the major limiting factor to production. Similarly, competition for light is implicated as the major factor inducing morphological changes in plants when plant density is increased (Herbert and Litchfield, 1984).

One indication of the prime influence of competition for light was stimulation of internodal elongation and promotion of plant height under mutual shading conditions (etiolation effects). The results show that new node production (node number) had completely stopped by 50 DAE, but increases in plant height continued up to 70 DAE before remaining constant (Figs. 2.4 and 2.5). Longer internodes in plants grown at high plant densities have also been observed by Doss and Thurlow (1974).

It may be worthwhile noting here that light distribution within the soybean canopy may also be important in affecting pod set. Irradiance is attenuated and spectral distribution changes as light penetrates the soybean canopy (Singh et al., 1968). As a consequence, leaf

photosynthetic rates are reduced for leaves lower down the plant (Johnston *et al.*, 1969). If assimilate supply regulates pod set, then pods per node, seeds per node and seed weight per node are expected to decrease at progressively lower levels in the canopy (Heindl and Brun, 1984). The results from the present study support this contention. Pod number per node on the main stem was relatively low at the basal region of Amsoy plants compared to the middle region (for example at 5.8 plants.m⁻² the middle region had 3.1 pods.node⁻¹ compared to 1.9 at the basal region : see Appendix 7 for more complete data). However, low pod number per node in the top region (0.6 pods.node⁻¹ at 5.8 plants.m⁻²) may not be explained by light interception, but may be explained by plant growth habit. During the reproductive phase, Amsoy plants grown under low competitive stress continued to grow vegetatively more than under the high stress conditions and reproductive structures produced during the late stages of development were located mainly on the top region of the main stem and branches. These reproductive structures, therefore, had a relatively shorter time to develop and were also under more intense competition from vegetative growth than reproductive structures at the middle and the bottom regions, resulting in lower pod numbers per node.

2.5.3 Crop growth and planting density

LAI is regarded as an indicator of the intensity of competition for light experienced by individual plants within a stand. In this study, light interception (Appendix 6) in plants grown at different densities started to change from about 30 DAE. Observations suggested that canopy closing occurred slightly earlier in Matara than in Amsoy, possibly due to differences in canopy structure and maturing character. Plants grown at high densities reached maximum light interception earlier than low densities (see Appendix 6).

Leaf area development in both cultivars in this study agrees with results reported previously (Buttery, 1969b; Enyi, 1973; Herbert and Litchfield, 1984; Willcott *et al.*, 1984). Generally, leaf area index (LAI) increased rapidly during the early reproductive stage and reached maximum LAI at about the end of flowering (compare Figs. 2.9b vs 2.11 and 2.10b vs 2.12). Thereafter, LAI declined progressively as a result of the increasing abscission of lower leaves.

A high correlation between CGR and LAI was also found in the present study suggesting that as plant growth progressed, increasing LAI resulted in an increasing occupancy of interplant spaces and consequently increasing light interception resulting in an increasing rate of dry matter production (Shibles and Weber, 1965; 1966).

CGR increased with planting density although maximum CGR was reached slightly earlier in high densities. These results have also been demonstrated previously (Buttery, 1969b; Herbert and Litchfield, 1984). In Matara, CGRs of plants grown at 61.2, 38.2 and 23.8 plants.m⁻² increased up to 40 DAE and then decreased rapidly after 60 DAE. CGRs tended to increase up to 60 DAE for plants grown at 14.8, 9.2 and 5.8 plants.m⁻² and declined rapidly after 75 DAE. In Amsoy, CGR increased up to 70 DAE irrespective of plant densities before decreasing. The decrease in CGR was concomitant with seed formation and leaf senescence. Shibles et al. (1975) indicated that substantial quantities of carbohydrates accumulated in leaves, petioles and stems prior to seed development are later utilized in seed growth. Thus seed growth in soybean partly relies on the redistribution of photoassimilates which is reflected in a reduction in CGR. Therefore, the higher early CGR in high density plants could be related to their high seed yield (Table 2.6).

2.5.4 Different responses in vegetative plant growth and development between cultivars

The different plant growth effects between the semideterminate Matara and the indeterminate Amsoy revealed in this experiment support the findings of Green et al. (1977). In general, the semideterminate cultivar was shorter in height and earlier in maturity, and had fewer nodes per plant than the indeterminate cultivar. Green et al. (1977) have further reported that these two types of stem growth respond similarly to row spacing, an effect which was clearly demonstrated in the present study since all growth parameters including seed yield and yield components (Tables 2.6 and 2.7) in these two growth types showed the same type of response to plant density variation. There was no significant interaction between variety and density.

2.5.5 Relationship between vegetative and reproductive growth

Figs. 2.19 and 2.20 summarise the response of selected vegetative and reproductive plant growth parameters at 3 plant densities: 61.2, 23.8 and 5.8 plants.m⁻². To highlight the effects of inter- and intraplant competition, the flowering period in each cultivar was divided into 3 phases. There was a slight difference in the time sequence between Matara and Amsoy. In Phase I (early flowering period), the initial daily flower production in Amsoy was similar at all three plant densities, whereas in Matara low density plants produced flowers at a higher rate than high density plants. This may be attributed to the earlier canopy closing in Matara than in Amsoy (as discussed in the previous section), and the fact that high density plants reached the point of interplant competition for light earlier than low density plants.

During Phase II (mid-flowering period), daily flower production increased sharply and reached a peak during this phase, daily maximum flower production per plant depending largely on plant density. In Phase III (late flowering period), daily flower production fell, although the rate of decline was substantially different in each plant density treatment. Between the end of Phase II and the beginning of Phase III, there was a second increase in flower production in low density plants in both cultivars. Increased branching in low density plants may play an important role in this second increase in flower production. Interplant competition created by plant density obviously suppressed branching and this in turn suppressed daily flower production.

When vegetative and reproductive growth are considered together, the effect of interplant competition became more obvious. Before plants entered the reproductive phase, little or no interplant competition was apparent at all plant densities. Particularly during the first 30 DAE, vegetative growth parameters such as plant height, plant dry weight and leaf area per plant were similar at all densities. During this early

growth period, light competition between plants was still low, leaves on each plant remaining free from contact with the leaves of neighbouring plants. At this stage, light penetration to ground level was still more than 20% even in the highest density (Appendix 6). This suggests that plants grown at all densities at 30 DAE had similar 'source strength' to produce the same number of flowers per plant per day. This certainly occurred in this experiment, since, as already mentioned, daily flower production was not significantly different during the early period of phase I (i.e. from first flowering to 32 DAE in Matara and to 38 DAE in Amsoy). However, towards the end of phase I, the level of interplant competition gradually increased in the highest density and was expressed by a decline in leaf growth. In medium and low densities active vegetative growth during the end of phase I enhanced plant size, resulting in a higher source strength for plants to produce higher daily flower numbers during phase II. At the beginning of phase II, high density plants stopped producing new leaves and medium density plants showed a decline in vegetative growth as a result of increasing interplant competition. Low density plants, on the other hand, still displayed very active vegetative growth because of less competitive stress. The reduction in vegetative growth in low density plants was delayed until after phase III. It seems likely that higher source strength (bigger plants and more branch leaves) at the beginning of phase III in low density plants was responsible for a second increase in daily flower production compared to the sharp decrease and completion of flowering in medium and high densities. This second increase in daily flower production reflected a lower level of interplant competition.

The results clearly show that interplant competition suppressed daily flower production and consequently caused smaller numbers of flowers to be formed per plant in high density situations, whereas intraplant competition (competition between vegetative and reproductive growth) existed at a higher level in low density grown plants.

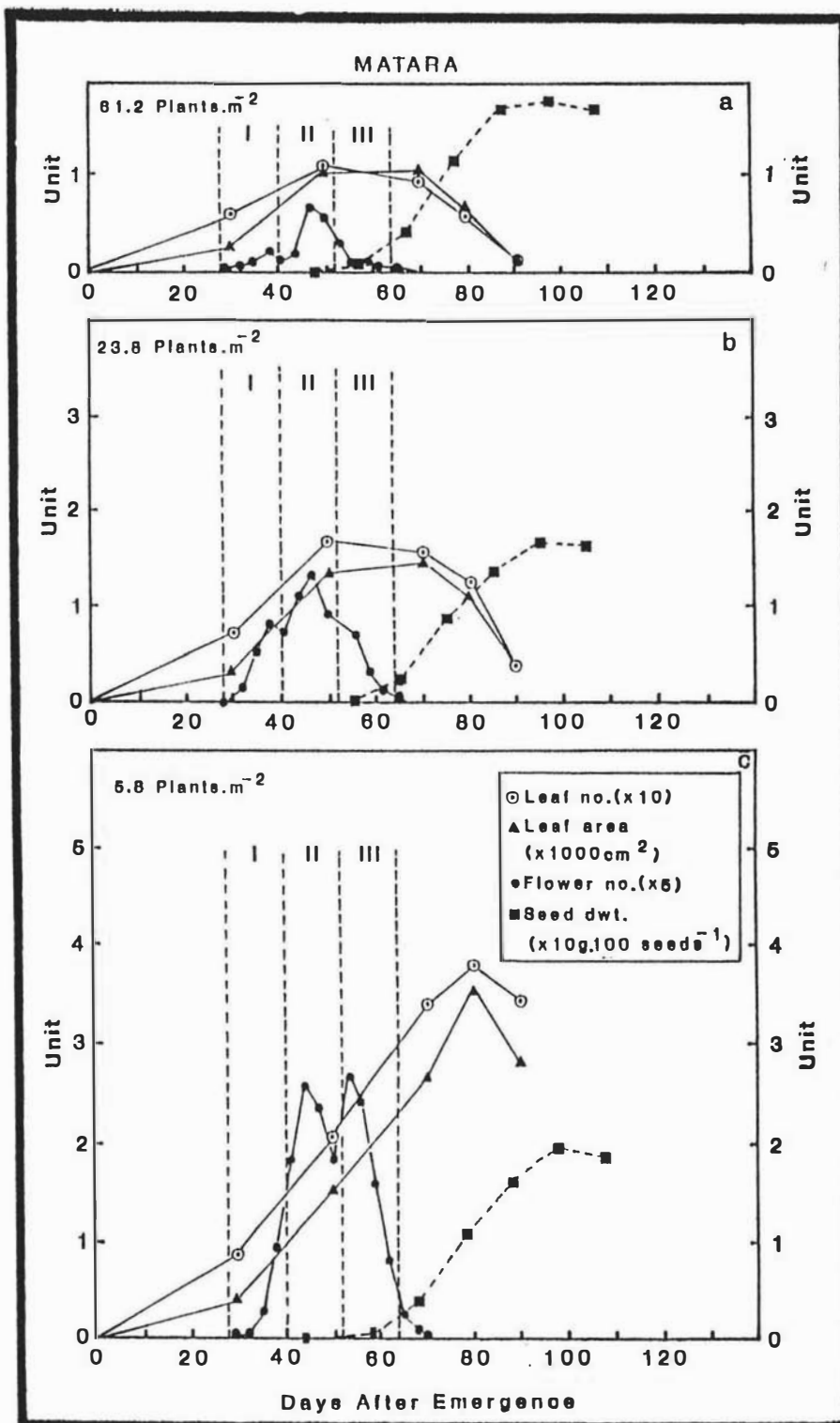


Fig. 2.19 Some aspects of vegetative growth (leaf number and leaf area per plant) and reproductive growth in Matara soybean at 3 different plant densities :
 - (a) 61.2 plants.m⁻², (b) 23.8 plants.m⁻² and
 (c) 5.8 plants.m⁻² (I, II and III indicate 3 phases of flowering; i.e. early, mid- and late flowering period, respectively)

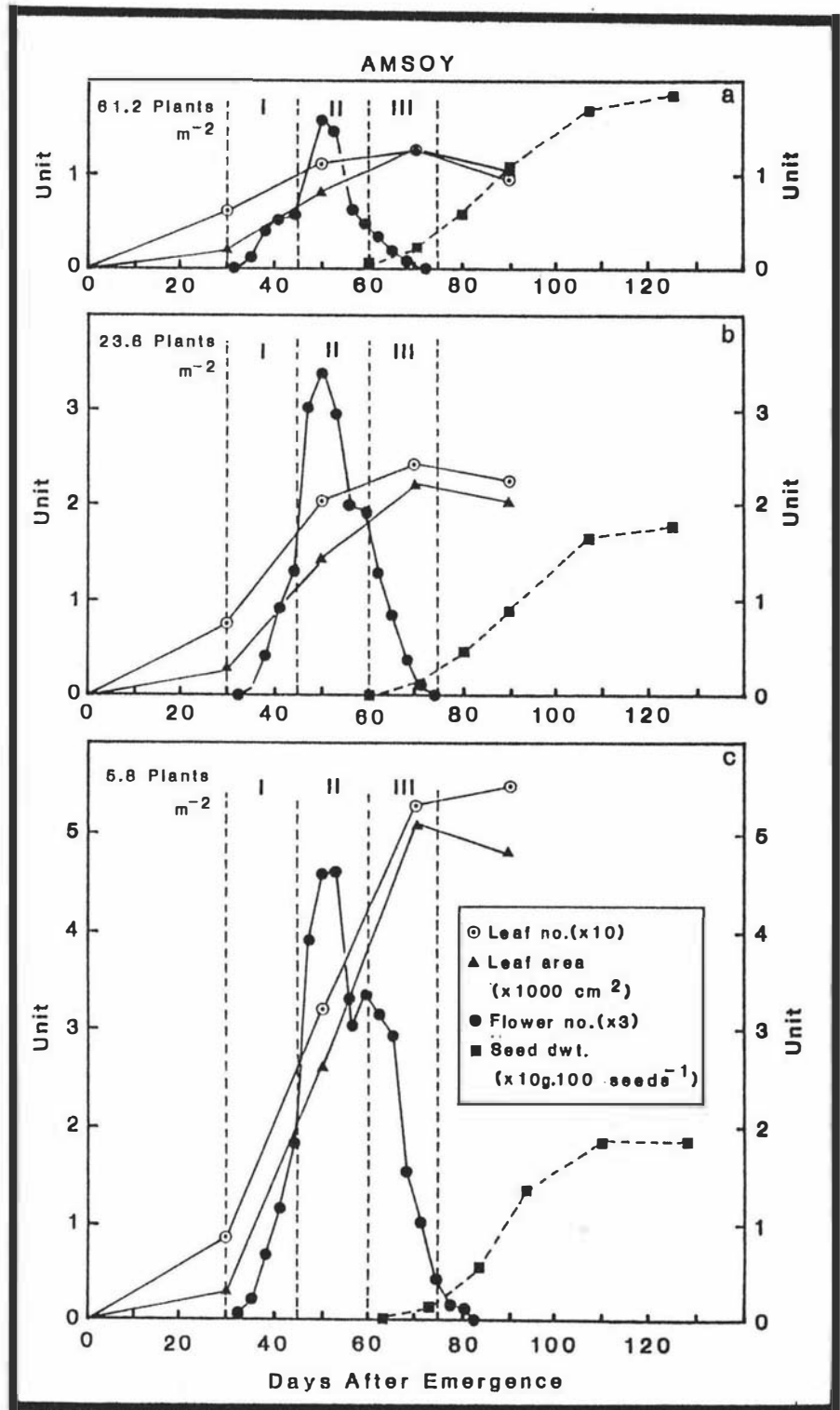


Fig. 2.20 Some aspects of vegetative growth (leaf number and leaf area per plant) and reproductive growth in Amsoy soybean at 3 different plant densities : (a) 61.2 plants. m^{-2} , (b) 23.8 plants. m^{-2} and (c) 5.8 plants. m^{-2} (I, II and III indicate 3 phases of flowering; i.e. early, mid- and late flowering period, respectively)

2.5.6 Reproductive growth and reproductive abortion

The percentage of reproductive abortion was remarkably consistent throughout the wide range of plant densities studied (Table 2.4). This result is contrary to those obtained by Buttery (1969a) and Dominguez and Hume (1978) who found that rate of reproductive abortion increased with plant density. However, the varieties used and different range of planting densities employed by the latter may have contributed to these different results. Buttery (1969a) studied the related variety, Harosoy 63 under 4 planting densities; 4, 8, 16 and 32 plants.m⁻², a range similar to some of the densities used in the present study, so it might be expected that the results should have been comparable. However, a different counting method was used by Buttery (1969a) who noted that his long counting interval (2 weeks) might miss many flowers completely and thus give considerable underestimates of flower numbers. As has already been discussed, the rate of flower production at lower densities is considerably higher which may mean that abortion rates in his study have been more severely underestimated at lower densities than high ones.

According to the pattern of pod development (Figs. 2.13a and 2.14a), large pod abortion (≥ 2 cm long) seemed to be minimal in this study. Therefore, the high reproductive abortion percentage here is attributable to the abortion of flowers or young pods (< 2 cm long), which is in agreement with previous work by Van Schaik and Probst (1958b).

Matara (semideterminate) and Amsoy (indeterminate) soybeans differed in their reproductive abortion levels (65 and 82%, respectively). Differences in reproductive abortion percentages among cultivars have also been reported by other researchers (Van Schaik and Probst, 1958a and 1958b; Dominguez and Hume, 1978). Studies by Dominguez and Hume (1978), for example, have indicated that 052-903 (a semideterminate variety) had a lower reproductive abortion percentage than Altona and Vansoy (indeterminate varieties).

Two main questions should be raised here :

1) why is the percentage of reproductive abortion so consistent in all planting densities ?

and,

2) what characteristics are responsible for differences in the abortion rate in these two cultivars ?

The results obtained provide some possible answers. In comparisons between plant densities, it seems that with decreasing plant density there is a progressive increase in intraplant competition. This effect is particularly obvious in low density plants where vegetative growth continued right through phase III (Figs. 2.19 and 2.20).

If reproductive abortion is controlled by the supply of photo-assimilates to the developing flowers and pods as has been suggested by Wiebold et al. (1981); Addicott (1982) and Antos and Wiebold (1984), then it can be suggested that the high reproductive abortion occurring in low density plants in the present study was greatly influenced by intraplant competition whereas the high abortion levels in high density plants was mainly affected by interplant competition.

2.5.7 Seed development

Seed growth rate and seed filling period were of interest in this study. For these aspects, Matara and Amsoy plants performed differently under different plant densities. It was evident in Amsoy that the rate of increase in seed dry weight was slower than in Matara (4 vs 5 mg.seed⁻¹.day⁻¹). To get to approximately the same size of seed, Amsoy required 3 to 17 days longer (based on days after peak flowering) to reach equivalent seed size to Matara depending upon plant density (compare Fig. 2.15b and 2.16b). It is presumed that the slower seed growth in Amsoy may be due to its continued vegetative growth during seed development. However, Amsoy plants could continue seed development over the extended periods, because they had a longer leaf duration (Figs. 2.6a and 2.7a), whereas Matara plants which were less

plastic in growth habit and had a shorter leaf duration, had a shorter seed filling period despite the fact that they had a genetically higher seed growth rate than Amsoy plants.

After reaching maximum seed fresh weight, there was a rapid loss of weight due to dehydration. The commencement of moisture loss was slightly earlier in high than in low density plants, although this trend was more marked in Matara than in Amsoy. This result suggests that density stress can hasten dehydration especially in early maturing soybeans. Similar results have been reported in density studies in maize (Poneleit and Egli, 1979).

The results on germination percentage as affected by planting density show that germination was lower in seeds from high density plants after they attained physiological maturity and also in seeds of the Amsoy cultivar compared to Matara (Figs. 2.17b and 2.18b and Table 2.5). The less favourable environment created by crowded growing conditions in high density plants and adverse climate such as high relative humidity during Amsoy seed maturation (Appendix 2) may be responsible for these effects. Crowding of plants in the field, may increase ambient relative humidity due to poor air movement and also increase levels of fungal infection. These may all be possible causes of reduced seed germination. Although, it is suggested that density effects may affect seed size and, in turn, affect seed germination in soybean and maize (Burris, 1973; Escasinas, 1984), in the present study a significant correlation coefficient (0.74) at probability <0.10 was found between seed weight and seed germination only in Matara. No such correlation was found in Amsoy (0.20). This suggests that seed size was unlikely be the main cause of lowered seed germination in seed from high density plants in Amsoy and may be confounded by the high level of cracked seeds caused by weathering effects due to its late maturing character.

2.5.8 Economic yield

The response in seed yield per plant to plant density in both soybean cultivars was similar. Increasing plant density from 5.8 to 61.2 plants.m⁻², seed yield per plant was dramatically decreased. When these figures were converted into seed yield per unit area (Table 2.6),

it was found that yield increased as plant density increased up to 38.2 plants.m⁻², but no significant difference was found between 38.2 and 61.2 plants.m⁻². Therefore, optimum plant density was considered to be at 38.2 plants.m⁻². However, optimum plant density may vary from year to year, location to location and cultivar to cultivar, depending upon environmental factors. The results from previous studies are summarised in Table 2.9.

Table 2.9 Summary of recommended optimum densities from previous studies on soybean

| Variety | Location | Recommended density (plants.m ⁻²) | Reference |
|------------|---------------------|---|-------------------------------|
| Harosoy 63 | Canada | 32 | Buttery (1969a) |
| Matara | New Zealand | 30 | Tolentino (1985) |
| L15* | USA (Indiana) | 28 | Wilcox (1974) |
| C1477** | USA (Indiana) | 28 | Wilcox (1974) |
| C1421*** | USA (Indiana) | 46 | Wilcox (1974) |
| Evans | USA (Massachusetts) | 68 | Herbert and Litchfield (1982) |

* 'Wayne' x 'Clark 63'

** 'Amsoy' x C1253 (Sel. from 'Blackhawk' x 'Harosoy')

*** 'Adelphia' x 'Mukden'

These results strongly suggest that the optimum plant density needed for maximising seed yield in soybean cannot be generalised, since it appears to depend strongly on differences in variety and environment. A comment made by Donald (1963) that the density required to give maximum yield increases as fertility status is improved, could be useful for soybean growers in selecting an optimum (appropriate) planting density. Therefore, it may be suggested that in highly

productive environments, plant densities ranging from 38 to 61 plants.m⁻² might be most suitable, and in lower productive environments plant densities should be reduced, possibly to within the range 28 to 38 plants.m⁻².

Yields per hectare were not statistically different between Matara and Amsoy. This confirms the statement by Anderson (1987) that 'yields of Matara have normally been equivalent to Amsoy in warm seasons' in New Zealand.

Differences in the vertical pattern of seed yield distribution in individual plants of Matara and Amsoy (Table 2.8) were governed by the degree of stem termination, plant density and perhaps light distribution within the canopy. Although total pod number per plant in Matara and Amsoy were not significantly different (Table 2.6), their distribution on the plants was. At comparable plant densities, the semideterminate Matara produced a greater percentage of seed yield in the top portion of the plant. In most cases, there were no differences in seed yield between the middle and bottom parts of the plant. However, it appeared that at the lowest density, seed yield from branches in the bottom region of Amsoy plants was significantly higher than the middle and the top parts. As discussed in section 2.5.2, light distribution may be responsible for this difference in Amsoy. Thus, the suggestion by Willcott et al. (1984) that greater efficiency of production could be obtained by concentrating breeding efforts for improved canopy structure, allowing deeper light penetration into the canopy is supported by the present study. Increased utilisation of incident light is only one part of the equation. Competition for assimilate between reproductive and vegetative growth is also important and thus this suggestion may be applied to only indeterminate soybeans. The results of the present study show that although the semideterminate Matara grown at the lowest density (5.8 plants.m⁻²) produced a lower seed yield at the bottom part compared to Amsoy (34% vs 49% of total seed yield), Matara plants could give similar seed yield per unit area in all densities to Amsoy. Moreover, the semideterminate Matara plants which produced a higher seed yield at the top part than the indeterminate Amsoy may have advantages in terms of density tolerance (pod growth at the top part can be better supplied by photosynthate from leaves at the top part even in high density plantings), reduced

competition from vegetative growth, and facilitating harvesting. In other words, Matara is a result of a good breeding program because of the increase in reproductive efficiency from its parental Amsoy variety and its equal yield when grown under warm environmental conditions.

2.6 CONCLUSION

The results from this study showed that plant growth and development in soybean is markedly influenced by the degree of plant competition. A dynamic (or plastic) response in vegetative and reproductive growth was encouraged by varying plant density.

The optimum plant density determined in this experiment was 38.2 plants.m⁻². Higher plant densities did not result in increased seed yield per unit area. However, it is suggested that environmental and edaphic conditions should be considered before choosing a suitable planting density in different climatic areas.

Seed quality at harvest was also found to be affected by plant density and variety. High density plantings caused a slight but significant reduction in seed germination (91% at 61 plants.m⁻² and 97% at 6 plants.m⁻²). External factors such as poor ventilation, humid conditions and fungal infection were suggested as possible causes of this effect, together with internal factors such as limitations in seed size or food reserves. Amsoy gave a poorer seed germination than Matara (90.7 and 95.7%, respectively) due to the less favourable late season climatic conditions during maturation.

Consistently high rates of reproductive abortion within each cultivar were found across all plant densities. This was presumably due to the interaction between interplant and intraplant competition. High reproductive abortion in high density plants may be mainly governed by interplant competition, while high reproductive abortion in the low density plants may be attributed more to intraplant competition. Further investigation is needed to determine whether high levels of abortion of reproductive structures occurred because of competition for photoassimilates between vegetative and reproductive growth or whether this effect was under genetic control.

Matara performed as a truly semideterminate cultivar as indicated by the lower level of vegetative growth during the reproductive phase as a result of earlier stem termination. Amsoy was approximately 2 weeks later in reaching plant maturity than Matara (based on days after emergence) and behaved in an obviously indeterminate manner. The differences between these two varieties was found mainly in terms of their vegetative growth. Amsoy tended to produce about twice as much vegetative growth as Matara, but in both cultivars reproductive growth was similar except for the rate of flower production, flower number per plant, seed growth rate and levels of reproductive abortion. Seed yield and yield components of Matara and Amsoy were also more or less the same. These results suggest that, especially in Amsoy, the wasteful loss of reproductive capacity through abortion was a major factor limiting their seed productivity and yield and that these parameters could be substantially increased if the abortion rate were reduced.

CHAPTER 3

MORPHOLOGICAL AND HISTOLOGICAL STUDY ON SOYBEAN FLOWERS AND PODS IN RELATION TO FLOWER ABORTION AND SEED ABORTION WITHIN PODS

3.1 INTRODUCTION

In the previous field study, it was shown that between 56 and 85% of the flowers formed on soybean plants aborted before reproduction was completed. The term 'abortion' describes the failure of a flower or immature pod to develop into a fully-expanded (≥ 2 cm) and seed-containing pod and the term 'seed abortion' refers to a young seed that fails to develop into a normal seed. The term 'abscission' is used to describe the natural separation of a flower or pod from the plant. In this Chapter, two separate experiments were conducted. The first experiment examined levels of fertilization of soybean flowers borne on plants grown in the glasshouse. The second experiment investigated seed abortion on plant material obtained from the previous field experiment. The main objectives of these studies were as follows.

- To observe the morphological development of flowers located on different parts of a soybean raceme
- To investigate whether flower abscission occurred following a lack of fertilization
- To ascertain the proportion of fertilized and unfertilized ovules
- To observe the probability of unfertilized ovules occurring in different positions in the ovaries
- To observe the frequency of seed abortion and seed development at each position within soybean pods

3.2 LITERATURE REVIEW

3.2.1 The soybean flower

Following the period of vegetative growth, which varies depending upon variety and environmental conditions, plants enter the reproductive stage. The flowers of the soybean develop in axillary racemes, usually consisting of 5 to 16 flowers (Guard, 1931), but sometimes with up to 35 flowers in a single inflorescence (Piper and Morse, 1923). The first flowers appear at node four or higher (Fehr et al., 1971) and appear progressively towards the tip of the main stem and also towards the tips of the branches. Gai et al. (1984) described that there are usually three axillary buds, but occasionally more, at a main-stem node. Under field conditions, the middle bud usually develops into a primary branch on the lower nodes and into a main raceme on the upper nodes. On the upper nodes, the other two axillary buds develop into subracemes or sub-branches with very small leaves on each side of the main raceme. On the lower nodes, the two axillary buds either do not develop or become small subracemes or sub-branches on each side of the primary branch. A secondary branch might develop on a primary branch in a luxuriant, late-maturing cultivar.

The soybean flower is a typical papilionaceous flower with a tubular calyx of five unequal lobes, a five-parted corolla that has a large posterior banner petal, two lateral wing petals and two anterior keel petals that are in contact but are not fused. The stamen comprises a typical diadelphous androecium in which the filaments of nine of the stamens are fused and elevated as a single structure with a posterior stamen remaining separate. The single pistil is unicarpellate and has one to four campylotropous ovules alternating along the posterior suture. The style, which is about half the length of the ovary, curves backwards towards the free posterior stamen and is terminated by a capitate stigma. Trichomes are present on the surface of the single pistil and also cover the outer surfaces of the calyx tube, the bract, and bracteoles. No trichomes are present on the petals or stamens (Guard, 1931; Carlson, 1973).

During anthesis, the opening of soybean flowers is controlled genetically and by some environmental conditions, especially

temperature and photoperiod. Erickson (1975b) studied the variability of floral characteristics and reported that soybean flowers could be cleistogamous, partially chasmogamous or chasmogamous. Chippewa 64 soybean, for instance, has been shown to be fully cleistogamous throughout flowering, while Hark soybean is more chasmogamous (Erickson, 1975a). Flower openness in some cultivars has been found to respond linearly to night air temperature, attaining highest values at higher temperature (22,26°C) compared to lower temperature (14,18°C) (Robacker et al., 1983). Photoperiod was also reported to control the production of cleistogamous or chasmogamous flowers in some plants (Kinet and Sachs, 1984; Morgan and Morgan, 1984).

3.2.2 Ovule development

Ovule development, megasporogenesis and megagametogenesis in soybean have been fully described by Carlson (1973), Prakash and Chan (1976), George et al. (1979) and Folsom and Peterson (1984).

Embryo sac development is of the polygonium type. Meiosis occurs in the functional megagametophyte at the chalazal end and the megaspore continues developing and enlarging while the three micropylar megaspores become disorganized and soon disintegrate. The first mitotic division of the functional megaspore results in a two-nucleate embryo sac. These nuclei are displaced to the opposite ends of the embryo sac by the formation of a large central vacuole. Two successive mitotic divisions result in an eight-nucleate embryo sac with four nuclei located at the chalazal end and four at the micropylar end. One nucleus from each end migrates to the centre of the embryo sac and functions as a polar nucleus. The six remaining nuclei each develop independent cell walls resulting in an embryo sac with three antipodals, two synergids and one egg. This stage of embryo sac development is called the eight-nucleate stage but has seven cells and contains large amounts of starch in the cytoplasm which frequently becomes tightly packed with starch grains.

One to four ovules are produced in each ovary. These ovules become campylotropous at maturity, with the micropyle directed towards the distal end of the ovary (Guard, 1931; George et al., 1979). Previous reports do not agree whether ovule development is synchronous or

asynchronous within an ovary. Pamplin (1963) reported similar rates of development amongst the three ovule positions. On the other hand, Kato et al. (1954) found that these rates differed before and after fertilization; Prakash and Chan (1976) and Stelly and Palmer (1985) both also reported different rates of ovule development, but with different results. The former observed that the basal ovule developed most quickly up to the eight-nucleate female gametophyte stage, whereas the later demonstrated that the medial ovule was the most advanced. However, Stelly and Palmer (1985) noted that all three ovules of the triovulate ovaries they observed reached maturity before anthesis.

The two polar nuclei, with large nucleoli, are the largest nuclei found within the mature megagametophyte and, in the majority of cases, both nuclei migrate along the side closest to the funiculus and finally come to lie below the egg apparatus in the middle of the megagametophyte (Prakash and Chan, 1976; George et al., 1979). There is some uncertainty about when the polar nuclei fuse. Pamplin (1963) and Shen (1983) recorded that fusion takes place prior to fertilization, but Prakash and Chan (1976) show a diagram where the polar nuclei have not yet fused at the mature embryo sac stage, and Tilton et al. (1984) showed evidence that the polar nuclei had not yet fused by the time of pollen tube discharge. Folsom and Peterson (1984) reported that the polar nuclei are initially separate, but prior to fertilization, while the embryo sac is densely filled with starch grains, they become closely paired with their outer membranes in direct contact. Although distinct pores were not observed in the double nuclear membrane, alternating electron-dense and electron-translucent regions are evident suggesting that the fusion process has begun. Jensen (1973) proposed a mechanism for double fertilization in angiosperms where the two polar nuclei partially fuse, firstly through the joining of endoplasmic reticulum attached to the outer membrane of the nuclear envelope, and secondly by the formation of numerous small bridges between the two nuclei. The process is then arrested until the arrival of the sperm nucleus.

3.2.3 Pollination and double fertilization

At the time of maturation of the stamens, the ovary has already matured and become receptive (Stelly and Palmer, 1985). After the diadelphous stamens have been elevated to a position so that the anthers form a ring around the stigma, the pollen is shed directly on the stigma, resulting in a high percentage of self-fertilization (Carlson, 1973). Shen and Yan (1981) observed self-pollination in flower buds hourly from 0300-0800 h and found that self-pollination started when the corolla was 0.5-1.0 mm below the top of the calyx and reached its peak when the corolla approached the top of the calyx. When the corolla was 0.5-1.0 mm above the top of the calyx, 97.6% self-pollination of the flower buds had already been accomplished. Flowers collected at 0800 h in their study were entirely pollinated (100%). However, Carlson (1973) noted that pollination may occur the day before the opening of the flower.

Natural crossing in soybean has been found to vary from less than 0.5 to about 1% (Carlson, 1973). However, in some circumstances, this figure may be an underestimate, because honey bees (Apis mellifera L.) are reported to be involved in soybean pollination (Erickson, 1975b; Robacker et al., 1983; Severson, 1984), and to cause 5 to 16% yield increases in some varieties (Erickson, 1975a).

After pollination, the pollen grains germinate and the tubes grow through the tissue of the style, enter the stylar canal, and grow along the surface of the placenta. During growth of the pollen tube, the generative nucleus divides and forms two male gametes. Finally the pollen tube grows through the micropyle of the ovule, penetrates the embryo sac and releases the two male gametes. One male gamete fuses with the egg and forms the zygote, and the other male gamete fuses with the polar nuclei, forming the primary endosperm nucleus. The fusion of the second nucleus to one of the polar nuclei triggers the completion of fusion of the polar nuclei. This process begins after the fusion of the egg and the sperm nucleus, but is completed in a shorter period of time (Jensen, 1973). The starch grains in the embryo sac diminish at the time of fertilization and usually disappear 1 or 2 days later. The time from pollination to fertilization varies from about 8 to 10 hours.

Thus, the day of full opening of the flower is very likely to be the day of fertilization (Carlson, 1973).

3.2.4 Embryo and early seed development

Carlson (1973) contributed a comprehensive literature review on reproductive development of soybean. He described that, following double fertilization, the vacuole in the egg becomes smaller and finally disappears entirely about the time of the first transverse division of the embryo, which usually occurs about 32 hours after pollination. Thus, it may be assumed that the resting period of the zygote is approximately one day following fertilization. Continuous cell division results in the formation of a club-shaped embryo at about 3 days, a well-defined protoderm at about 5 days, the 'heart' stage at about 8 days and the late cotyledon stage at about 14 days.

The nuclear division of primary endosperm starts almost immediately following fertilization and by the time the zygote has undergone the first division, the endosperm has several free nuclei. Divisions of the endosperm nuclei continue and displace towards the outer surface of the embryo sac. By 5 to 8 days after fertilization, the endosperm becomes cellular and surrounds the heart-shaped embryo. The embryo and the endosperm grow at approximately the same rate until about 14 days and then the growth rate of the cotyledons increases and they absorb the endosperm rapidly. By 18 to 20 days after fertilization only the remnants of endosperm remain and appear as a thin aleurone layer and a few crushed endosperm cells in the mature seed.

Young seed abortion can happen at any time after fertilization. Abortion frequencies differ among the various ovule positions in pods. Generally, medial seeds are the heaviest while the slower growing basal seeds have the highest abortion frequency (Halsted, 1914; Woodworth, 1930; Egli et al., 1978a; Palmer and Heer, 1984; Stelly and Palmer, 1985).

3.2.5 Relationship between fertilization and flower abscission

In soybean, abscised flowers and pods are very common throughout the reproductive period. No major differences in the process of abscission

are found between reproductive abscission and leaf abscission (Morgan, 1984). Abscission layer formation is found at the base of the pedicel of a flower or pod and causes subsequent yellowing and withering of tissues at a later stage.

Lack of fertilization might be one of the factors causing this problem, possibly as a result of pollen infertility or egg cell infertility or by the failure of the pollen tubes to grow to the eggs (incompatibility). Johns and Palmer (1982) studied the cause of low seed set in a soybean mutant (Genetic Type Collection Number T269), which was a flower-structure mutant with cleistogamous flowers. They found that young mutant flower buds had longer carpels and larger receptacles than normal flower buds. The abnormal petal development prevented staminal tube elongation, and a spatial separation between the anthers and stigma existed at anthesis, preventing self-pollination. They noted that the low seed set on T269 plants was due both to a lack of self-pollination and to partial female sterility.

Kato and his colleagues in Japan studied the histology of abscised flowers and pods in normal soybean and reported that 94% of the abscised flowers and pods were fertilized; 55% of them were in the 3- to 8-cell stage of proembryo development, 16% were in the proembryo stage (about 100 cells), and 23% abscised just after cotyledon differentiation (Kato and Sakagushi, 1954 and Kato et al., 1955). Abernethy et al. (1977) checked these observations under United States growing conditions with American cultivars to characterize the controlling mechanisms in soybean flower abscission. They found similar results, in that a high percentage of the abscising flowers were fertilized and only 6 to 7% were unfertilized. Predominantly, the ovules had proembryos of 4 to 8 cells. They also observed the retained flowers and reported a very high percentage (98 to 99%) of the ovules were fertilized. The conclusion was that failure of fertilization seemed to play a negligible role in soybean floral abscission. The same conclusions were drawn with Vicia faba L. (Gates et al., 1983) and Phaseolus vulgaris L. (Sage and Webster, 1987).

The work of Abernethy and his co-workers (1977) involved the collection of flowers primarily from the apical region of the plant and only during developmental stage R2 (described by Fehr et al., 1971). It was

the objective of this study to check these results by collecting the flowers from different parts of the plant and at different stages of growth.

3.2.6 Clearing techniques for observation of fertilization

Histological techniques are necessary to confirm fertilization has occurred. Several techniques are available for histological and cytological studies on plant tissue. Embedding-sectioning methods have been widely used, but the procedures are time consuming. The alternatives are squashing after enzymatic digestion (Forbes, 1960) and clearing techniques (Herr, 1971, 1982; Crane, 1978; Young et al. 1979). The use of clearing techniques is particularly effective as it permits rapid whole ovule observation without gross disruption of 3-dimensional relationships. Procedures and applicability of two clearing methods for ovules have been described. One uses a mixture of lactic acid, chloral hydrate, phenol, clove oil and xylene (2:2:2:2:1, by weight) (Herr, 1971; 1982). The second involves methyl salicylate (synthetic oil of wintergreen) as the clearing agent (Crane, 1978; Young et al., 1979).

George et al. (1979) tested the usefulness of Herr's clearing fluid, modified by the addition of one part by weight of benzyl benzoate to the original cocktail. The effectiveness of this fluid was noted in studies of early ovule development, megasporogenesis and megagametogenesis in Glycine max and Phaseolus aureus. Young et al. (1979) compared the methyl salicylate clearing method developed by Crane (1978) and the plastic embedding-sectioning method in the classification of embryo sacs of an aposporous apomictic grasses, and reported that the clearing method was technically easier, consumed only 10% of the time of the sectioning method, and had equivalent accuracy.

3.3 MATERIALS AND METHODS

3.3.1 Plant culture

Seeds of Amsoy and Matara soybean cultivars were sown in the glasshouse at the Seed Technology Centre, Massey University, Palmerston North, New Zealand, on 13th August 1986. The seeds were sown in pots (15 cm in diameter and 10 cm in height) containing a mixture of peat, pumice and sand. This is a completely sterile mixture containing balanced proportions of fertilizer and slow release trace elements plus Terrazole soil fungicide. A set of (daylight) fluorescent lamps producing a light intensity of $80-100 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{sec}^{-1}$ (Photosynthetically Active Radiant, PAR) at the top of mature plants was used as supplementary lighting $13.5 \text{ hours}\cdot\text{day}^{-1}$. The glasshouse was adjusted to control temperature between 20°C and 30°C and an attempt was made to keep the relative humidity above 70% during flowering (see Appendix 8). One hundred millilitres of Hoagland's nutrient solution (Appendix 9) was applied every alternate day to each pot starting from the developmental stage R1 (first flowering) (Fehr and Caviness, 1977) until maturity (pod yellowing). Malathion (maldison, $250 \text{ g}\cdot\text{kg}^{-1}$ wettable powder) was sprayed at the rate of 200 g of product per 100 litres of water at 40 days after planting and 'Attack' (pirimiphos-methyl plus permethrin, $475 \text{ g}\cdot\text{litre}^{-1}$ plus $25 \text{ g}\cdot\text{litre}^{-1}$ emulsifiable concentrate, at the rate of 100 ml of product per 100 litres of water) was used to control two-spotted mite 3 times at 10-day intervals.

A second set of plants of each variety was sown in $17\times 17\times 17$ cm pots in the same potting mixture and placed outside on 20 October 1986. Hoagland's nutrient solution was supplied every second day as in the previous planting. On 24 December 1986, plants were transferred into the glasshouse and used for additional histological studies on the flowers.

3.3.2 Pollination observations

Fifteen flowers of each variety were collected at 0800 h on the first day of corolla appearance. Pollination was observed in fresh material under a microscope (300x) with 10% cotton blue staining.

3.3.3 Histological observations

3.3.3.1 Description of embryogenesis

To obtain a descriptive sequence on embryogenesis, flowers were collected at 0800, 1400, 2000 h on the day that their corolla appeared and then daily for 7 days. The flowers were fixed in formalin acetic acid-ethanol (FAA; 95% ethanol : water : 39-40% formaldehyde : glacial acetic acid, 10:7:2:1 by volume) until required for examination. Plant material can be effectively stored in this solution for up to 4 months (Young et al., 1979).

Pistils were dissected from the flowers and transferred through a series of dehydration and clearing steps as follows : 50% ethanol; 75% ethanol; 85% ethanol; 100% ethanol (three changes); ethanol : methyl salicylate 1 : 1, ethanol : methyl salicylate 1 : 3; 100% methyl salicylate (two changes) (Young et al., 1979). In this study groups of five pistils were wrapped in small pieces of soft cloth and placed in separate vials, and each dehydration or clearing step was conducted using 5 ml of liquid for at least 30 minutes. Cleared pistils were stored in vials containing methyl salicylate.

Cleared ovules were dissected from pistils under a binocular microscope and placed sequentially from apical (nearest to the stigma) to basal (nearest to the pedicel) on a microscope slide in a drop of methyl salicylate. This material was then mounted under a cover-slip. Fertilization was observed and recorded using a Zeiss standard light microscope equipped with (Zernike) phase contrast optics and a Zeiss MC-63 35-mm automatic camera system.

Using this technique, a description of embryogenesis was obtained as shown in Fig. 3.1. These pictures were drawn from views seen under the

phase contrast microscope. Plates 3.1a and 3.1c were obtained using black and white Kodak Technical Pan 2415 35-mm film exposed at iso 25; developed with HC110 Developer Dilution F for 8 minutes, but Plates 3.1b and 3.1d were reproduced by black and white Agfa film (ASA 100) from Kodak slide film (EPY 50, ASA 50, Ektachrome). The quality of the photographs obtained is limited because of a lack of depth of field compared to the thickness of the specimens. By adjusting the fine adjustment on the microscope and travelling through the section, 3-dimension perspective views could be clearly seen and the details of the ovules recorded.

Observations on embryogenesis made at different times in this experiment showed that there is considerable variation in the stage of embryo development within each sampling time. Generally, flowers removed at 1400 h and 2000 h were mostly in the resting stage of zygote development (Fig. 3.1b to d). A primary endosperm nucleus was frequently present in the ovules collected at 0800 h and 1400 h (Fig. 3.1b and Plate 3.1a) and soon divided continuously until it contained about 6 endosperm nuclei by the time of first zygote division (Fig. 3.1d). On the second and third days following first corolla appearance, the majority of ovules were in the 2- to 4-celled and 4- to 8-celled stage of zygote division, respectively, with endosperm nuclei located nearby (Fig. 3.1e to g and Plate 3.1b). At day 4, most of the ovules were found to be in the form of a club-shaped stage embryo surrounded by cellular endosperm (Fig. 3.1h and Plate 3.1c). Spherical embryos and well developed suspensor embryos were seen on about days 6 or 7 at which time endosperm nuclei were lining up towards the outer surface of the embryo sac (Fig. 3.1i).

The ovule in Fig. 3.1a was classified as unfertilized because the two polar nuclei had not fused with a gamete. Such a condition were found occasionally in flowers collected at 0800 h. Ovules with primary endosperm (Fig. 3.1b) were the most commonly found type of development observed in flowers from 0800 h and were classified as a fertilized ovule (Carlson, 1973; Abernethy *et al.*, 1977). Fig. 3.1c to i were also classified as fertilized ovules. Ovules that contained large amounts of starch granules packed together inside the embryo sac (Fig. 3.1j) or that were dispositioned from the horizontal plane under the cover slip where structure was unable to be clearly seen, were

judged as unclassifiable ovules. Unfertilised ovules also included those in which the egg cell and the polar nuclei had disappeared (Fig. 3.1k and Plate 3.1d).

3.3.3.2 Fertilization examination on 'normal flowers'

For the examination of level of fertilization, flowers were collected from plants at growth stages R2 to R5 (see Appendix 10). This period was chosen because flower production is in an active stage and it includes peak flowering. Flowers from different parts of soybean plants were marked with acrylic paint on the first day of corolla appearance and then randomly collected on the second and third days, by which stage some endosperm initials or divided zygotes were expected to be observed if fertilization had occurred. Each flower was removed at a stage before its fate as an abscised flower or a retained flower, could be determined. The term 'normal flowers' was used to refer to this group of flowers.

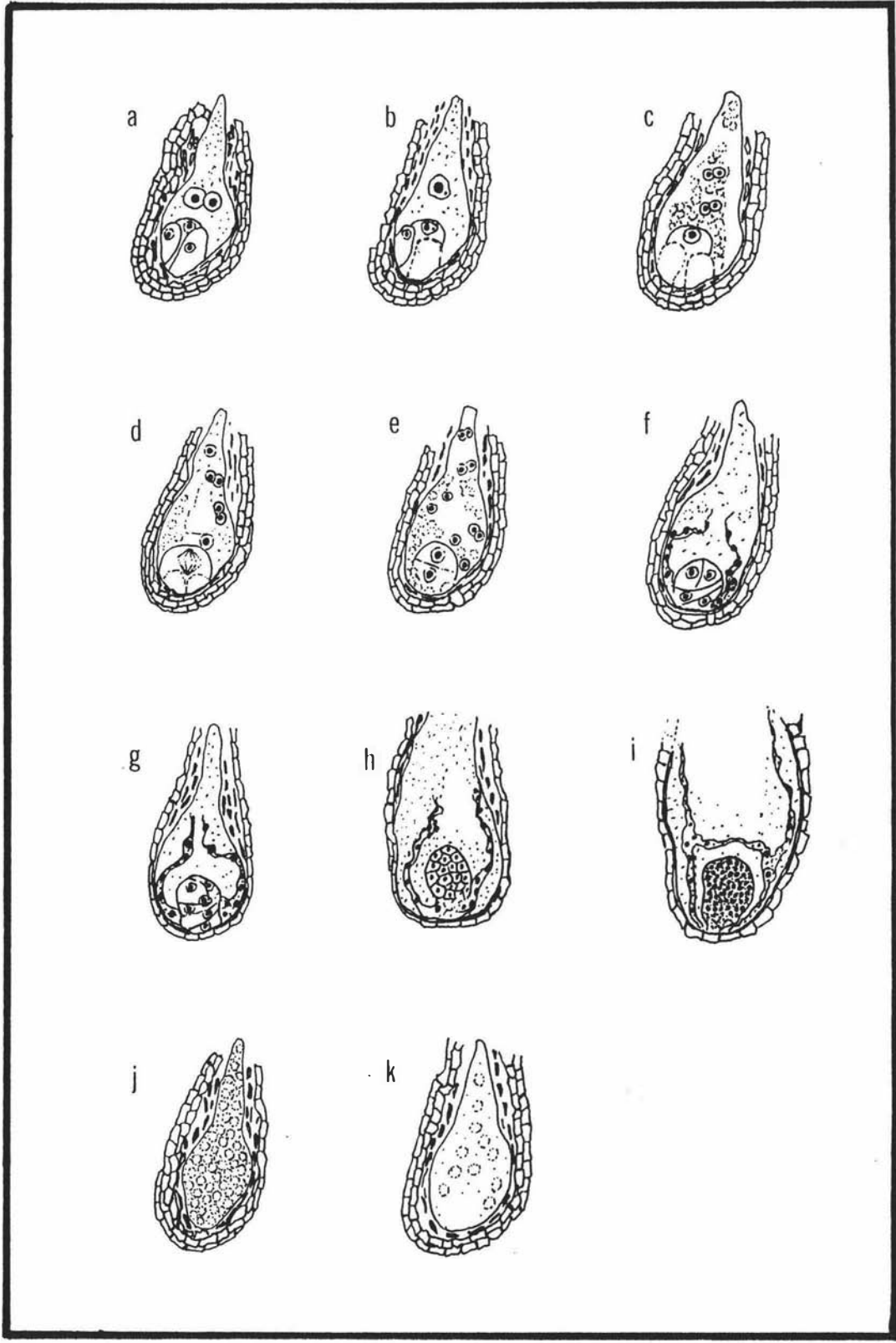
Flowers were fixed and cleared as described in section 3.3.3.1. Eighty-eight pistils from Matara and 61 pistils from Amsoy were collected from plants sown on 13 August 1986 and another 27 pistils of Amsoy were retrieved from the 20 October planting.

3.3.3.3 Fertilization examination on 'abscising flowers'

'Abscising flowers' from both varieties were collected from different parts of the plants. A gentle touch on flowers with forceps resulted in a separation at the base of the pedicel. One hundred flowers of each cultivar were collected from plants of the late grown set (20 October) and fixed by passing through the same process as described for 'normal flowers'.

Fig. 3.1 Description of sequence of embryogenesis in soybean

- | | | |
|---|---|--|
| a) Eight-nucleate stage embryo (unfertilized) | b) Embryo with primary endosperm nucleus | c) Resting stage embryo with dividing endosperm nuclei |
| d) First mitotic dividing zygote with dividing endosperm nuclei | e) Two-celled stage embryo | f) Four-celled stage embryo |
| g) Eight-celled stage embryo | h) Club-shaped stage embryo | i) Spherical zygote embryo |
| j) Embryo with starch granules tightly packed (unclassifiable) | k) Embryo with absence of zygote and endosperm (unfertilized) | |



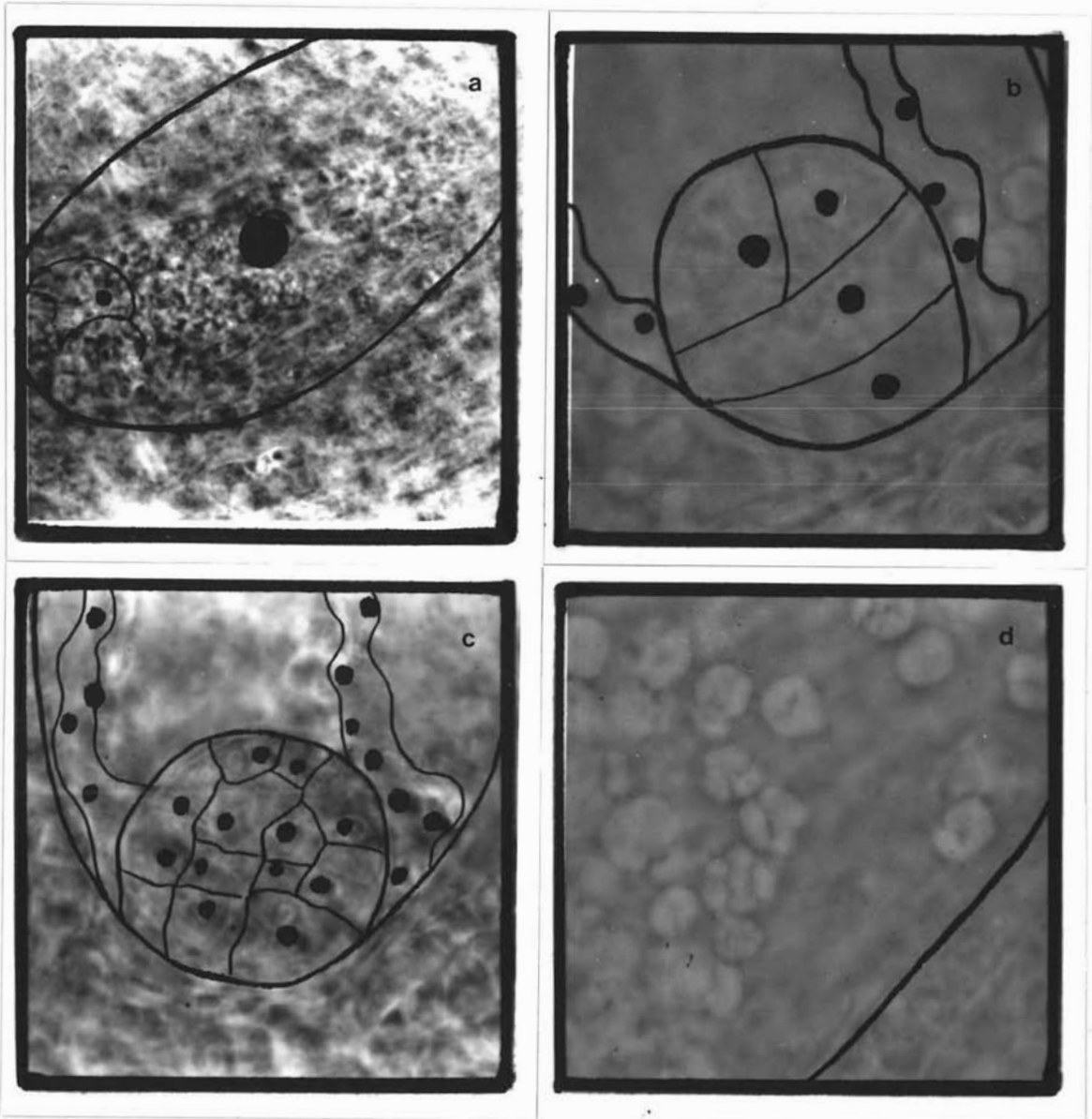


Plate 3.1 Fertilized (a - c) and unfertilized (d) ovules : a) with resting stage zygote (1000x), b) with four-celled stage, c) with club-shaped stage embryo (1000x), d) without egg cell or zygote (1000x).

Overlaid line diagrams are drawn from three dimensional observations on these specimens.

3.3.4 Observations on seed abortion and changes in seed dry weight at different positions within pods during seed development

Surplus soybean pods from the plant density groups in the previous field study were mixed and kept at 20°C. Observations on these samples were made 5 months after harvesting.

Within a pod, seed may be present as either a full and healthy seed, an aborted seed (shriveled seed) or only as a vestige of ovule (Plate 3.2). In all cases calculations of seed numbers per pod took into account only shriveled seed and full seeds.

3.3.4.1 Seed abortion within pods

Pods of both cultivars (303 for Matara and 455 for Amsoy) were randomly sampled from the bulk and were sorted into 4 types of pod, i.e. uni-seeded, 2-seeded, 3-seeded and 4-seeded pods, to calculate the proportion in each pod group. Pods with at least 1 aborted (shriveled) seed that has its thickness less than one-fourth of its width were separated from another group of 1,343 pods for Matara and 674 pods for Amsoy and were examined to determine the position(s) within the pods that seeds aborted.

3.3.4.2 Changes in seed dry weight at each position within 3-seeded pods determined during seed development

One hundred 3-seeded pods of Matara were randomly selected from each harvesting time 10 to 60 days after peak flowering (DAPF). Seeds were grouped into basal seeds, medial seeds and apical seeds and dried at 103°C for 17 hours to determine seed dry weight at each position.



Plate 3.2 Soybean pods showing seed abortion at different positions
 a) aborted young pods; 1 = whole, 2 = with 3 vestiges of ovules, 3 = with one vestige of an ovule and one aborted seed; b) pods from tri-ovulate ovaries, showing a vestige of ovule in pods no.2 and 3; c) pods from tri-ovulate ovaries, showing a vestige in pod no. 2 and an aborted seed in each of pods no. 2 and 3; d) mature pods suspected of coming from 4-ovulate ovaries, left pod is classified as 2-seeded, right pod is classified as 3-seeded. Circles highlight vestiges and the arrow marks the point of attachment that an ovule was expected to be. (a to c = glasshouse grown soybeans collected at 40 days after anthesis; d = field grown soybean)

3.4 RESULTS

First flowers appeared 33 and 34 days after planting at node numbers 4 and 5 for Matara and Amsoy respectively. Matara was fully cleistogamous (Fig. 3.2) while Amsoy was partially chasmogamous. Matara flowers were slightly smaller in size than in Amsoy. Observations on racemes borne at nodes 4 to 7 on main stems revealed that corolla exertion of a flower occurred hierarchically from the proximal to the distal end on a raceme. In general, flowers borne at the proximal end opened and developed faster during the early stages and were the most successfully productive. Flowers borne distally opened later than those at the proximal end and sometimes appeared to grow more slowly (measured in length). Typically, flower abortion was found to occur more commonly at the distal end and rarely occurred at the proximal end.

3.4.1 Pollination observation

All flowers removed at 0800 h on the first day of corolla appearance, were found to be self-pollinated. Typically, the style bent down towards the site at which the single stamen was located, resulting in the touching of the stigma and one of the dehisced anthers (Fig. 3.2). In about two-thirds of the flowers, pollen appeared to be recently dehisced from the anthers as indicated by fresh anthers with some pollen grains left inside, whereas one-third of the flowers were observed with empty and withering anthers. This implies that self-pollination in some flowers has occurred some time before observation, i.e. before the first external observation of corolla extrusion.

3.4.2 Fertilization examination on 'normal flowers'

A total of eighty-eight flowers of each cultivar were observed in this study. Fig. 3.3 shows that, for both varieties, more than 50% of the flowers were of the tri-ovulate type: 53.4% for Matara and 65.9% for Amsoy. Uni-ovulate flowers were found in only 1.1% of cases in Amsoy and were not observed at all in Matara. The average ovule number per ovary was about the same in both varieties (2.74 and 2.72 for Matara and Amsoy, respectively).

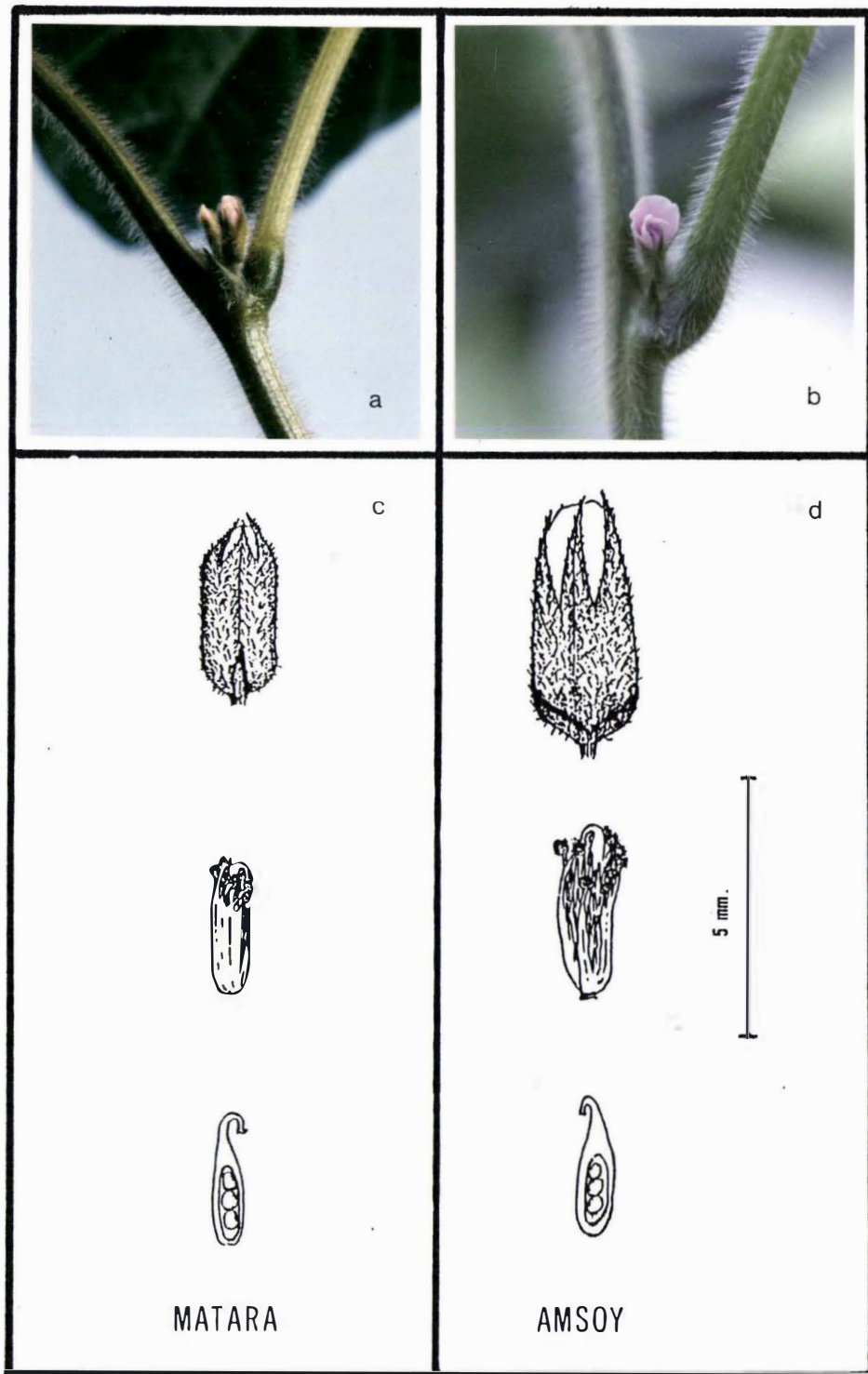


Fig. 3.2 Flowers and flower structures of soybean : a) cleistogamous type found in Matara; b) chasmogamous type found in Amsoy; c) a flower of glasshouse grown Matara observed at 0800 h on the first day of corolla appearance showing pollination and the structure of a pistil; d) a flower of glasshouse grown Amsoy compared to that of Matara

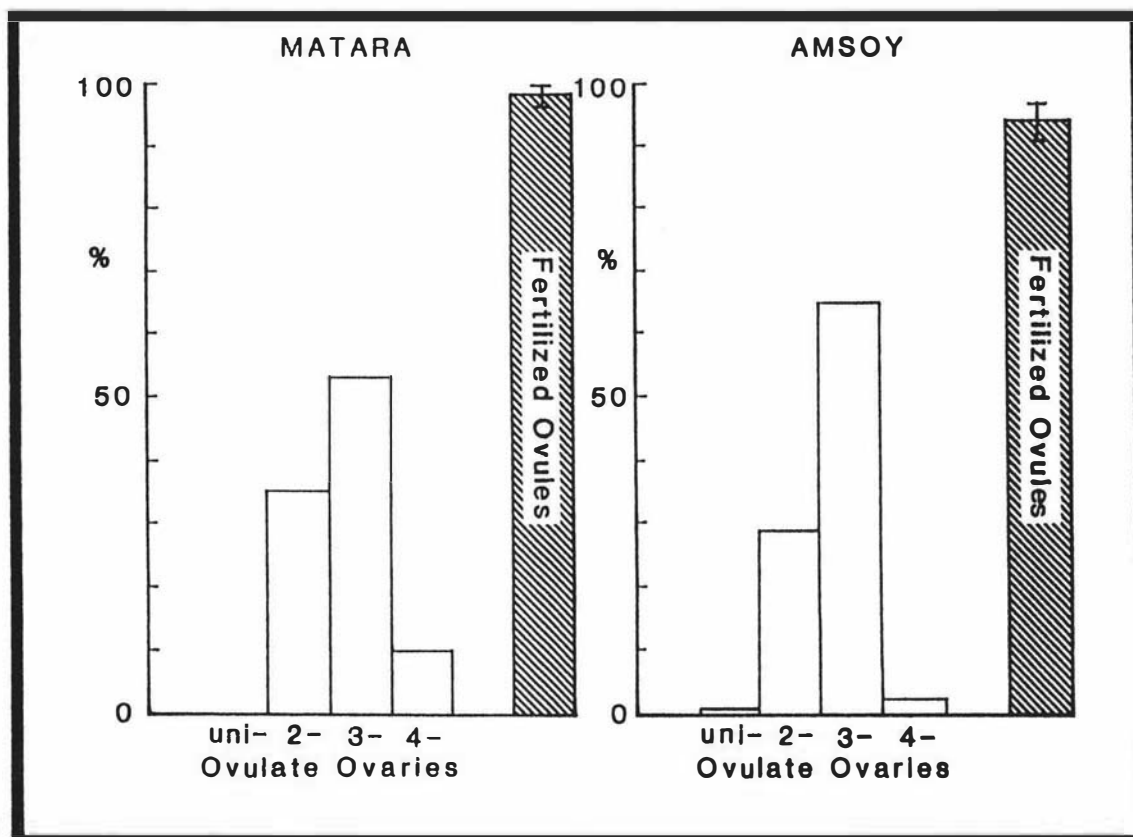


Fig. 3.3 Percentage of each ovary type in normal flowers and percentage of fertilized ovules (based on the total number of classified ovules with 95% confidence interval) in Matara and Amsoy soybeans

A high percentage of fertilized ovules based on the total number of classifiable ovules was found in both varieties (98.6% in Matara and 94.8% in Amsoy) (Fig. 3.3). The stage of development of the fertilized ovules ranged from the resting stage to club-shaped embryo stage (Fig. 3.1b to h), with the majority between nuclear division of the primary endosperm and the 8-celled zygote stage (Fig. 3.1c to g). In most unfertilized ovules observed in this study, the egg cell and the polar nuclei were absent (Fig. 3.1k and Plate 3.1d)). Only a few of ovules were in the 8-nucleate stage (Fig. 3.1a). Of 241 ovules examined in Matara 21 could not be classified as were 25 of the 239 examined in Amsoy. Some of these were ovules tightly packed with droplets and starch grains (Fig. 3.1j) and some were ovules which could not be examined clearly due to ovule dispositioning during mounting.

The percentages of unfertilized ovules (based on the total number of classified ovules) at the basal position (nearest to the pedicel) and the apical position (nearest to the stigma) are shown in Table 3.1. Data in the table excluded the medial position because no unfertilized ovules were observed. It was found that, regardless of ovary type, the basal position showed a higher percentage of unfertilized ovules than in the apical position.

Table 3.1 Percentages of unfertilized ovules (based on the total number of classified ovules) at basal and apical positions in Matara and Amsoy soybean. No unfertilized ovules were found in medial positions.

| Cultivar | % unfertilized ovules | |
|----------|------------------------|-----------------|
| | Basal position | Apical position |
| Matara | 4.0(±3.7) [*] | 0 |
| Amsoy | 12.0(±6.2) | 2.5(±2.8) |

^{*} 90% confidence interval

3.4.3 Fertilization examination on 'abscising flowers'

Thirty-three abscising flowers (containing 101 ovules) of Amsoy were cleared and observed under the phase-contrast microscope. Most ovules from abscising flowers were shrunken as shown in Plate 3.3b to d, compared to the ovules from 'normal flowers' (Plate 3.3a). These ovules were sometimes difficult to remove from the ovary wall and often were lost among extraneous material. The structures inside the ovules were unclear, because the zygote and endosperm had begun to degenerate. However, out of these 101 ovules examined, 37 of them were identifiable as fertilized. The majority of these fertilized ovules were seen in the nuclear division stage up to the 32-cell zygote stage. The remaining 64 ovules were undefinable with unclear structures. No ovules were clearly identifiable as being unfertilized.

3.4.4 Seed abortion at different positions within pods

Fig. 3.4 shows the proportion of pod types in 2 soybean cultivars. Three-seeded and then two-seeded pods were the most common in both cultivars. Matara tended to have a higher proportion of 4-seeded pods and Amsoy a higher proportion of uni-seeded pods.

The average percentage of seed abortion was higher in Amsoy than in Matara (18.0% vs 8.9%). In Amsoy, the more seeds a pod contained, the more likely it was to have aborted seeds (Fig. 3.4). In Matara, however, there was a higher frequency of seed abortion in 3-seeded pods than in any other.

Table 3.2 presents the percentage of seed abortion in various positions in pods. In all types of pod, the basal position was found to be the most likely site of seed abortion.

3.4.5 Changes in seed dry weight at different position within pods

The development of seeds at various positions in 3-seeded pods as shown in Fig. 3.5 were different as early as 10 DAPF and became more obvious after 30 DAPF. The basal seeds showed a lower seed dry weight at every sampling time throughout the developmental period.

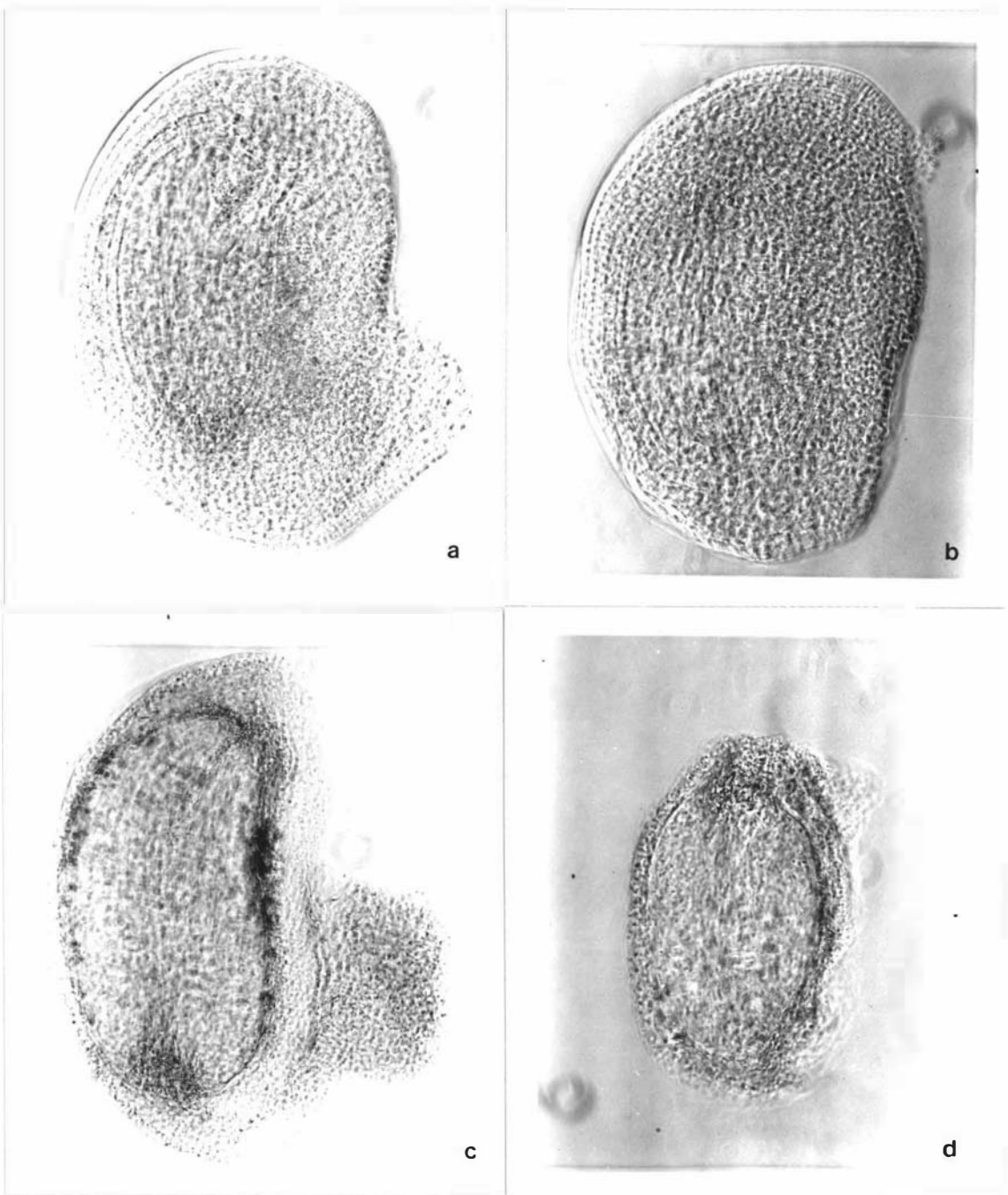


Plate 3.3 Ovules from abscising flowers showing mild to severe shrinking (b-d) compared to an ovule from a normal flower (a) (250x)

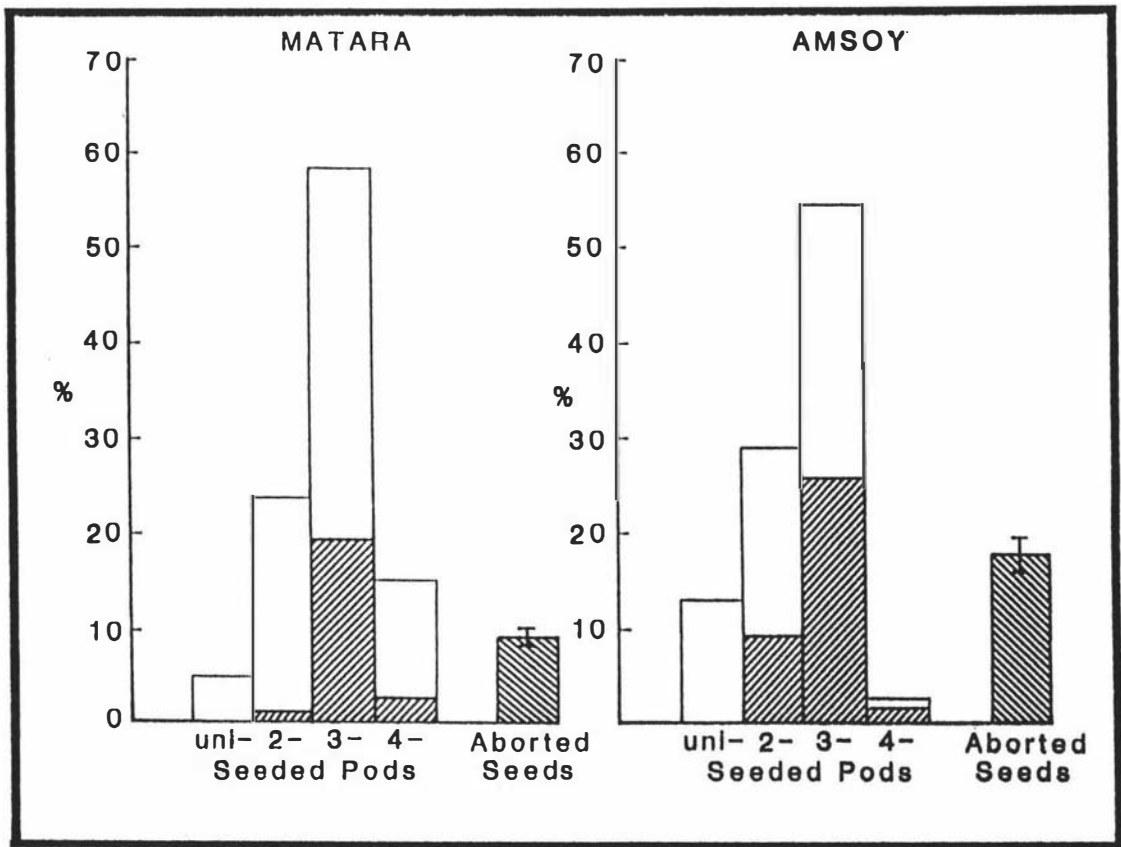


Fig. 3.4 Percentage of each pod type (□) and percentage of pods containing at least one aborted seed (▨) in Matara and Amsoy soybeans grown in the field. Percent total aborted seeds for the two cultivars is shown on the right of each graph with a vertical bar giving the 95% confidence interval.

Table 3.2 Percentage of aborted seeds in samples of field grown soybeans examined at each position within a pod

| Cultivar | Pod type | Ovule positions from basal to apical | | | |
|----------|----------|--------------------------------------|--------------------|--------------------|--------------------|
| | | 1 | 2 | 3 | 4 |
| Matara | 2-seeded | 3.7(± 2.0) [*] | 0.6(± 0.8) | | |
| | 3-seeded | 26.7(± 3.0) | 5.3(± 1.5) | 3.3(± 1.2) | |
| | 4-seeded | 15.5(± 5.0) | 5.0(± 3.0) | 1.0(± 1.4) | 2.0(± 1.9) |
| | | | | | |
| Amsoy | 2-seeded | 20.1(± 5.2) | 8.5(± 3.6) | | |
| | 3-seeded | 35.3(± 4.6) | 12.4(± 3.2) | 8.4(± 2.7) | |
| | 4-seeded | 46.2(± 19.2) | 30.8(± 17.7) | 23.1(± 16.2) | 11.5(± 12.3) |

* 95% confidence interval

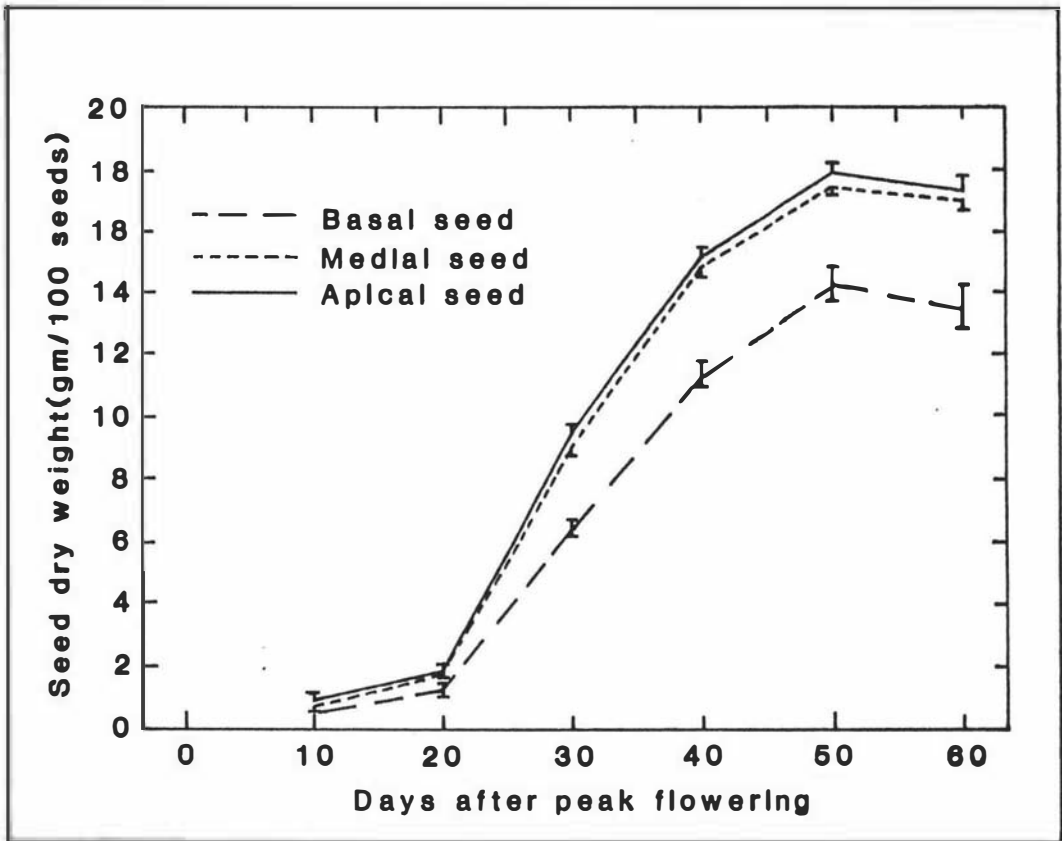


Fig. 3.5 Seed dry weight at each position in 3-seeded pods during seed development in field grown soybean var. Matara. Vertical bars represent SE of the mean.

3.5 DISCUSSION

The soybeans grown in the glasshouse in this study took about the same time from 50% seedling emergence to first flowering as did the field-grown soybeans in the first experiment. Fifty percent seedling emergence of Matara and Amsoy was observed at 3 and 4 days after planting in the glasshouse and first flowering was noted 30 days later.

Cleistogamy was consistently found in Matara both in the field and in the glasshouse (see Fig. 3.2a). Amsoy was chasmogamous (Fig. 3.2b) in the field study, but partially chasmogamous in the glasshouse. This variation is due to the effects of environmental conditions such as daylength, temperature and soil minerals (Erickson, 1975b and Robacker et al., 1983). Flowers borne at the base were smaller and less open than flowers at the top of the plant. Light intensity which was lower in the glasshouse might also be involved in this phenomenon. However, the openness of flowers did not affect reproductive development and self-pollination in these studies. Many other researchers have also reported that megagametophyte development in soybeans grown under field conditions is markedly similar to development in soybeans grown under glasshouse conditions. Therefore the embryological data collected from plants grown under glasshouse conditions can reflect the sequence likely to occur in plants in nature (Carlson, 1973; George et al., 1979).

Observations of flower development on racemes borne between nodes 4 and 7 showed that most aborted flowers occurred at the distal end of the raceme. This agrees with similar results by Huff and Dybing (1980) and Spollen et al. (1986a).

Observations on self-pollination confirm the results of Shen and Yan (1981) that when the corolla is 0.5-1.0 mm above the top of the calyx, self-pollination reaches almost 100%. However, many flowers were pollinated several hours before the time of observation as indicated by the structure of anthers. Dzikowski (1936) also noted that pollination in soybean may occur within the bud or the day before full opening of the flowers.

Microscopic examination of pollen samples was also done by Van Schaik and Probst (1958b). They reported ample supply of full-bodied, viable pollen grains to ensure successful pollination and no evidence was found to show that abscission was due to a failure of the pollen to bring about fertilization or of the ovules to be viable.

The results from the histological studies clearly show that lack of fertilization is not the major cause of floral abscission in soybean. High percentages of fertilized ovules, based on the total number of classified ovules (98.6% in Matara and 94.8% in Amsoy) were found in 'normal flowers' compared to 99.3% in 'Amsoy 71' and 97.8% in 'Wayne' soybean cultivars reported by Abernethy et al. (1977). Abernethy et al. (1977) collected flowers primarily from the top part of the plant and only during stage R2. The results from this present study showed that the large majority of flowers sampled over the whole plant and at a much wider range of developmental stages were fertilized.

Although observations on 'abscising flowers' were not always successful by the clearing technique employed, some conclusions can be made. All identifiable ovules (37% of the total observed) were found to be fertilized. The undefinable and shrunken ovules were found to be structurally distorted and the zygote absent. In these cases, the zygote might have degenerated after fertilization because no cell division had occurred. Cytokinins, which are important to cell division, may be lacking in these 'abscising flowers' (see discussion in the final chapter).

From the observations on ovule development and embryogenesis, differences in ovule size and stage of embryogenesis were found among ovule positions in the ovaries. In general, basal ovules were less developmentally advanced especially in size, than ovules in other positions. These observations suggest that the ovule development in an ovary is asynchronous as reported by many researchers (Kato et al., 1954; Prakash and Chan, 1976; Stelly and Palmer, 1985). Stelly and Palmer (1985) suggested that the development of the medial ovule usually preceded that of the basal and apical ovules, but that development was similar for basal and apical ovules. These findings differ from the results in the present study in which apical ovules were more advanced than basal ovules. The observations on seed dry

weight from each position during development shown in Fig. 3.5 suggest that low competitive ability of the basal ovules may have existed since the ovule developmental stage. The higher percentages of unfertilized ovules at the basal position shown in Table 3.1 also supports this suggestion.

The proportions of pod types shown in Fig. 3.4 are related to those of the ovary type in Fig. 3.3. Uni-ovulate ovaries in the glasshouse study were found only rarely (none observed in Matara and 1.1% in Amsoy), but uni-seeded pods were more commonly found in the field (3.6% for Matara and 13.2% for Amsoy). This difference is not because the field-grown soybeans produced large number of uni-ovulate ovaries, but because the uni-seeded pods were initially 2- or perhaps 3-ovulate ovaries which had aborted 1 or 2 ovules before or, more probably, soon after fertilization. These aborted ovules could be seen as small particles in uni-seeded pods. This suggests that seed abortion may take place very early after fertilization. Woodworth (1930) reported that aborted ovules or seeds (he called 'aborts') possessed an embryo, therefore, fertilization had occurred.

The percentage of seed abortion in pod samples was higher in the Amsoy variety (18.0%) than in Matara (8.9%). Halsted (1914) found the same range of seed abortion from three varieties, namely, Early Brown, Ito San and Wilson (i.e. 15.0, 14.2 and 6.8%, respectively). These results confirm that certain varieties differ considerably and significantly in the percentage of aborted seeds. The higher seed abortion in Amsoy may be associated with the indeterminate growth habit which causes higher intraplant competition.

Observations on the location of aborted seeds showed that basal ovules aborted more frequently (Table 3.2). This confirms the observations on the abortive behaviour in soybean pods reported more than 50 years ago (Halsted, 1914 and Woodworth, 1930). It would seem logical that basal seed, being nearest the source of nutrition, would be most likely to develop but, it was clear that the apical seed rather than the basal had a better chance of development. Moreover, these studies showed that the dry weight of basal seeds at each sampling time from 10 to 60 DAPF in Matara variety was significantly lower than in seeds at other positions within 3-seeded pods. During the early growth stages (10-20

DAPF), the lower dry weight of the basally positioned seeds seemed to be due to their slower growth rate (smaller young seeds are seen in the plate enlarged in the front page of this thesis). Seed abortion at the basal position occurred in a higher proportion than in the other two positions resulting in the much lower seed dry weight during late growth stages (30-60 DAPF). No significant differences in dry weight between medial and apical seeds were found (Fig. 3.5). These findings agree with results by Egli et al. (1978a).

3.6 CONCLUSION

- Flower abortion was more frequently observed at the distal end of the raceme.
- Self-pollination is likely to take place several hours before 0800 h on the first day of corolla appearance.
- Lack of fertilization is not the main cause of flower abscission, at any stage observed (R2-R5) and at any position on the plant. Among various ovule positions, the basal ovule seems to have highest possibility of being unfertilized.
- Available evidence from 'abscising flowers' shows that these had been fertilized, but the clearing technique used was more suitable for studying 'normal flowers'.
- Abortion can occur as early as immediately after fertilization.
- The percentage of pods containing aborted seeds and the percentage of aborted seeds were higher in the indeterminate soybean cultivar Amsoy than in the semideterminate cultivar Matara, possibly due to more intense intraplant competition.
- Seed abortion was most frequent in the basal position of the pod.
- Seed dry weight increases during the developmental stage were the same between medial seed and apical seeds, but were lower for the basal seed due to both slower growth rates and seed abortion.

CHAPTER 4

EFFECTS OF YOUNG LEAF REMOVAL ON FLORAL ABORTION AND POD SET

4.1 INTRODUCTION

The results of the field experiment suggest that competition for assimilates plays an important role in regulating soybean yield and yield components. Daily flower production was largely affected by interplant competition (created by plant density) probably because of the source-strength (plant size) at the time of first flowering. On the other hand, the percentage of reproductive abortion was not affected by plant density. Interplant competition is probably the cause of high abortion rates in high density plants. Low density plants also had high rates of abortion even though they were grown under less density-stressed conditions. In this situation, intraplant competition for assimilates seems to be an important factor, causing flower and pod drop in both low and medium density plants. During flowering and early seed development, new leaves were progressively produced, whereas in high density plants, leaf growth stopped before peak flowering. These young leaves serve as strong sinks for assimilates from roots and older leaves. The higher reproductive abortion percentage found in Amsoy was probably attributable to the indeterminate type of growth which caused increased intraplant competition between reproductive and vegetative structures during the flowering period. These stresses were less intense in the semideterminate Matara.

A study by Thrower (1962) clearly demonstrated the source and sink roles of single leaves of soybean. It was shown that leaves only import assimilates (sink activity) without any export of assimilates (source activity) when the leaf area was below 30% of the final mature size. When leaves were between 30% and 50% of the fully expanded size, there was simultaneous import and export, and thereafter export increased without full replacement of imported assimilates. A young

leaf at about 25% of its fully expanded size was a very active sink. Therefore, young leaves which are produced during reproductive development compete for assimilates very intensely and there may also be hormonal interactions with reproductive structures.

No report on young leaf removal in relation to changes in yield and yield components in soybean has been found in the literature. It is nevertheless likely that young leaf removal at different stages of reproductive development may affect seed yield component compensation, and may enhance seed yield because competitive sinks are reduced.

The aim of this experiment was to investigate the role of competitive sink reduction in intraplant competition by removing young leaves at 2 rates of removal and at 3 different stages of reproductive development in the soybean cultivars Matara and Amsoy. The objectives of this experiment were as follows:

- To study the effect of young leaf removal on reproductive development and abortion, and yield components in semideterminate and indeterminate soybean plants.
- To detect any differences in pod set and seed growth between early flowers and late flowers.
- To improve an understanding of the source-sink relationships in soybeans.

4.2 LITERATURE REVIEW

4.2.1 Introduction

Ultimately, soybean seed yield depends on the total number of seeds per unit area. However, to some extent, yield is related to the number of flowers produced (Dominguez and Hume, 1978; Wiebold et al., 1981), or inversely related to the percentage of total flower and pod abortion (Hardman and Brun, 1971; Clapp, 1975; Brevedan et al., 1978) (See Fig. 4.1)

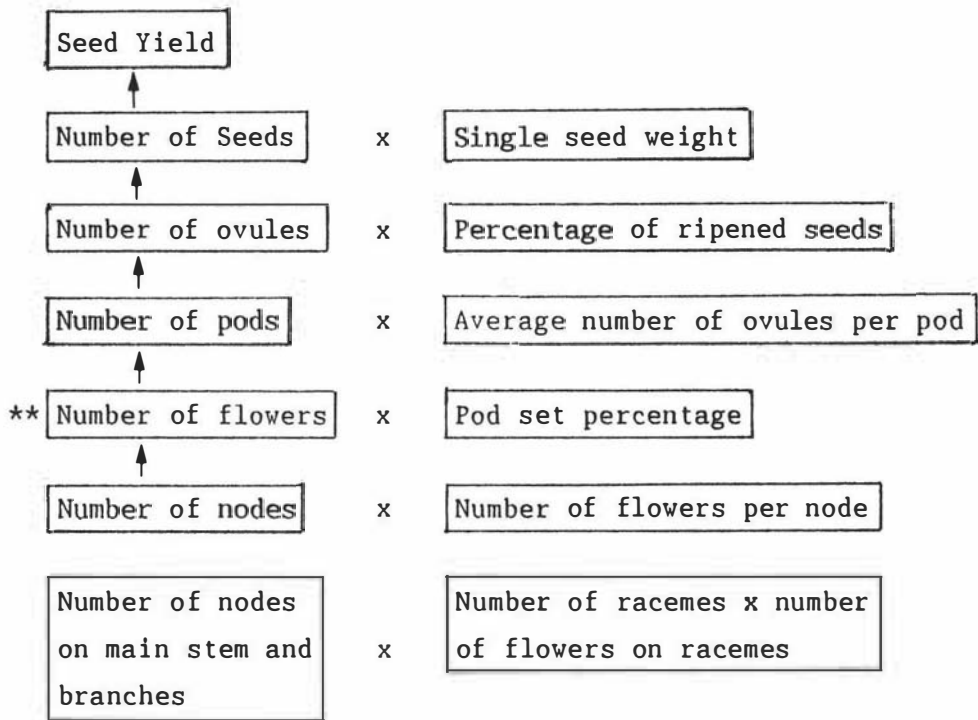


Fig. 4.1 Diagram showing factors associated with seed yield of soybeans (Konno, 1977)

The number of flowers and pod set percentage have been found to be the most variable factors of those listed in the diagram above. Flower production in soybean has been reported to vary from 38 (McBlain and Hume, 1981), up to 800 flowers per plant (Crane and Walker, 1984). Wiebold *et al.* (1981) studied 11 field-grown, determinate soybean cultivars (Maturity Groups V, VI, VII, VIII) and reported that the number of flowers per plant ranged from 170 for Bossier to 332 for Hardee and percent total abscission ranged from 67% for 'McNair 800' to 82% for 'Hale 3' (average 75%). Cultivar differences for percent abscission were also found in the studies of Van Schaik and Probst (1958a, 1958b), ranging from 32 to 83%. Gai *et al.* (1984) also found flower numbers ranging from 168 to 411 for determinate soybean cultivars and from 107 to 358 for indeterminate cultivars. It is not clear whether there is a relationship between type of stem termination and levels of abscission. Normally, late maturing cultivars of both determinate and indeterminate types produced many more flowers than

early maturing cultivars. Abortion percentages varied from 60 to 82% in determinate and 54 to 77 in indeterminate soybean varieties. Hansen and Shibles (1978) studied two indeterminate cultivars (Hark and Hawkey; Maturity Groups I and II, respectively) and found that both cultivars aborted 63% of their flowers and pods. Hardman (1970) also reported 55 and 65% abortion from two planting dates of Hark soybean, while McBlain and Hume (1981) revealed that abortion did not differ among Canadian cultivars Altona, Maple Arrow and McCall (Maturity Group 00), averaging 64% from studies over two years.

The terms used by researchers to define reproductive abortion are different. In this review, 'reproductive abortion' means the combined abortion of flower buds, flowers, young pods and large pods which fail to develop to fully mature and harvestable pods, whether they abscise from their locations or not.

Attempts to increase soybean seed yield by reducing or preventing flower and pod abortion have been made for many years. Treatments include plant growth regulators (James *et al.*, 1965; Burton and Curley, 1966; Hicks *et al.*, 1967; Clapp, 1975; Boize, 1982; Noodén and Noodén, 1985), nutrients (Mordaseva, 1964; Brevedan *et al.*, 1978) and mechanical removal of flowers or pods (McAlister and Krober, 1958; Hicks and Pendleton, 1969). Although many scientists claim to be able to increase soybean pod numbers per plant (Burton and Curley, 1966; Hicks *et al.*, 1967; Clapp, 1975; Brevedan *et al.*, 1978; Boize, 1982; Noodén and Noodén, 1985), very few have reported a consistent increase in yield (Clapp, 1975; Brevedan *et al.*, 1978). This review discusses the possible factors involved in regulating pod set and seed fill and the possibility of reducing reproductive abortion in soybean.

4.2.2 Flower development and reproductive abortion

4.2.2.1 The physiology of flowering and factors affecting flower development

Flower initiation is controlled by temperature (Garner and Allard, 1930; Parker and Borthwick, 1943), photoperiod and genotype. The role of photoperiod in controlling flower development was recognized in

early work by Garner and Allard (1920, 1923) who found that in some species, including soybean, tobacco, and aster, flower initiation occurs after a minimal number of inductive cycles. Photoperiod not only affects the rate of development but also the extent of abortion of the reproductive structures. Photoperiod also has various morphogenetic effects such as the production of cleistogamous or chasmogamous flowers in some plants (Kinet and Sachs, 1984). The soybean is a short-day plant, and cultivars differ in their critical day-length requirement. In general, the shorter-seasoned the cultivar, the longer the photoperiod under which it will flower and mature (Shibles et al., 1975).

Temperature has been reported to have only a minor effect on the floral initiation stage in soybean, but it has a very significant effect on subsequent reproductive development including the time of anthesis, and floral and pod abscission rates (Thomas and Raper, 1978, 1981). Susceptibility to floral aberrations of cleistoflory and cleistogamy (flowers which only partially open or do not open at all, respectively) in soybeans is also governed by temperature (Erickson, 1975b). Cool day/night temperature combinations of 18/14°C were observed to cause malformed pods and multiple flowers in soybean (Thomas and Raper, 1978; 1981).

At latitudes greater than 40° (Palmerston North is located 40° 21'S), where soybeans are planted during a cold spring, the length of time between emergence and flowering for adapted cultivars is mainly a function of accumulated temperature and is little influenced by natural photoperiod (Shibles et al., 1975). The difference in time of flowering between cultivars at these latitudes may be controlled by their varying response to temperature, or by a quantitative effect of the difference between critical and experienced photoperiod (Fisher, 1955).

4.2.2.2 Reproductive abortion in crop plants

Many plant species produce far more flowers than they can possibly develop into fruits. The excess flowers or potential fruits may be abscised at any time during development, but the abscission takes place most commonly in the early-bud stage; before flower opening; in the young fruit stage; or at fruit maturity (Addicott, 1982).

Over-production of flowers is a biological advantage (Summerfield et al., 1974); having the effect of ensuring an adequate seed set in the face of adverse weather, predation by insects and abortion of young fruits. However, it can be an agronomic disadvantage, and is implicated as a major factor in poor yield and harvest index (Ojehomon, 1972; Adedipe and Ormrod, 1975; Hansen and Shibles, 1978). From either point of view, an investigation of the factors likely to result in high reproductive abortion is important in understanding reproductive development in plants. Factors influencing flower and fruit abortion in many plant species have also been extensively reviewed and discussed by Stephenson (1981).

The proportion of reproductive abortion varies among species, varieties and under different environmental conditions. Apart from soybean, many other crop plants have high reproductive abortion rates. In lupin (Lupinus angustifolius L.) abortion of flowers under favourable conditions usually exceeds 60% (Greenwood et al., 1975; Perry, 1975; Herbert, 1979), and reaches higher levels under moisture stress (Biddiscombe, 1975).

In cotton (Gossypium hirsutum L.), El-zik et al. (1980) reported that usually there was relatively little abscission at the time of anthesis, but during the period five to ten days after anthesis many varieties abscised approximately two-thirds of the young fruits. Cotton bolls seldom abort when older than 14 days (McMichael et al., 1973). The average abortion under most conditions is about 65% of the flowers. The abortion of early formed structures was found to affect late formed structures. Kerby and Buxton (1981) reported the abortion of an early formed square (flower) enhanced the probability of boll retention at adjacent positions. Boll retention in a late formed square was depressed when the early square did not abort until it had reached the young boll stage.

Plancquaert and Raphalen (1984) reported an average of 89% reproductive abortion for winter faba bean (Vicia faba var. Survoy) and 82 to 85% for spring faba bean (var. Ascott). In common bean (Phaseolus vulgaris L.), it was also found that abortion ranged from 28 to 63% in the greenhouse and 52 to 76% in the field by Subhadrabandhu et al. (1978). The higher abortion rate under field conditions in all

cultivars might be attributed to greater variation in environmental conditions such as moisture stress, heat, wind and disease. Also, under field conditions, many more flowers were produced than under greenhouse conditions. Early flowers and late flowers were also found to have different abortion rates in common bean. Tayo (1986) and Pechan and Webster (1986) found a similar result, most of the pods which were retained to maturity being formed from early flowers that opened within 3 to 4 days of anthesis and were positioned basally on the raceme. Competition for carbon assimilates among pods and hormonal control of older, basally positioned pods over younger, more apically positioned pods may be the factors influencing the pattern of pod retention in all these species.

4.2.2.3 Reproductive abortion in soybean plants

i) Site of flowers produced on soybean plants

The numbers of flowers produced on individual nodes are unequal. Gai et al. (1984) reported a detailed description of the blooming habit of both determinate and indeterminate soybeans. For both types, there were approximately 35% of total flowers on the main stem and 65% on the branches. In contrast, Hansen and Shibles (1978) found upto 81.2% and 72.7% flowers on the main stem of two indeterminate soybean cultivars (Hark and Hawkeye, respectively).

In general, the middle part of the plants produced larger numbers of flowers than the top and the bottom parts. For example, Wiebold et al. (1981) reported that in determinate soybean cultivars, each canopy level of top, middle and bottom (determined by node number); contributed 38, 48 and 14% of the total flower number, respectively (averaged from 11 cultivars). Similar results were found in Hark and Hawkeye soybeans (indeterminate). In these two cultivars, nodes beyond number 19 produced very few flowers (less than 10%). Maximum flower number was produced at node 8 for Hark and node 10 for Hawkeye. This difference may be related to canopy structure in that the more open canopy of Hark allowed greater irradiance to penetrate the canopy, resulting in greater photosynthate

production at lower levels of the plant than occurred with the more closed canopy in Hawkeye (Hansen and Shibles, 1978).

ii) Site of reproductive abortion on soybean plant

The amount of flower and young pod abortion varies from node to node and even from position to position in a soybean raceme. In general, results from many studies have shown that flowers and pods carried in the lowest portion of the canopy show the greatest abortion (Hansen and Shibles, 1978; Wiebold et al., 1981; Antos and Wiebold, 1984). Heindl and Brun (1984) found in Evans soybean (indeterminate, Maturity Group 0) that reproductive abortion in the lowest part (nodes 3 - 6) was 90% compared to 28, 43 and 78% in nodes 7 - 11, nodes 12 - 16 and nodes 17 upwards, respectively. For determinate cultivars, percentage reproductive abortion was also greatest at the bottom of the plant, but was least in the top rather than the middle (Wiebold et al., 1981).

There are a few reports involving a comparison of the fates of flowers located on different parts of the soybean raceme. In the cultivar Clark isoline containing the E_1t alleles, which produces long racemes, less than 20% of the flowers located at the proximal (basal) end of the raceme aborted, whereas more than 75% of the flowers located at the distal end aborted (Huff and Dybing, 1980; Brun and Betts, 1984). Spollen et al. (1986a) studied the competitive relationship among pods within a raceme for field-grown soybeans without the E_1t gene (cv. Williams), and found a similar pattern of results with abortion as high as 99% at the distal end.

Heitholt et al. (1986a) found that early flowers aborted less frequently than late flowers. Although the flower's raceme positions could not be determined in their study, they claimed that the early flowers probably came from the basal position of the raceme and late flowers could have come from the distal position of the primary raceme or from a secondary raceme.

iii) The timing of reproductive abortion in soybean

The processes that ultimately lead to flower abscission may commence as early as the day of anthesis of the abscised flowers. Brun and Betts (1984) reported that the determination of soybean reproductive abscission occurred at or very near the day at which each flower reached anthesis, whereas Huff and Dybing (1980) found many flowers abscised within 3 days following anthesis. Dybing et al. (1986) and Ghiasi et al. (1987) reported that processes leading to eventual shedding of fertilized ovaries commence soon after anthesis.

Abortion is not restricted to flowers, it also occurs in a significant proportion of young pods usually before the onset of rapid seed growth (Van Schaik and Probst, 1958b; Wiebold et al., 1981). Some flowers and young pods were found to abort from 9 to 17 days after anthesis (Heindl and Brun, 1984; Heitholt et al., 1986a).

In the field, many of the early opened flowers that have developed into immature pods can remain as immature pods for up to 20 or 25 days without yellowing or abscising. However, by 30 days, many of these immature pods may have yellowed and died (Heitholt et al., 1986a). The timing of flower and young pod abortion can vary, depending on the cultivar or environmental conditions.

Heindl and Brun (1983) reported 35% flower abscission in the soybean cultivar Evans grown in the field. This was followed by young pod and pod abscission in 80% of the remaining flowers. Other reports have shown that over 50% of the total abortion in soybean can occur after immature pod formation (Hansen and Shibles, 1978; McBlain and Hume, 1981).

In contrast, Heitholt et al. (1986a) found that the relative contribution of flower abortion to total reproductive abortion was greater than 50% both in greenhouse (using cultivar McCall, indeterminate, Maturity Group 00) and field conditions (using cultivar Kent, indeterminate, Maturity Group IV). Similar

results were also reported for other soybean cultivars (Van Schaik and Probst, 1958a; Huff and Dybing, 1980).

4.2.3 Factors affecting reproductive abortion

At present, the mechanisms responsible for high reproductive abortion are unclear. A number of hypotheses have been proposed to explain this effect. Available results provide evidence that three possible factors are involved in reproductive abortion: i.e. nutrient deficiencies, chemical control (or hormonal control) and vascular constrictions.

4.2.3.1 Nutrient deficiencies

It has long been known that mutual shading and competition for light is especially evident in soybeans. Under field conditions, the middle and bottom soybean leaves do not reach their photosynthetic potential, because of both shading and an overall degeneration of metabolic activity with age. Apparent photosynthesis ($\text{mg CO}_2 \cdot \text{dm}^{-2} \text{ leaf area} \cdot \text{h}^{-1}$) can be increased by artificially lighting the bottom of the soybean canopy. Johnston et al. (1969) revealed that apparent photosynthetic rate of bottom leaves increased 73% and of the middle leaves increased 41% when fluorescent lamps were turned on. Plants treated with artificial light, had more seeds, nodes, pods, branches, pods per node, seeds per pod, and a higher oil content than untreated plants. Light enrichment increased seed yields of bottom, middle, and top canopy positions of plants by 30, 20 and 2%, respectively, compared to controls. Schou et al. (1978) also found a 40% yield increase, mostly from lower nodes, in light-enriched plants. They indicated that light enrichment increased yield by increasing the number of pods which were formed and retained. Delayed senescence and higher photosynthetic rate in lower leaves were observed to affect final pod number. Pod abortion was found to be lower in light-enriched plants (27%) compared to 34% in untreated plants observed during the pod filling period.

Research on light reduction or shading in soybean provides complementary results to light enrichment studies. Seed yield from shaded plants was observed to be lower than from normal plants (Schou et al., 1978), especially when shading occurred during the early seed filling period (Baharsjah et al., 1980). Mann and Jaworski (1970)

reported that shading to 63% of ambient light levels, begun during flowering, caused 58% fewer pods than controls due to pod abortion. All the findings from light enrichment and shading studies strongly suggest the need for more photoassimilates especially in the middle and bottom canopy positions to enhance pod retention and seed development. In other words, yield increase in soybean is limited by the availability of photoassimilates during reproductive development.

Competition between pods on the same raceme may lead to the abortion of structures unable to compete for available assimilates. Studies generally agree that most of the carbohydrate produced by a leaf is used in filling the pods which occur at the same node as the leaf (Blomquist and Kurst, 1971; Stephenson and Wilson, 1977a). Very little carbohydrate is transported to pods higher or lower on the stem. Thus, a localised decrease in photosynthesis could cause a localised abortion increase. This could account for the relatively higher abortion within the lower regions of the canopy (reviewed in section 4.2.2.3).

Ghiasi et al. (1987) found that aborting ovaries appear to continue to increase in fresh weight, maintain metabolic activity (in terms of protein and nucleic acid synthesis) and continue cell division almost until the date of their separation from the raceme. However, the growth rates of these aborting ovaries were low compared to setting ovaries. Although causes of the slowing in growth are not known, it is likely that these weaker flowers, being unable to compete for nutrients, degenerated physiologically and were no longer able to inhibit their abscission.

Changes in reproductive sink demand may influence foliar assimilate partitioning. Kollman et al. (1974) observed a 64% decrease in leaf blade carbohydrate concentration and a 40% decline in stem plus petiole carbohydrate concentration as pod numbers increased from 0 to 2.7 per node. Increased sink demand (increased pod number) by light enrichment caused a significant decrease in the proportion of label incorporated into the starch fraction of soybean leaves and increased the activity accumulated in the pod wall 24 hours after exposure of the subtending leaf to $^{14}\text{CO}_2$ (Carlson and Brun, 1985). These results indicate that variation in sink demand also regulates assimilate partitioning in leaves. The possibility has also been raised that other kinds of 'feed

back' from sink to source, including hormonal signals, may be operating.

4.2.3.2 Hormonal control

It is conceivable that several plant hormones and the interactions among them play very important roles in a series of morphogenetic events which occur during floral initiation and development. A great number of experimental results have shown various flower-inducing and inhibiting actions of phytohormones in different plant species, but sometimes the data seem to be inconsistent or even contradictory, making their interpretation rather difficult. Changes in hormone concentration at the hormone-responsive active site may account for many of the hormone-related changes in growth and development in plants (Davies, 1987). The flexibility and diversity required for such control are provided by modulation of hormonal levels, interactions between different hormones (Guern, 1987), interconversions of different hormones (Pharis and King, 1985) and sensitivity of plant tissues to the hormone (Trewavas, 1981). This section will deal in turn with each hormone involved in reproductive development in plant systems.

i) Auxin

In polycarpic fruit species, the role of hormones in fruit set and development has been well recognised for many decades. There is good evidence that fruit development requires auxin normally produced by the young seeds which are rich sources of auxin, as are germinating pollen grains. Also, the auxin content in the various tissues of the pistil sometimes increases progressively as the pollen tube grows through it. The retarding effect of seed removal upon growth of some fruits can also be overcome by adding auxin to the ovaries (Salisbury and Ross, 1985).

Early work on lupin (Lupinus luteus L.) by Van Steveninck (1957) revealed by selective removal experiments that proximal flowers on an inflorescence exhibited a dominant effect over pod set of more distal flowers. The effect appeared to operate

only over a short distance in the inflorescence and was oriented vertically in direction. Further, a substance was extracted from young pods that hastened abscission of lupin flower pedicels in an explant assay (Van Steveninck, 1959). In soybean, Huff and Dybing (1980) reported a similar result which showed that flower shedding was induced in distal flowers by substances from the more proximal fertilized ovaries. They tested chemical effects by replacement of the three lowermost flowers with lanolin preparations containing test chemicals (IAA, ABA, GA₃, and Glycine). They found that when lanolin containing 1% of IAA was substituted for flowers below the fourth flower, pod set was markedly reduced. IAA also hastened abscission from 5.7 days to 2.6 days. James et al. (1965) also found more shedding when soybeans were sprayed with NAA at the pod developmental stage. It is likely that high auxin concentration from setting proximal flowers may have a role in flower shedding.

Noodén and Noodén (1985) suggested that auxin (possibly from the leaves) plays a role in regulating pod numbers in soybean at an early stage of development. The evidence is that auxin-transport inhibitors such as TIBA (2,3,5-triiodobenzoic acid) and morphactin have a capacity to increase pod numbers, because they inhibit the transport of auxin from its production sites to the reproductive buds. However, the anti-auxin effect of these chemicals may be indirectly related to pod set by changing the distribution of photosynthate between vegetative and reproductive growth (e.g. Hicks et al. 1967; Tanner and Ahmed, 1974; Peat and Jeffcoat, 1982).

IAA has been suggested as a correlative signal from seeds involved in the control of development of other organs (Huff and Dybing, 1980; Tamas et al., 1981). The presence of IAA has been demonstrated in individual seed parts throughout embryogenesis by Hein et al. (1984a). They found that the concentration of IAA in the embryonic axis was highest when the pod was increasing in length at its most rapid rate. In the seed coat, IAA concentration was generally higher than in other parts of the seed. They noted that the IAA in the seed coat

may serve as a pool for transport to other tissues of the seed embryo or maternal plant. In further studies, they found that IAA moved acropetally toward laminae in petioles. The highest amount of IAA ester(s) was found in petioles during the mid- and late-stages of seed filling. Removal of pods reduced the amount of IAA ester in the petiole, suggesting that fruits were a source of IAA conjugate (Hein et al., 1984b). IAA from seeds may also be a correlative signal controlling leaf senescence since removal of seeds from bean fruits delays leaf senescence (Wareing and Seth, 1967) and reduces chlorophyll loss in leaves (Tamas et al., 1981). Application of IAA to deseeded bean fruits has also been shown to increase leaf senescence (Wareing and Seth, 1967) and induce loss of chlorophyll in leaves at a rate equal to, or greater than, that of plants with intact seeds (Tamas et al., 1981). It seems that IAA plays an interrelated role between soybean leaves and fruits. IAA from leaves may be involved in the inhibition of pod set at some stages (Noodén and Noodén, 1985), whereas IAA from seeds may be involved in the control of leaf senescence, chlorophyll content and pod set at some stages.

ii) Gibberellins

Gibberellins are recognised as the first group of chemicals that can induce flower formation in many plants under noninductive conditions (Zeevaart, 1983). In general, GA treatment can overcome the cold or long day requirement for flower induction in rosette plants, but does not cause flowering in most short day plants. This, together with the evidence that developing seeds are sources of gibberellins, has suggested that the inhibitory influence of young fruits on flower formation in short day plants may be due to gibberellins being released from the immature seeds in young fruits.

Birnberg and Brenner (1987) reported that the major effect of treating soybean leaves with GA₃ was a decrease in pod set, at least at the subtending node where development was monitored. This effect was most pronounced if GA₃ was applied before anthesis, but was not found on the soybean genotype T210 whose

vegetative parts do not show a growth response to GA_3 . Accordingly, they reasoned that GA_3 has no direct effect on pod set, but in normal genotypes the treatment caused photoassimilates to be diverted from reproductive structures toward vegetative ones and thus led to lower pod set.

In monocarpic fruit, such as tomato, Leonard and Kinet (1982) reported that abortion was associated with a low level of cytokinin activity and a high level of gibberellin activity. They suggested that although gibberellins are required for the development of flowers to anthesis, it is possible that high levels of gibberellins at that time inhibit development. This is supported by the fact that a reduction in the number of flowers formed in the first inflorescence of tomato was associated with high gibberellin-like substance activity in diffusates from young leaves (Abdul and Harris, 1978).

iii) Cytokinin

Cytokinin application was found to promote flower development in bougainvillea 'San Diego Red', a short day plant (Tse et al., 1974). It was suggested that the role of short days in promoting inflorescence development in bougainvillea may be one of redirecting the flow of assimilates by its influence on cytokinin synthesis and distribution. Application of exogenous cytokinin to the floral raceme has also resulted in increased mature pod numbers in soybean (Crosby et al., 1981; Carlson et al., 1987; Dyer et al., 1987). Carlson et al. (1987) reported that a single application of 2 millimolar BA (6-benzylaminopurine) when pods appeared in 25 to 50% of the proximal floral positions resulted in a 58% increase in pod set due primarily to a 33% reduction in floral abscission. Applications of BA at later intervals also resulted in significant reductions in total abscission. When applications of BA were given to the upper five nodes of field grown soybeans, total pod number and seed weight were significantly increased in this section of the canopy by 27 and 18%, respectively. These results suggest that endogenous cytokinins play a major role in the regulation of pod set in soybean.

Cytokinins and cytokinin-like activity have been reported to increase or attain maximal levels in the root pressure exudates of several species after floral induction (Devey and Van Staden, 1976; 1978; Heindl et al., 1982). Carlson et al. (1987) detected zeatin, dihydrozeatin, zeatin riboside, dihydrozeatin riboside, and isopentenyladenine in root pressure exudate of soybean plants throughout the flowering period. They found that total cytokinin flux peaked from 0 to 9 days after flowering began, and then dropped to one-half of this level by 15 days post-anthesis. The probability that a flower would initiate a pod was directly related to the concentration of total cytokinins present in the exudate when the flower opened. They discussed two mechanisms which may be responsible for mediating flower set and subsequent reproductive development. Increased abscission in the lower canopy may be mediated by decreased irradiance and a deficit in assimilate availability, whereas increased abscission of late flowers and pods in the mid to upper part of the canopy may be explained by a decrease in the concentration of cytokinins in the xylem sap.

iv) Ethylene

Ethylene plays an important role in abscission of plant organs through its ability to inhibit auxin transport and concomitantly promote abscission (Beyer and Morgan, 1971). Considerable evidence indicates that ethylene regulates senescence in leaf blades and flower petals. Morgan (1984) reviewed the recent work on ethylene and explained that no major differences are known between leaf abscission and abscission of flower buds, flower parts, and fruits. Production of ethylene by cotton flowers during, and immediately after, anthesis reached levels which would explain abscission. The dehiscence of some fruits is an abscission process, and extensive evidence indicates that ethylene regulates dehiscence. Nutritional and water stresses also increase ethylene production and flower or fruit abscission.

Urwiler and Stutte (1986) revealed that ethylene generated from ethephon increased the ethylene levels within soybean tissue

and subsequently increased flower abscission especially during 1 to 7 days after ethephon application. They suggested that the stimulation of abscission may be mediated by endogenously generated ethylene. They also noted that stress can trigger ethylene biosynthesis in soybeans.

v) Abscissic acid (ABA)

ABA has also been reported to be involved in the abscission of plant organs. The evidence is summarized as follows: a) the presence of ABA in leaves, branches, flowers, young fruits and mature fruits is correlated with the occurrence of abscission; b) application of ABA promotes abscission; and c) ABA will cause abscission in the absence of ethylene (Morgan, 1984).

In soybean, however, Huff and Dybing (1980) found that ABA did not significantly promote shedding of flowers when applied in lanolin in place of the three lowermost flowers on a raceme. Yarrow et al. (1988) also found that shade-induced premature reproductive abscission in soybean is not stimulated by high levels of ABA within reproductive structures, but that ABA may inhibit abscission of reproductive structures by playing a role in preferential assimilate partitioning to them. Recent evidence suggests the possible functions for ABA in developing soybean seeds including, a) stimulation of phloem unloading of sucrose into the seed coat apoplast, b) suppression of precocious germination, and c) promotion of storage protein accumulation (Hein et al., 1984a).

Although many positive identifications of phytohormones in the fruits of many plant species have been carried out, conclusive evidence for the regulation of any phase of fruit development by any group of plant hormones is lacking (Wang and Sponsel, 1985). However, it has been emphasized that the net physiological effect is probably due to more than one regulatory hormones (Morgan, 1984; Purohit, 1985).

One of the difficulties in correlating endogenous hormone concentration with differences in growth and development is the problem of what is

measured when the hormone is assayed, even if this is done by highly accurate physico-chemical means. Quantification is normally done by measuring total extractable hormone. Often this is of little relevance because the total hormonal amount tells us little about the hormonal concentration in the tissue in question, let alone in the cell compartment, or at the hormone receptor site (Davies, 1987). Furthermore, changing sensitivity of tissues to hormones can be just as or more important than changes in hormone concentration (Trewavas and Cleland, 1983).

Additionally, a growing body of evidence showing a variety of plant responses to small oligosaccharides strongly suggests that the diversity of chemical messages used by plants to react to external signals and/or to integrate their functions at the whole plant level is far greater than that corresponding to plant hormones (Guern, 1987). The effects of these natural plant growth substances still need to be elucidated.

Seeds in fruits are not only rich sources of auxins, but also of gibberellins and cytokinins (Zeevaart, 1983). Crane (1969) indicated hormones in developing seeds can act as mobilization centres, increasing the sink strength and thus diverting the flow of nutrients from vegetative organs into reproductive organs and that, to some extent, vegetative growth may be greatly depressed by this phenomenon. After flowers have set pods, seed growth is found to be important in the development of other reproductive structures. The evidence suggests that mobilization of plant constituents is also related to processes such as abscission and senescence.

The involvement of hormones in assimilate movement and partition is evident. Patrick and Wareing (1981) considered the mechanism of these hormonal effects in relation to the loading of assimilates at the source and to effects at the sink end of the phloem pathway. In the transport system of a plant, the phloem pathway between source and sink forms a relatively impermeable barrier against lateral exchange of assimilates; thus the 'permeability' of this barrier must decrease within sink regions. Hormonal control of pathway 'permeability' to lateral assimilate movement could be exerted at the phloem boundary (i.e. phloem unloading) or on uptake into the surrounding ground cells

(i.e. sink loading). The form of regulation will depend on whether assimilate transfer from the phloem to ground tissues is via the apoplastic or symplastic route. IAA, GA₃ and kinetin are known to promote assimilate movement to the hormone-treated stem stumps when they are applied to decapitated stems of bean (Patrick et al. 1979). Patrick and Wareing (1981) suggested that assimilate partitioning is predominantly under sink control. Sink produced auxins could facilitate assimilate transfer by stimulating some active mechanism propelling longitudinal flow through the phloem. Furthermore, the effects of sink-produced hormones could be further amplified by attracting root-produced cytokinins and gibberellins swept along in the assimilate stream. They proposed that symplastic unloading at apices may be promoted by IAA, whereas apoplastic unloading may be stimulated by kinetin.

Finally, the effects of plant hormones cannot be considered independently from environmental impact. A group of researchers has been working on the effect of light on reproductive abscission in soybean and has raised the possibility that reproductive abscission in soybean may be photomorphogenetically controlled. Heindl and Brun (1983) found that low-irradiance supplemental light in the lower part of the canopy decreased reproductive abscission. The effect was only observed if the supplemental light reached the flowers. Illuminating the leaves while blocking light to reproductive structures had no effect. In addition, they showed that red and white supplemental lights increased fruit set equally, thus implying that the response did not involve photosynthesis. They also observed that supplemental illumination of soybean flowers increased their importation of ¹⁴C from subtending leaves. Further experiments by Myers et al. (1987) showed that flowers receiving supplemental light were more intense sinks for ¹⁴C-source than were controls. Forty-two percent of flowers treated with supplemental light set pods, while only 26% of control flowers set pods. Red supplemental light produced 55% fruit set, compared to 41% set for far-red light, and 35% for controls (far-red not statistically different from control). They suggested that soybean racemes contain a photoreceptor, possibly phytochrome, capable of regulating sucrose accumulation. It may be noted that secondary messengers for phytochrome action may be identical to those in hormone action. The empirical observation that the red/far-red light ratio decreases and

flower abscission increases in the lower canopy is supportive evidence for this hypothesis. However, this hypothesis fails to account for the high abscission rates in the top part of indeterminate soybean canopies.

4.2.3.3 Vascular constriction

Gates and his colleagues have studied the anatomy of vascular development in relation to the reproductive development of *Vicia faba* L. (Gates et al., 1983; White et al., 1984). They found that there was a rapid and massive increase in vascular development in peduncles and pedicels after fertilization, preceding pod development and seed growth. At anthesis the cross-sectional area of pedicel vascular bundles was small and the pedicel/peduncle connection was fragile. Deposition of strengthening tissue in the vascular system could be detected soon after fertilization where the development of pedicel vascular bundles was characterised by inter-fascicular meristematic activity generating a thick annulus of lignified xylem, surrounded by a thinner annulus of phloem. Development of the outer parenchyma was restricted to cell expansion. The vascular and supportive tissues of the raceme were likely to be a major sink for assimilate at this stage.

The changes in seed dry weight were dependent on sequential vascular development in the supporting vascular tissues of the raceme, and it was observed that aborted seeds were generally supplied by vascular bundles which exhibited arrested development. It was proposed, therefore, that seed abortion is a result of vascular development failure, which may in turn be the result of differences in time of fertilization of individual ovules (Gates et al., 1983; White et al., 1984).

However, recent studies in sunflowers have failed to support the argument that central seeds may be inadequately supplied with nutrients because of restricted vasculature. Steer et al. (1988), working with sunflower concluded that the vasculature to the centre of capitulum can adequately supply nutrients to central seeds, since there were no differences in single-seed weights or nutrient contents when controlled pollination treatments allowed only the inner or outer seeds to develop, and that outer seeds control the growth of inner seeds,

probably by competition for preferential sequestration of nutrients. From their conclusion, it is likely that vascular restriction may merely be a secondary cause of flower and seed abortion.

Again, hormonal control may be involved in vascular differentiation. Auxin levels along the transport pathway can dictate the rate of vascular differentiation (Patrick and Wareing, 1981). Therefore, when sink activity is reduced, hormone levels (i.e. auxin and/or cytokinin) change resulting in restricted vascular development.

4.2.4 The plasticity of yield components

Despite the wide range of factors which can affect different components of crop yield, there is a tendency, within limits, for plants to compensate for losses at one stage of reproductive growth by augmenting other stages.

A concept widely accepted by plant breeders was proposed by Grafius (1964), explaining the yield components of barley as a box of xyz cubic volume. The number of heads per unit area (x), the average number of kernels per head (y), and the average kernel weight (z), multiplied together equals w, yield. This is basically a biological concept expressed in geometric form. There is no way in which yield can be changed without changing one or more of the components. There can be no genes for yield which by-pass the components. On the other hand, changes in x, y or z may tend to counterbalance each other, giving, in effect, homeostasis for yield. Hence, all changes in the components need not be expressed as changes in yield, but all changes in yield must be accompanied by changes in one or more of the components.

Photoassimilates can be limiting to one or another of the components at critical stages in their development. In soybean, for instance, Laohasiriwong (1982) reported yield component compensation in the soybean cultivar Maple Arrow grown in controlled climate rooms when plants were affected by water stresses at different times. Water stress from first flowering (growth stage R1) through to the beginning of maturity (growth stage R7) severely reduced yield by depleting the number of pods per plant and a slight decrease in seed weight. If water stress was applied for only part of this period, yields were

increased (compared with severe stress) either by increased seed weight when pod and seed numbers were decreased due to early water stress, or by increased pod numbers compensating for decreased seed numbers per pod and seed weight due to late water stress.

In addition, many studies have shown that removals of flowers or pods causes an increase in seed weight in soybean (McAlister and Krober, 1958; Hicks and Pendleton, 1969; Schonbeck et al., 1986). Peet (1984) studied soybean plants with different source-sink ratios by manipulating the numbers of leaves and pods per plant to 15:1 and 5:1 pod/leaf ratio. The results showed that plants with a 5:1 pod/leaf ratio had significantly higher total pod weight (including seeds) than 15:1 ratio plants. When CO₂ enrichment was given to those plants, she found that total pod weight was significantly increased only in 15:1 pod/leaf ratio plants but not in 5:1 pod/leaf ratio plants. This suggests that plants in the 5:1 ratio enriched treatment were sink-limited, but plants in 15:1 ratio were source-limited. All of these findings point to the developmental flexibility of plant systems. In soybean yield compensation is mostly effected by pod number per plant and seed weight, whereas seeds per pod was found to be a highly heritable characteristic (McAlister and Krober, 1958).

4.2.5 The competitive sink reduction concept

Net importers of assimilates such as roots and shoots, apical meristems, young leaves, axillary branches, fruit and storage tissues, etc. are competitive sinks to reproductive growth. Research has shown that sink manipulation can alter reproductive development. Removal of axillary branches, for instance, has been found to reduce reproductive abortion in different Lupinus species (Farrington and Pate, 1981; Porter, 1982). Conversely, root initiation and particularly root expansion inhibits floral initiation in Anagallis arvensis (a long day plant), particularly if the onset of rapid root elongation coincides with long day induction (Bismuth et al., 1979).

One of the importers of assimilates reported to be a strong competitive sink is the young leaf (Thrower, 1962; Tse et al., 1974; Larson et al., 1980; Turgeon, 1980). Young leaf removal is found to promote floral initiation and development in tomato (De Zeeuw, 1956),

Bougainvillea (Tse et al., 1974) and tobacco (Wardell, 1976). It is likely that young leaves are sources of gibberellins, auxins, and perhaps other promoters of competing sinks. Sachs and Hackett (1983) suggested that GA-induced inhibition of inflorescence differentiation in Bougainvillea may result from GA-induced activation of competing meristems, particularly of the rib meristems (e.g. those active in stem elongation and leaf blade elongation).

Amuti (1983) reported that single removal of all reproductive structures and plant apex above the 9th trifoliate leaf at an early reproductive stage significantly increased flower numbers and pod numbers in greenhouse and field grown soybeans. The number of pods containing 3 or more seeds was also increased but seed weight per plant was not consistently increased. However, this experiment did not distinguish the competitive effect of the shoot apex from other competitive sinks (flowers and pods), so no evaluation of the relative importance of vegetative and reproductive sinks could be made. In Phaseolus vulgaris, it was found that by removal of the shoot apex (above node 2) alone, fruit set was increased 52 to 100%, whereas removal of the shoot apex plus axillary buds increased fruit set 105 to 239% over the control (Bennie and Clifford, 1980). This shows that removal of competitive sinks enhances reproductive growth and possibly enhances yield.

Soybeans sometimes produce too many leaves after reproductive development has begun. The hypothesis that partial young leaf removal may reduce competitive sink strength and thus enhance yield has apparently not been reported in soybean before.

4.3 MATERIALS AND METHODS

4.3.1 Plant culture

Seeds of Amsoy and Matara soybean cultivars were sown in the glasshouse at the Seed Technology Centre, Massey University, Palmerston North, on 13 August 1986, using round pots (15 cm in diameter and 10 cm in

height). Seedlings in each pod were thinned at 1 week after sowing to leave one plant per pot. The soil used, plant culture techniques and glasshouse climatic conditions were the same as described in Chapter 3.

4.3.2 Experimental design

Data of Amsoy and Matara were analysed separately using a Completely Randomized Design with 5 replicates (one pot per replicate). Percentage values were transformed into arcsin $\sqrt{\quad}$ values before calculating the ANOVA (Appendix 13). To compare the mean values, Duncan's New Multiple Range Test was employed. There were seven treatments as follows:

- Control = No young leaf removal
- R1-50 = 50% young leaf removal, started at growth stage R1
- R1-100 = 100% young leaf removal, started at growth stage R1
- R3-50 = 50% young leaf removal, started at growth stage R3
- R3-100 = 100% young leaf removal, started at growth stage R3
- R5-50 = 50% young leaf removal, started at growth stage R5
- R5-100 = 100% young leaf removal, started at growth stage R5

The description of reproductive development described by Fehr and Caviness (1977) is given in Appendix 10.

4.3.3 Young leaf removal

'A young leaf' was a visible trifoliate folded leaf or, occasionally, a leaf not larger than 5% of the final leaf size and/or unfolded but not more than one-fourth of the size of a fully unfolded leaf.

Young leaves were removed every two days (by cutting the petioles) starting from growth stage R1, R3 or R5 according to the treatments throughout the growing season. One hundred percent young leaf removal was done by removing all young leaves. Fifty percent young leaf removal was done by removing every alternate young leaf starting from the lowest node upwards. The remaining counted young leaves were marked by tagging with small and light wires to ensure that they would not be included in the next defoliation. If there was an odd number of

young leaves, the last one (normally on the top of the main stems) was left unmarked and was included in the next set of young leaf removals.

4.3.4 Reproductive structure classification

Days to seedling emergence (50% emergence) were recorded at 3 and 4 days after planting (DAP) for Matara and Amsoy, respectively. First flowers (with corolla exerted) appeared 30 days after emergence in both cultivars. Counting, marking and observations for each cultivar were done on alternate days where possible and at not more than 5 day intervals.

Starting from first flowering, flowers (with corolla exerted) of each cultivar were counted and identified by placing acrylic paint on the calyx. At 6 days after first flowering, some young pods were found to have developed directly from flower buds (which had not shown corolla exertion). To ensure this situation did not lead to inaccurate evaluations of reproductive development and abortion, flower bud counts were also carried out and used for the evaluation of reproductive abortion rates.

To identify reproductive structures for this study, terms for flowers were defined as shown in Fig. 4.2. A 'flower bud' was a flower bud without apparent corolla. A 'developed flower' was a flower with visible corolla, either opened (for Amsoy) or unopened (for both Matara and Amsoy). Because the opening of flower buds was influenced by the glasshouse conditions and was not affected by young leaf removal (as shown in Appendix 11), flower buds and developed flowers were combined and collectively termed 'flowers' in this study.

Flowers were divided into 2 groups: early flowers (developing before growth stage R4) and late flowers (developing subsequently).

Developing pods from early flowers which were longer than 2 cm were counted and marked by placing acrylic paint at the tip of each pod. These were classified as 'early pods'. Pods developed from late flowers were named 'late pods'.

All these activities were performed for each node of each plant. Reproductive structures occurring on branches were recorded for the node at which the branch originated.

During reproductive development until seed maturity, numbers of young pods (0.5–2.0 cm) and large pods (>2.0 cm) abscising were recorded every alternate day.

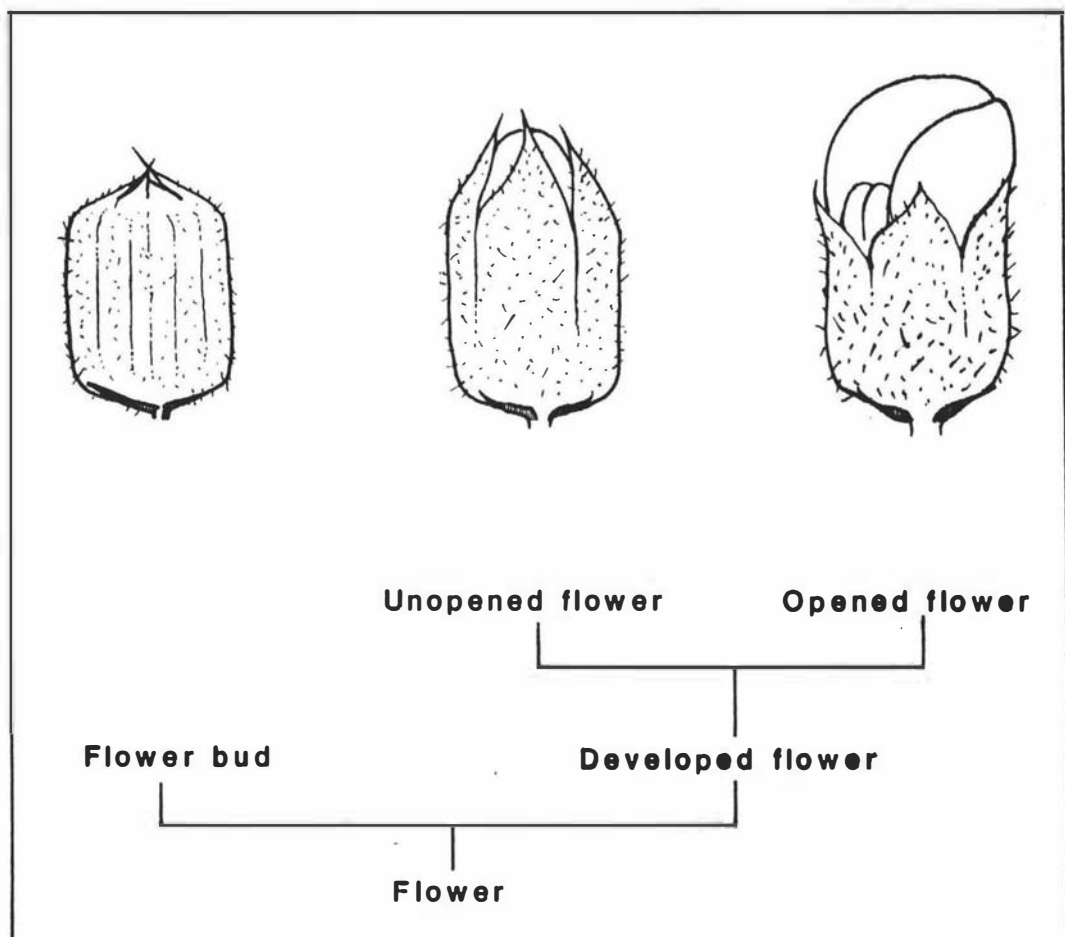


Fig. 4.2 Soybean flower identification for this study

4.3.5 Yield and yield component determination

The soybean plants were harvested on 1 December 1986 (109 DAP) for Matara and on 14 December (122 DAP) for Amsoy. Numbers of pods per plant (early pods per plant and late pods per plant) were determined at each node. Number of seeds per pod (excluding undeveloped seeds which are described as vestiges and aborted seeds in Chapter 3) and average seed weight ($\text{mg}\cdot\text{seed}^{-1}$) at 10% seed moisture content (see Chapter 1) were determined for whole plants. Separation between early and late for seeds per pod and seed weight was done only in the Amsoy cultivar.

Seed yield ($\text{g}\cdot\text{plant}^{-1}$) was calculated from the number of pods per plant, number of seeds per pod and seed weight. Again the partitioning between early and late formed seed yield was done only in the Amsoy cultivar.

4.4 RESULTS

The records of the reproductive developmental stages of glasshouse-grown soybean varieties Matara and Amsoy are shown in Fig. 4.3. First flowers appeared at 33 and 34 days after planting (DAP) for Matara and Amsoy, respectively. The onset of pod formation (growth stage R3) in Amsoy was 3 days later than in Matara, and to reach full maturity (growth stage R8), Amsoy plants took 13 days longer than Matara plants. The total flower production period was also 4 days longer in Amsoy than in Matara.

4.4.1 Effect of YLR on leaf numbers

The amounts of young leaf removal (YLR) each time are also shown in Fig. 4.3. The figures show that the leaf initiation period generally ended later in Amsoy than in Matara (about 65 and 55 DAP, respectively).

Leaf numbers per plant were recorded at growth stage R6 and are shown in Table 4.1. At this stage, control plants had 19.8 and 21.6 leaves per plant for Matara and Amsoy, respectively. YLR caused a significant reduction in the number of remaining leaves. The severity depended on the intensity and time of YLR. Although leaf area was not measured, Amsoy were observed to produce larger leaves than Matara plants.

The number of removed young leaves in each treatment for both varieties obviously showed that 100% YLR starting at the earliest stage (R1) was the most severe treatment followed by 100% YLR starting at later stages, i.e. R3 and R5 (Table 4.1). YLR by 50% starting at various stages resulted in approximately the same total amounts of removed young leaves. It is interesting that plants responded differently to YLR in terms of total numbers of leaves produced per plant (Table 4.1). In Matara, there were no significant differences between treatments whereas in Amsoy total numbers of leaves produced per plant were increased by YLR. 100% YLR at growth stage R1 and R3 in Amsoy increased the numbers of young leaves initiated by 30.6 and 27.8% respectively.

Young leaf removal (YLR) had no effect on node number per plant (average 11.8 and 13.7 nodes per plant for Matara and Amsoy, respectively, data not shown).

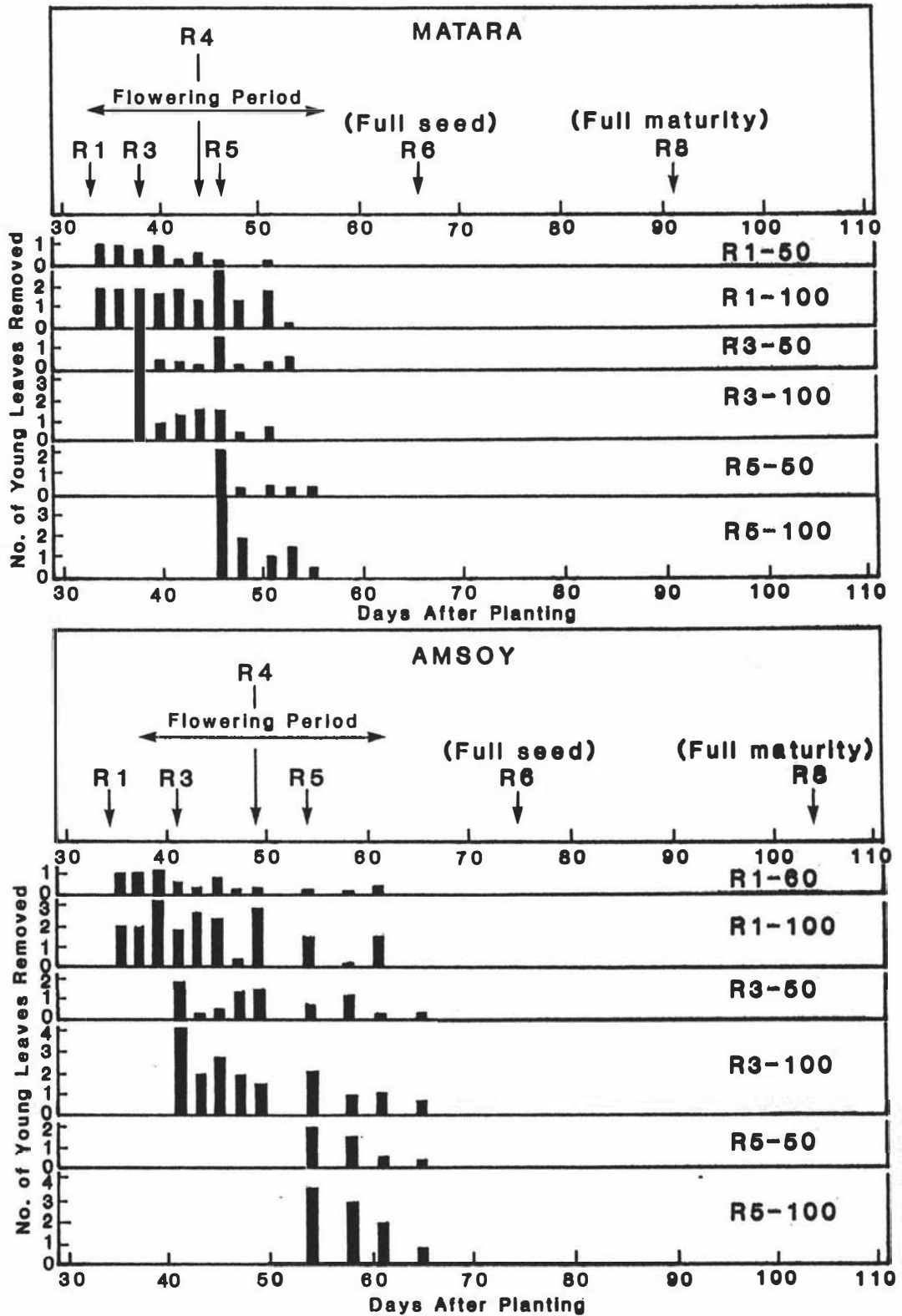


Fig. 4.3 Reproductive developmental stages in glasshouse-grown soybeans varieties Matara and Amsoy and frequencies of young leaf removal for each treatment

Table 4.1 Effect of young leaf removal on the remaining leaf number per plant (at growth stage R6, 66 DAP for Matara and 75 DAP for Amsoy), number of removed leaves and total number of leaves produced in Matara and Amsoy soybean

| Matara | | | |
|-----------|----------------------------------|--------------------------|---------------------------------|
| Treatment | Remaining leaf numbers per plant | Number of removed leaves | Total number of leaves produced |
| Control | 19.8 a* | 0.0 d | 19.8 a |
| R1-50 | 13.6 b | 5.0 c | 18.6 a |
| R1-100 | 7.2 bc | 16.8 a | 24.0 a |
| R3-50 | 14.6 b | 5.6 c | 20.2 a |
| R3-100 | 9.2 c | 10.6 b | 19.8 a |
| R5-50 | 16.6 b | 3.6 c | 20.2 a |
| R5-100 | 15.0 b | 9.6 b | 24.6 a |
| Average | 13.7 | 7.3 | 21.0 |
| CV (%) | 21.5 | 41.0 | 23.5 |
| Amsoy | | | |
| Treatment | Remaining leaf numbers per plant | Number of removed leaves | Total number of leaves produced |
| Control | 21.6 a | 0.0 d | 21.6 b |
| R1-50 | 14.4 c | 6.4 bc | 20.8 b |
| R1-100 | 7.6 e | 20.6 a | 28.2 a |
| R3-50 | 15.4 c | 8.4 b | 23.8 ab |
| R3-100 | 9.8 d | 17.8 a | 27.6 a |
| R5-50 | 19.4 b | 4.6 c | 24.0 ab |
| R5-100 | 15.6 c | 9.6 b | 25.2 ab |
| Average | 14.8 | 9.6 | 24.5 |
| CV (%) | 12.5 | 33.2 | 15.7 |

* Mean values within a column followed by the same letter are not significantly different at probability .10

4.4.2 Effect of YLR on flower numbers

4.4.2.1 Cumulative flower number per plant

Only graphs of cumulative flower production of treatments R3-50, R3-100 and control have been selected to show in Figs. 4.4 and 4.5.

In Matara (Fig. 4.4), there was a tendency for an increase in flower number in treatment R3-100 only during 40 to 50 days after planting (DAP). After this period, cumulative flower production slowed down and dropped below the control. Treatments R1-50, R1-100, R5-50 and R5-100 (data not shown) followed more or less the same pattern as R3-50 which was not different from the control.

In Amsoy (Fig. 4.5), YLR showed a clearer effect on flower production. Plants immediately responded to 50% YLR starting at growth stage R3 by increasing flower number over the control until the end of flowering when statistical differences were found (Table 4.2). Treatments R3-100 and others (data not shown) showed the same pattern of flower production as the control.

4.4.2.2 Total flower number per plant

As shown in Table 4.2, the effect of YLR on total flower number per plant was statistically different between treatments only in Amsoy. These differences were attributable to differences in late flower production (data not shown). No differences in total flower numbers per plant were found in Matara. In Amsoy, the average flower number per plant of the control plants was slightly higher than in Matara (89.4 vs 83.6).

The remarkable treatment in Amsoy was R3-50 which promoted a substantial increase in flower number per plant (44.1% over the control). Other treatments caused no significant changes.

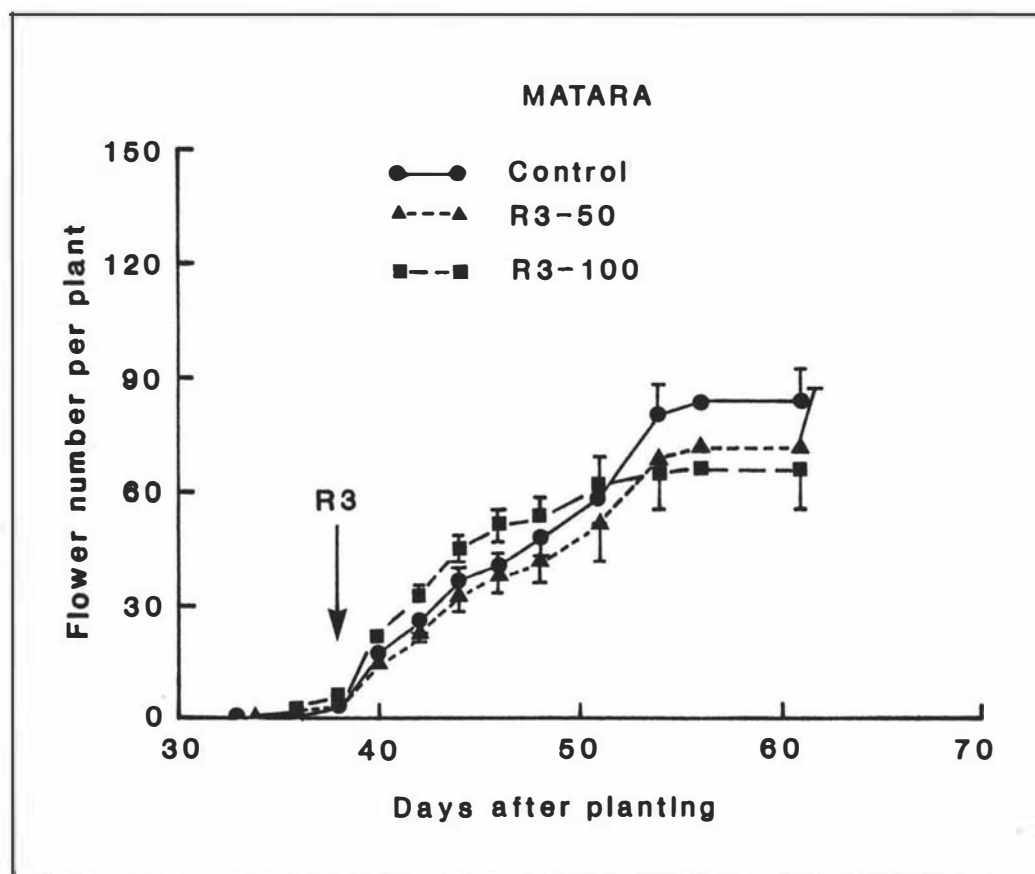


Fig. 4.4 Effect of YLR starting at growth stage R3 on cumulative flower production per plant of Matara. Vertical bars represent SE's of the means.

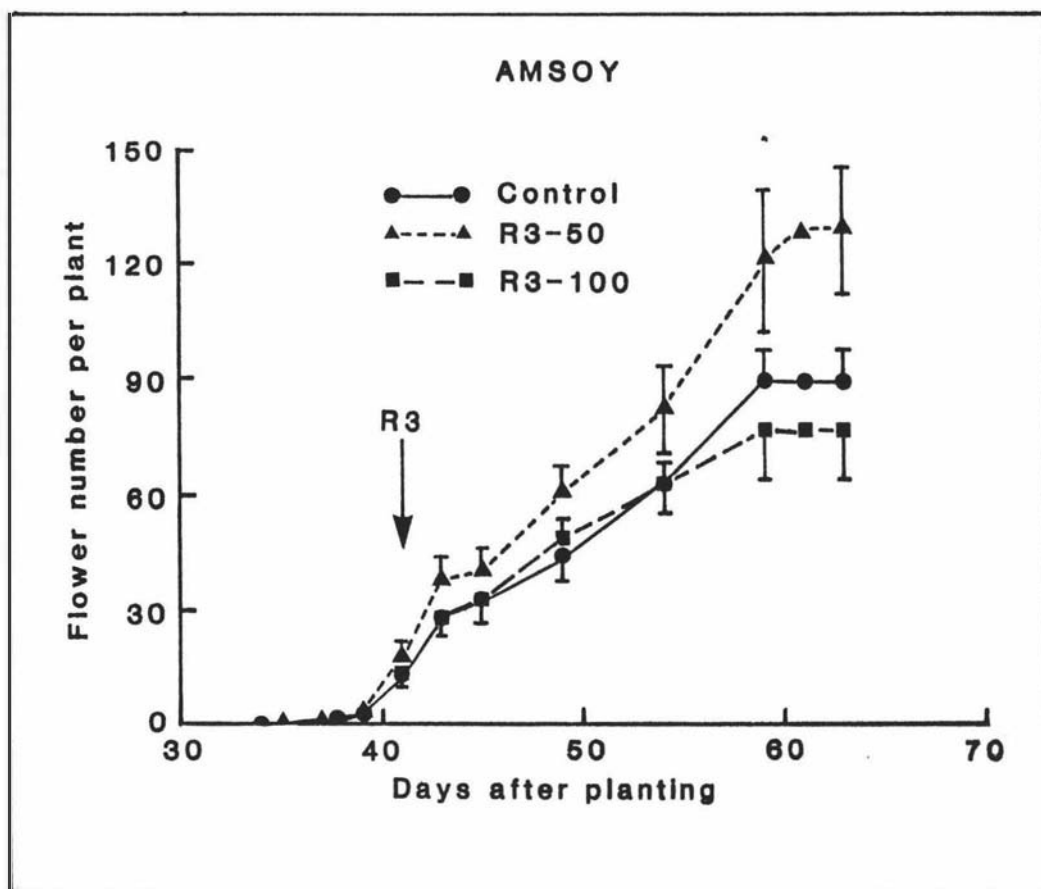


Fig. 4.5 Effect of YLR starting at growth stage R3 on cumulative flower production per plant of Amsoy. Vertical bars represent SE's of the means.

Table 4.2 Effect of YLR on flower number per plant in Matara and Amsoy soybean

| Treatment | Matara | Amsoy |
|-----------|---------|-----------|
| Control | 83.6 a* | 89.4 bcd |
| R1-50 | 63.6 a | 101.4 abc |
| R1-100 | 79.8 a | 69.0 d |
| R3-50 | 71.8 a | 128.8 a |
| R3-100 | 65.8 a | 76.4 cd |
| R5-50 | 70.8 a | 93.8 bcd |
| R5-100 | 84.6 a | 116.6 ab |
| average | 74.3 | 96.5 |
| CV (%) | 31.2 | 28.0 |

* Mean values within a column followed by the same letter are not significantly different at probability .10

4.4.2.3 Vertical distribution of flowers on control plants

Fig. 4.6 shows the production of flowers at each node on control plants of Matara and Amsoy varieties.

Control plants produced flowers up to node 11 in Matara and node 15 in Amsoy. The proportions of flowers on branches to the total flowers were 57% for Matara and 47% for Amsoy. Branches borne on node 1 produced relatively higher flower numbers than branches on upper nodes. On the main stem, nodes 2 to 7 in Matara and nodes 2 to 9 in Amsoy were the main areas of flower production.

4.4.2.4 Vertical distribution of flowers on plants as promoted by YLR in Amsoy

Fig. 4.7 shows the distribution of reproductive structures on Amsoy plants in the R3-50 treatment. Compared with the control, flower production was increased 49.4% on the main stem and 38.2% on branches. Increases occurred at all nodes, but were more pronounced in the basal region of the plants, particularly nodes 2 to 8 on the main stem and on branches borne at nodes 3 and 4.

4.4.3 Effect of YLR on pod set

There were no significant differences in young pod numbers per plant between treatments in either Matara or Amsoy (data not shown). Overall averages of young pod numbers per plant were 23.6 for Matara and 26.9 for Amsoy.

4.4.3.1 Cumulative large pod numbers per plant

The effect of 50% and 100% YLR at R3 on cumulative numbers of large pods (>2-cm long) per plant, is shown in Figs. 4.8 and 4.9, and was found to be very similar to that of cumulative flower numbers.

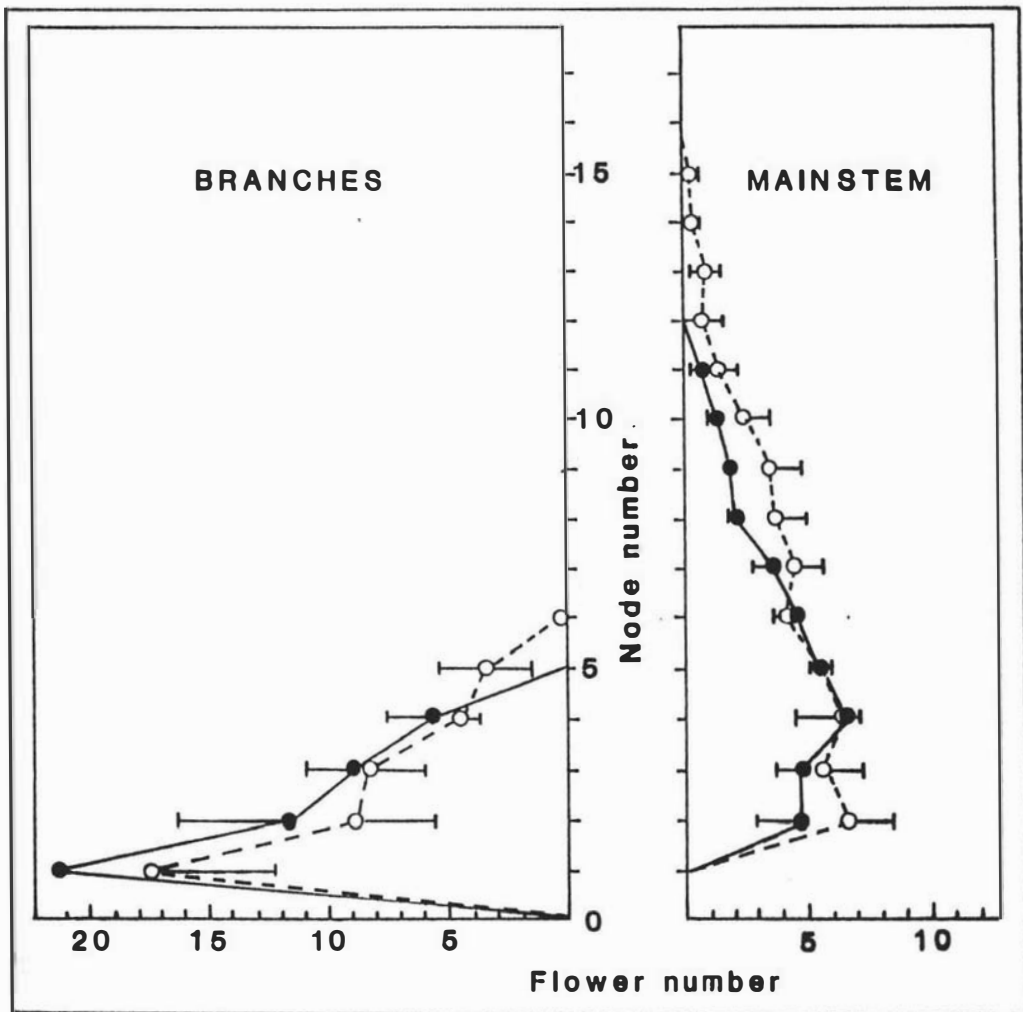


Fig. 4.6 Flower production at each node on control plants of Matara (●—●) and Amsoy (o--o). Horizontal bars represent SE's of the means.

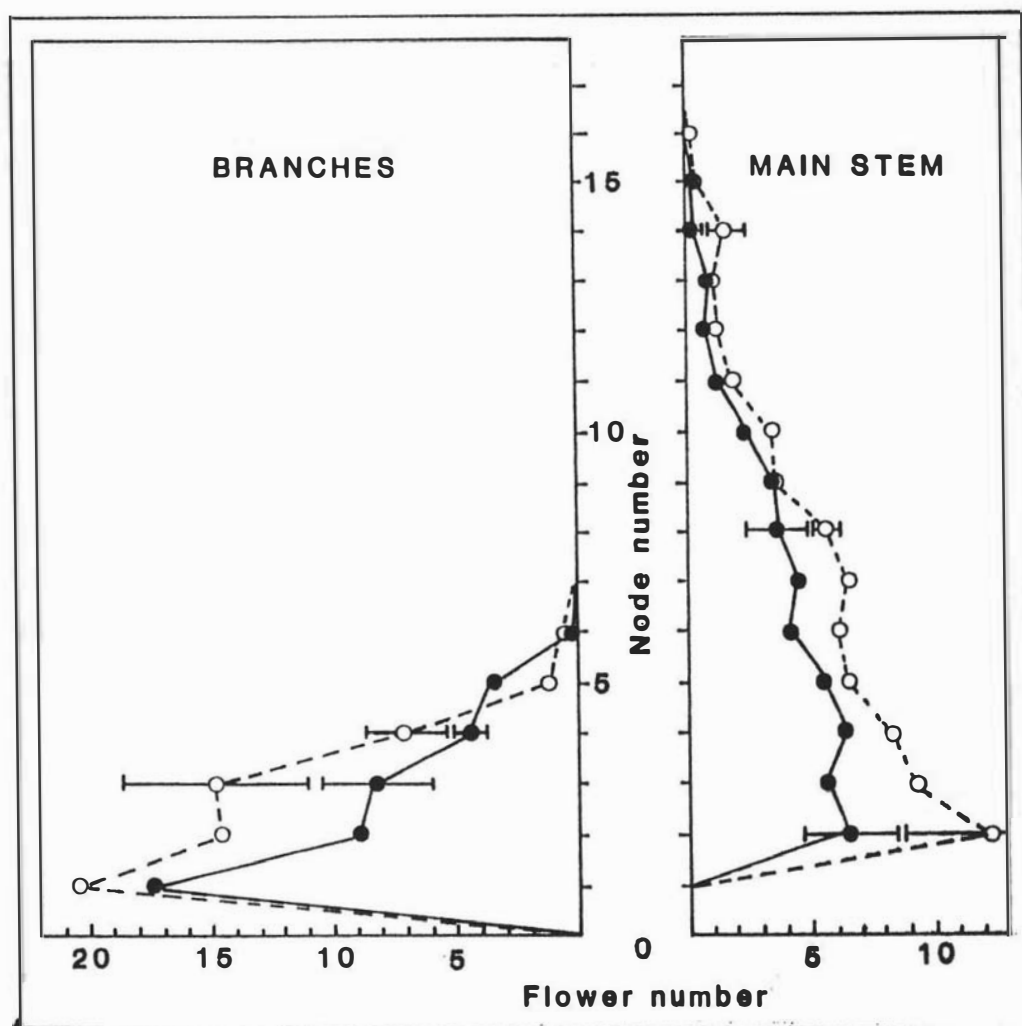


Fig. 4.7 Flower production at each node on Amsoy plants from treatment R3-50 (o--o) compared with the control (●—●). Horizontal bars represent SE's of the means.

In Matara (Fig. 4.8), although YLR showed a trend towards depressing final large pod number per plant, there was an indication that plants responded to 100% YLR by increasing the number of large pods produced per day over a short period of about 10 days during 46 to 56 DAP. As source strength became exhausted during later stages of pod growth, the number of large pods declined to levels below the control. This trend was also found in R1-100 and R5-100 (data not shown). It may be noted that 50% YLR at any stage in Matara caused no transient increase in large pod numbers. At the final count (91 DAP) there were no significant effects of any treatment in Matara (see ANOVA in Appendix 13 : Table A13.15), although there was a tendency for any leaf removal treatment at R1 or R3 to depress large pod number per plant.

In Amsoy (Fig. 4.9), the tendency of a short-period increase in large pod produced was not as clear in R3-100 as in Matara, while all other treatments except R3-50 followed the same pattern as the control. In the case of R3-50, the increase in large pods produced from after 60 DAP was dramatic and persisted until the end of the experiment, being significantly higher from 74 DAP onwards compared with the control (see ANOVA in Appendix 13 : Table A13.16).

After reaching the large pod stage, very few pods aborted. Mature pod set which was closely related to yield is considered in the next section.

4.4.3.2 Mature pod number per plant

The responses of plants to YLR in terms of mature pod numbers per plant differed in the two cultivars. In Matara, YLR had a generally deleterious effect on mature pod number. Treatments R1-100 and R3-100 in particular, showed a significant decrease in mature pod numbers by 39%, although the other treatments showed no significant reduction compared with the control. In Amsoy, treatment R3-50 increased mature pod number by 43.6% over the control, but no significant differences were found between other treatments and the control. The increase in mature pod number by R3-50 was due to the increase in late pod numbers (data shown in Table 4.3).

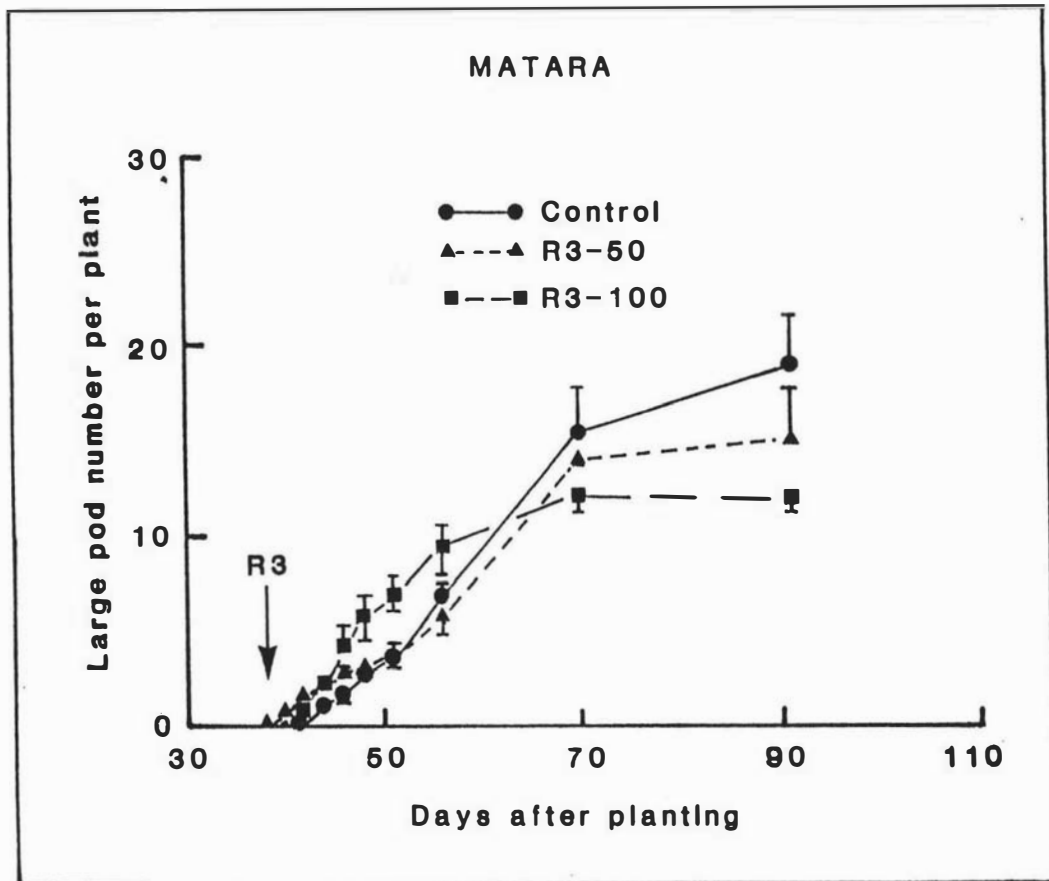


Fig. 4.8 Effect of YLR starting at growth stage R3 on cumulative large pod production per plant of Matara. Vertical bars represent SE's of the means.

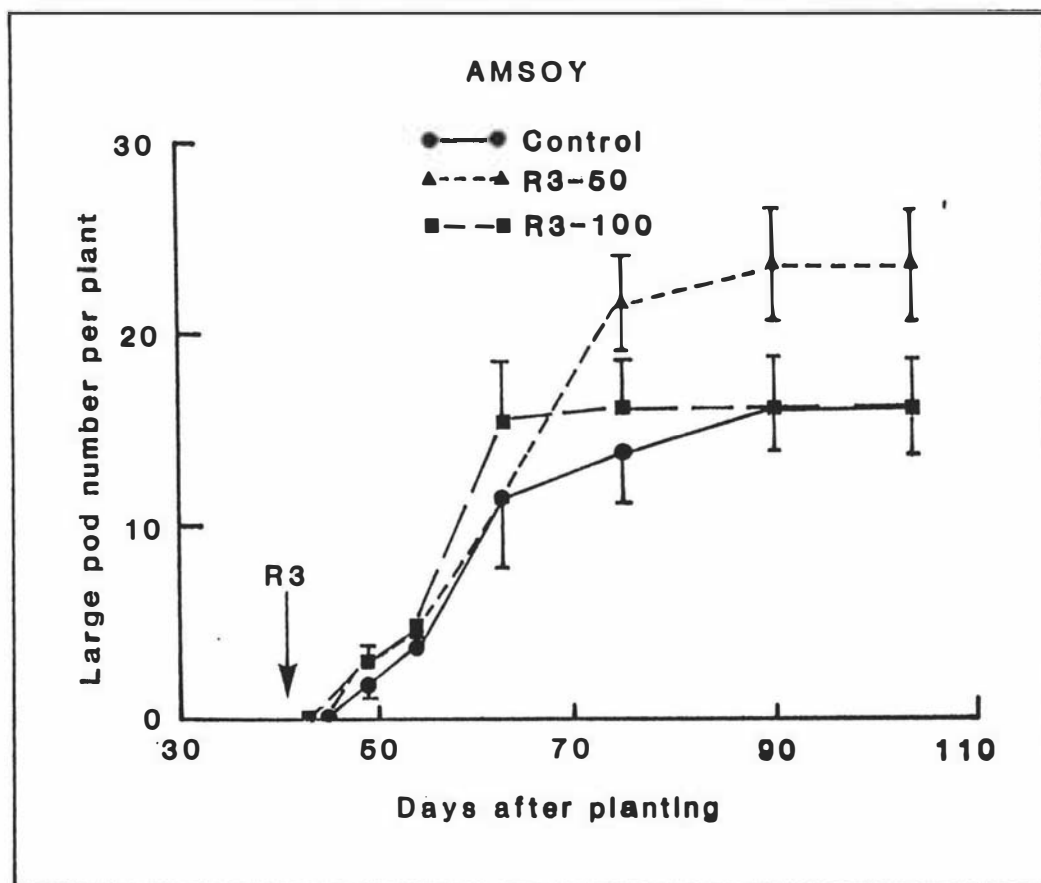


Fig. 4.9 Effect of YLR starting at growth stage R3 on cumulative large pod production per plant of Amsoy. Vertical bars represent SE's of the means.

Table 4.3 Effect of YLR on mature pod number per plant in Matara and Amsoy soybean

| Treatment | Matara | Amsoy |
|-----------|---------|----------|
| Control | 18.8 a* | 15.6 bc |
| R1-50 | 14.2 ab | 16.6 abc |
| R1-100 | 11.4 b | 13.4 c |
| R3-50 | 15.0 ab | 22.4 a |
| R3-100 | 11.4 b | 13.0 c |
| R5-50 | 15.0 ab | 19.4 ab |
| R5-100 | 18.4 a | 17.6 abc |
| average | 14.9 | 16.9 |
| CV (%) | 30.1 | 29.5 |

* Mean values within a column followed by the same letter are not significantly different at probability .10

4.4.3.3 Vertical distribution of mature pods on control plants

Both varieties produced about half their pods on branches (51.1 and 53.8% of the total mature pods for Matara and Amsoy, respectively, Fig. 4.10). On the main stem, the main area of pod production in Matara was in the middle region, especially at node 5. In Amsoy, pods were much more equally produced throughout the plant profile.

4.4.3.4 Vertical distribution of mature pods on plants as affected by YLR in Amsoy

It is obvious from Fig. 4.11 that 50% YLR starting at growth stage R3 increased mature pod set in the middle part of the plants (particularly at nodes 5 to 8). Increased pod set on branches was relatively unimportant (an increase of 9.5%) compared to the 83.3% increase in pod numbers borne on the main stem.

4.4.4 Effect of young leaf removal (YLR) on yield and yield components

Among the yield components of both varieties, only the numbers of pods per plant were significantly affected by YLR. Seeds per pod and seed weight were consistent throughout the treatments (Table 4.4).

Statistical analysis for total seed yield per plant showed differences between treatments in Matara, but not in Amsoy (Table 4.4). Seed yield in soybean was mainly influenced by the numbers of pods per plant. Seed yields of Matara plants in treatment R1-100 and R3-100 were significantly decreased due to the reduction in pods per plant. The correlation coefficient between pods per plant and yield in Matara was highly significant ($r = 0.932$). In Amsoy, although R3-50 was a

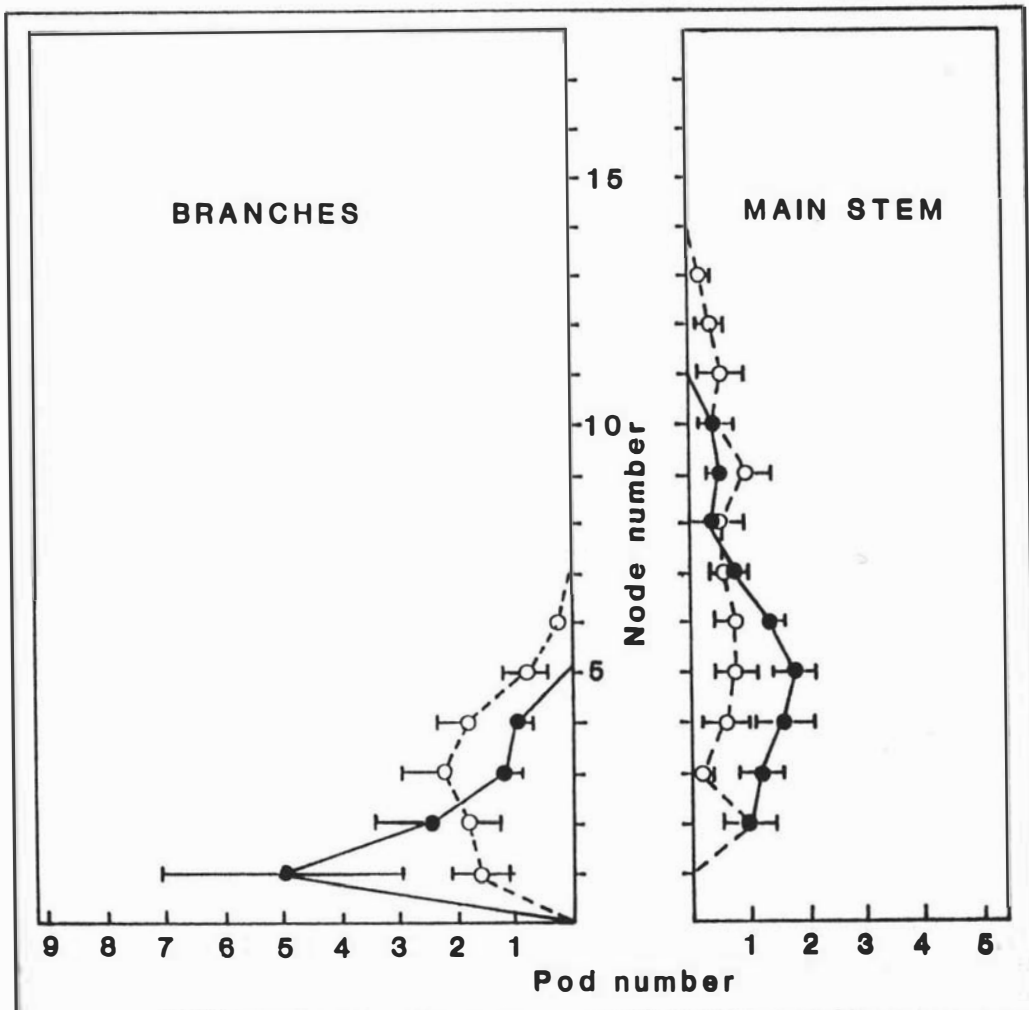


Fig. 4.10 Mature pod production at each node on control plants of Matara (●—●) and Amsoy (○--○). Horizontal bars represent SE's of the means.

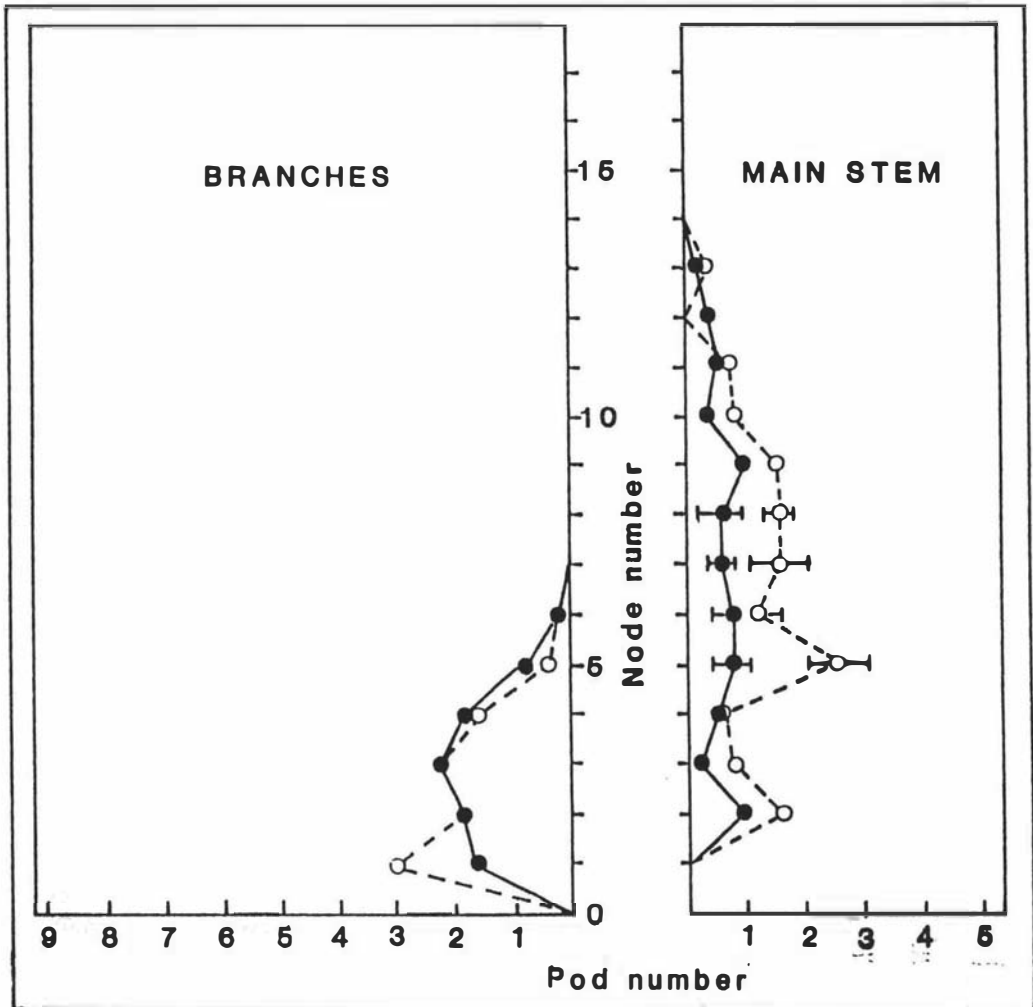


Fig. 4.11 Mature pod production at each node on Amsoy plants treated for R3-50 (o--o) compared with the control (●—●). Horizontal bars represent SE's of the means.

Table 4.4 Effect of YLR on yield and yield components in Matara and Amsoy soybeans

| Matara | | | | |
|-----------|------------------|---------------|--------------------------------------|--|
| Treatment | Yield components | | | Seed yield (g.plant ⁻¹) |
| | Pods per plant | Seeds per pod | Seed weight (mg.seed ⁻¹) | |
| Control | 18.8 a* | 2.01 a | 167.5 a | 6.21 a* |
| R1-50 | 14.2 ab | 2.07 a | 188.2 a | 5.46 ab |
| R1-100 | 11.4 b | 1.98 a | 180.7 a | 3.86 c |
| R3-50 | 15.0 ab | 2.06 a | 173.9 a | 5.03 abc |
| R3-100 | 11.4 b | 2.10 a | 185.4 a | 4.47 bc |
| R5-50 | 15.0 ab | 2.17 a | 178.8 a | 5.73 ab |
| R5-100 | 18.4 a | 1.98 a | 175.4 a | 6.33 a |
| average | 14.9 | 2.05 | 178.6 | 5.3 |
| CV (%) | 30.1 | 10.0 | 7.6 | 21.7 |
| Amsoy | | | | |
| Treatment | Yield components | | | Seed yield (g.plant ⁻¹) |
| | Pods per plant | Seeds per pod | Seed weight (mg.seed ⁻¹) | |
| Control | 15.6 bc | 1.96 a | 151.7 a | 4.67 a |
| R1-50 | 16.6 abc | 1.88 a | 161.0 a | 5.16 a |
| R1-100 | 13.4 c | 2.29 a | 158.7 a | 4.89 a |
| R3-50 | 22.4 a | 1.96 a | 151.8 a | 6.60 a |
| R3-100 | 13.0 c | 2.29 a | 160.0 a | 4.87 a |
| R5-50 | 19.4 ab | 2.22 a | 157.9 a | 6.91 a |
| R5-100 | 17.6 abc | 2.04 a | 150.2 a | 5.55 a |
| average | 16.9 | 2.09 | 155.9 | 5.52 |
| CV (%) | 29.5 | 20.6 | 8.1 | 38.0 |

* Mean values within a column followed by the same letter are not significantly different at probability .10

promising treatment in increasing pod number per plant, its effect on seed yield was not consistently high enough to cause a significant increase. However, seed number per pod and seed weight were not altered by YLR. The high coefficient of variation in this experiment is probably responsible for masking the effect of treatment on seed yield per plant. The correlation coefficient between pods per plant and seed yield in this case was significant at probability $< .05$ (0.866^*). Therefore, it is possible that YLR treatment (especially R3-50) which caused an increase in pod number per plant has the potential to have a beneficial effect on seed yield.

Yield and yield components of Amsoy plants were partitioned into two groups: that derived from early formed flowers and that from late formed flowers. The results in Table 4.5 show the flexibility of yield components. Seed yield and seeds per pod were consistent in both early and late groups (data not shown). Average values of seed yield for early and late groups were 2.82 and 2.66 g.plant⁻¹, and seed numbers per pod were 2.23 and 1.95, respectively. Plants set about the same numbers of early pods in all treatments, but late pods were significantly different in treatment R3-50 in particular, which gave a significantly higher late pod number than the control.

Data on seed weight showed that seed growth of early formed pods was influenced by YLR. Plants treated for R1-50 and R3-100 produced heavier seeds than the control plants whereas plants given other YLR treatments did not. The seed weight in late formed pods was not affected by YLR.

Table 4.5 Effect of YLR on pod number per plant and seed weight of early and late formed reproductive structures in Amsoy soybean

| Treatment | Number of pods per plant | | Seed weight (mg.seed ⁻¹) | |
|-----------|-----------------------------|----------|---|---------|
| | early | late | early | late |
| Control | 6.2 a* | 9.4 bc | 155.8 c | 147.6 a |
| R1-50 | 6.2 a | 10.4 abc | 183.0 a | 139.1 a |
| R1-100 | 8.2 a | 5.2 c | 170.2 abc | 147.1 a |
| R3-50 | 7.2 a | 15.2 a | 166.8 bc | 136.8 a |
| R3-100 | 6.4 a | 6.6 bc | 174.2 ab | 145.7 a |
| R5-50 | 8.2 a | 11.2 ab | 160.5 bc | 155.3 a |
| R5-100 | 7.8 a | 9.8 abc | 159.8 bc | 140.7 a |
| average | 7.2 | 9.7 | 167.2 | 144.6 |
| CV (%) | 46.8 | 49.6 | 7.9 | 9.2 |

* Mean values within a column followed by the same letter are not significantly different at probability .10

4.4.5 Reproductive abortion

4.4.5.1 Reproductive abortion in control plants

Fig. 4.12 shows a diagram of the relative pod set and abortion changes occurring during each stage of growth of control plants. For every 100 flowers, 32.1 produced young pods in Matara and 29.0 in Amsoy. Of these young pods, 22.7 and 18.0 developed into large pods, respectively. Eventually, large pods reached the mature pod stage with very little change in the level of large pod abortion (0.2 and 0.0, respectively).

When the percentages of total abortion were calculated, Matara and Amsoy plants had 77.5% and 82.0% combined abortion, respectively. This figure emphasizes the importance of abortion at the flower stage, flower abortion rates (67.9 and 71.0%) being the major component of the combined abortion in both cultivars.

4.4.5.2 Reproductive abortion as affected by YLR

The percentages of reproductive abortion as affected by YLR are shown in Table 4.6. In both cultivars, there was no significant effects of YLR on combined reproductive abortion.

In Matara, YLR only affected large pod abortion, although the magnitude of effects was small. Large pod abortion was significantly higher in treatments R1-100, R3-100 and R5-100 than in the control, although the contribution to combined abortion was negligible.

In the Amsoy cultivar, YLR affected both young pod abortion and large pod abortion, but these changes in Amsoy plants were different from the changes in large pod abortion of Matara plants. Treatment R1-100, where plants bear the smallest number of mature leaves during the later stages of reproductive development, showed a significantly lower percentage of young pod abortion than the control. At the later stage, however, large pod abortion was greater in treatments R3-50 and R3-100. However, again abortion of young and large pods was only a small component of the combined abortion.

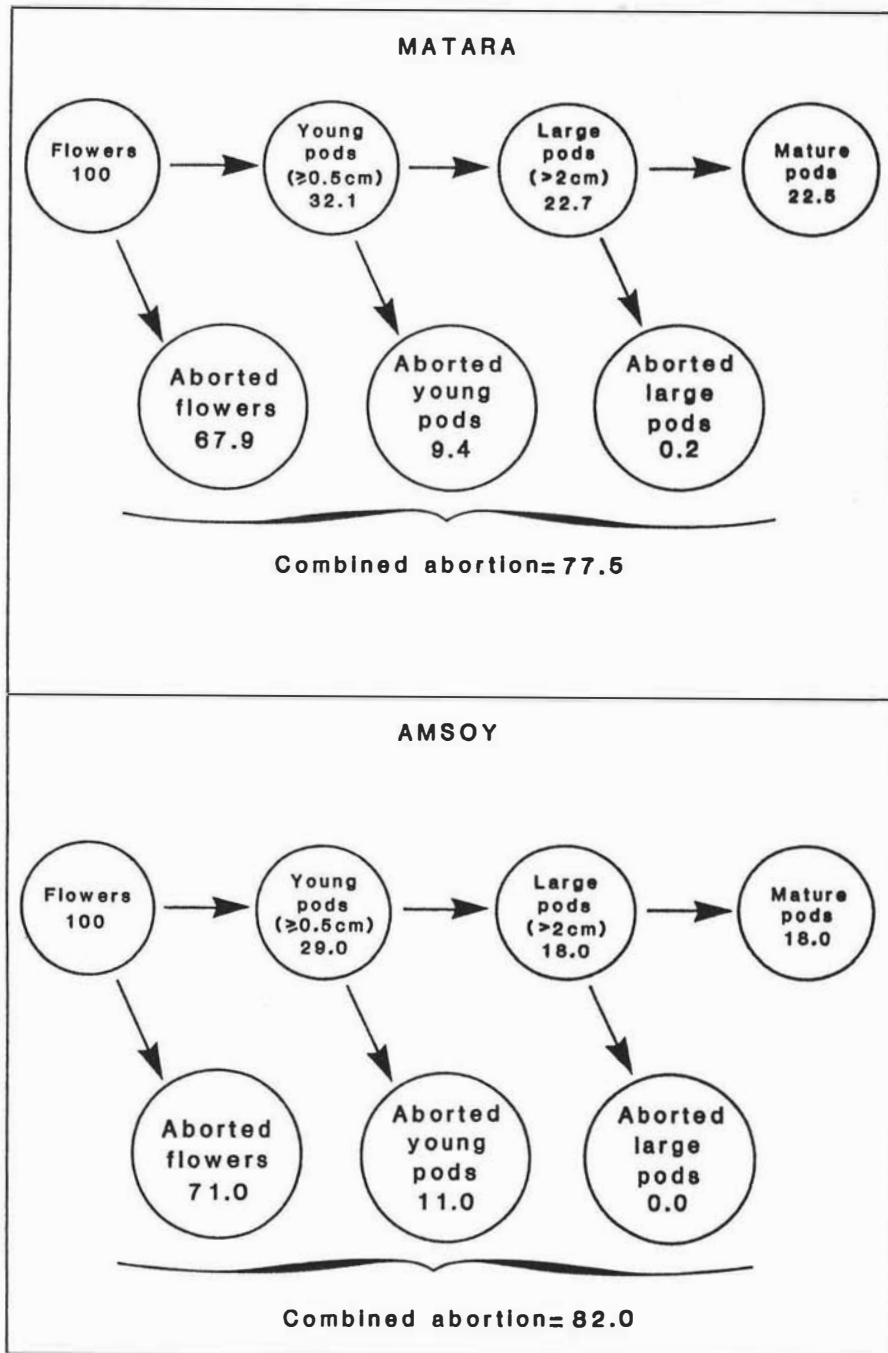


Fig. 4.12 Diagram showing events of pod set and abortion at each stage of the control plants. Starting with 100 flowers, the diagram shows the number of set pods and aborted pods at each stage.

Table 4.6 Effect of YLR on the percentage of flower abortion, young pod abortion, large pod abortion and combined abortion (of total flower number) in Matara and Amsoy soybean

| Matara | | | | |
|---------|-------------------|----------------------|----------------------|---------------------|
| | % flower abortion | % young pod abortion | % large pod abortion | % combined abortion |
| Control | 67.9 a* | 9.4 a | 0.2 cd | 77.5 a |
| R1-50 | 66.1 a | 10.8 a | 0.6 bcd | 77.4 a |
| R1-100 | 71.2 a | 13.4 a | 1.8 a | 86.4 a |
| R3-50 | 62.3 a | 15.3 a | 0.0 d | 77.6 a |
| R3-100 | 68.9 a | 9.8 a | 1.2 ab | 79.9 a |
| R5-50 | 71.4 a | 6.8 a | 0.3 cd | 78.5 a |
| R5-100 | 68.8 a | 7.2 a | 1.1 ab | 77.1 a |
| average | 68.1 | 10.4 | 0.7 | 79.2 |
| CV (%) | 7.3 | 27.8 | 103.3 | 6.6 |
| Amsoy | | | | |
| | % flower abortion | % young pod abortion | % large pod abortion | % combined abortion |
| Control | 71.0 a | 11.0 a | 0.0 b | 82.0 a |
| R1-50 | 78.5 a | 3.3 ab | 0.5 b | 82.3 a |
| R1-100 | 78.4 a | 1.5 b | 0.6 b | 80.4 a |
| R3-50 | 67.1 a | 13.3 a | 1.9 a | 82.3 a |
| R3-100 | 72.8 a | 6.4 ab | 2.3 a | 81.5 a |
| R5-50 | 73.1 a | 5.0 ab | 0.2 b | 78.3 a |
| R5-100 | 70.8 a | 13.7 a | 0.0 b | 84.5 a |
| average | 73.1 | 7.7 | 0.8 | 81.6 |
| CV (%) | 10.3 | 64.1 | 124.8 | 7.3 |

* Mean values within a column followed by the same letter are not significantly different at probability .10

4.4.5.3 Reproductive abortion of early and late flowers

Effect of YLR on the percentage of reproductive abortion of early flowers and late flowers is shown in Table 4.7. Soybean plants showed some flexibility in reproductive development from early formed flowers and late formed flowers. Differences in reproductive abortion of early and late flowers due to YLR were found only in Matara. Treatments R1-100 and R3-100 increased abortion rates of early flowers and late flowers, respectively, whereas treatment R5-100 resulted in reduced abortion rates in early flowers. 50% YLR did not change the percentages of reproductive abortion in either group of flowers.

In Amsoy, plants showed a higher degree of flexibility in terms of their flower production than in Matara. There were no significant differences in either early or late flower abortion in Amsoy between treatments. The average value of reproductive abortion of early and late flower groups was 83% and 77%, respectively.

4.4.5.4 Reproductive abortion at each node

Rates of reproductive abortion were relatively consistent both on branches and on the main stem (compare Figs. 4.6 and 4.10). Based on the number of flowers on each part, the percentage of reproductive abortion of Matara control plants were 79.7% on branches and 74.6% on the main stem. In Amsoy, the respective mean values were 80.2 and 84.7%. Abortion on the main stem was generally higher in the bottom region than in the middle and top regions, respectively.

Amsoy plants treated for R3-50 (compare Figs. 4.7 and 4.11) also exhibited about the same rates of abortion on branches and on main stem (84.3 and 81.2%, respectively). The lower part of the main stem also had the highest rate of reproductive abortion.

Table 4.7 Effect of YLR on percentage of reproductive abortion of early and late flowers in Matara and Amsoy soybean

| Treatment | % abortion for Matara | | % abortion for Amsoy | |
|-----------|-----------------------|---------|----------------------|--------|
| | Early | Late | Early | Late |
| Control | 77.5 b* | 76.5 bc | 84.4 a | 79.4 a |
| R1-50 | 79.6 b | 68.8 c | 85.9 a | 68.5 a |
| R1-100 | 88.9 a | 82.5 bc | 78.5 a | 77.5 a |
| R3-50 | 82.0 b | 74.3 bc | 86.3 a | 78.3 a |
| R3-100 | 80.0 b | 92.0 a | 85.6 a | 74.7 a |
| R5-50 | 77.3 b | 78.7 bc | 81.9 a | 74.7 a |
| R5-100 | 68.6 c | 84.9 b | 77.3 a | 87.2 a |
| average | 79.1 | 79.7 | 82.8 | 77.2 |
| CV (%) | 6.8 | 12.6 | 14.0 | 19.8 |

* Mean values within a column followed by the same letter are not significantly different at probability .10

4.5 DISCUSSION

It was clear in this study that plant responses to YLR differed between the two cultivars. The semideterminate Matara showed only negative effects while the indeterminate Amsoy showed positive responses in terms of pod set and yield potential. Responses of both cultivars depended on the time and intensity of YLR.

This section will discuss the factors involved in the differences in plant responses to YLR. A model is proposed which is intended to simplify the rather complicated plant responses and to test the hypothesis of nutrient deficiency in pod set. Possible causes of reproductive abortion are also discussed.

4.5.1 Effects of YLR on reproductive development

It is well known that pod number per plant is the most important component of seed yield in soybean. An interesting result in this study was that YLR altered pod number per plant in both cultivars but in opposite ways. It is important to know when Matara plants lost their yield potential as a result of YLR and what caused the increase in pod set in Amsoy plants.

4.5.1.1 Responses of Matara plants

There was a tendency for a transient increase in cumulative large pod set in all growth stages when 100% of the young leaves were removed (data shown only at stage R3, Fig. 4.8). These transient increases were probably because competition between leaf growth and pod growth was substantially removed during these stages. During the late stage of pod development, however, there was a tendency for a reduction in large pod numbers per plant. 50% YLR had little or no effect on cumulative large pod number, reflecting the low degree of intraplant competition in the semideterminate Matara.

At harvest, treatments involving 100% YLR at growth stages R1 and R3 resulted in a 39.4% reduction in pod numbers per plant (Table 4.3). It was clear that this reduction occurred mainly during the late stages of pod development as there were no significant differences in flower

production (Table 4.2) nor in young pod set (data not shown). Lack of photoassimilates during late stages of pod development due to the small number of remaining leaves was probably responsible for this reduction (Table 4.1). Bhattacharjee and Ghude (1985) also reported that source limitation by defoliation (mature leaves) during reproductive growth substantially reduced pods per plant.

4.5.1.2 Responses of Amsoy plants

In Amsoy, results showed that R3-50 caused a 43.6% increase in pod number, while other treatments did not significantly change pod number per plant (Table 4.3). This increase was due to the much greater number of pods on the main stem (83.3% more than the control), mainly located in the middle region (nodes 5 to 8) (Fig. 4.11). Pod growth and development has been reported to rely mainly on the corresponding subtending leaf (Blomquist and Kurst, 1971; Stephenson and Wilson, 1977a). Therefore, the increased pod set on nodes 5-8 reflects not only reduced intraplant competition but the continued efficiency for photosynthesis of leaves at these nodes during pod development and maturation. Stephenson and Wilson (1977b) reported in soybean that between pre-flowering and early pod development, assimilate was stored in stems and transferred to pods during later development, a finding also noted for *Vicia faba* by Ismail and Sagar (1981). Removal of some young leaf material probably reduces the competition for this temporary store of assimilates, allowing more to be available for additional pod set. Leaves at nodes 5-8 are in the best position for light interception in treated plants and are therefore more likely to maintain the photosynthate supply required by additional pods until maturity. The improvement of mainstem pod set by branch removal is also found in lupins (Herbert, 1977).

On branches, although little increase in mature pods (9.5%) was found (Fig. 4.11), young pod number was increased by 30.9% compared to the control (data not shown). Unfortunately, most of these young pods aborted during development. Mutual shading or low light intensity on branch leaves may be responsible for higher young pod abortion on branches. Hansen and Shibles (1978) also found in untreated plants that the highest degree of abscission occurred on branches and lower stems.

Interestingly, the changed pattern of flower production due to YLR does not entirely parallel the resulting changes in pod numbers. 50% YLR at growth stage R3 not only increased pod set, but also increased flower number (by 44.1% over the control) (Table 4.2 and Fig. 4.5). Unlike the increase in pod set, this increase in flower number was contributed by a 49.4% increase on the main stem and a 38.2% on branches. On the main stem, R3-50 increased flower number mainly at nodes 2 to 8 (Fig. 4.7).

The increase in flower number on branches was located at nodes 2-4 where there were about 2-3 mature leaves on the branches located at these nodes at growth stage R3. Young leaves were also produced in branches at these nodes. This major increase in flower number (Fig. 4.7) may also be because competitive sinks were reduced on these branches resulting in a localised surplus of photoassimilate for increasing flower number and young pods in this area. However, as already noted most of the flowers in this area were not very productive.

These results suggest that a high degree of intraplant competition existed in Amsoy plants during the early stages of reproductive development and partial reduction of competitive sinks caused a redirection of photoassimilates in favour of flower initiation and pod set. YLR seemed to be effective in stimulating an increase in flower number about 2-4 days after starting treatments, but the significant effect on flower number was on late flower production (Fig. 4.5). As might be expected, the time before pod numbers increased in response to YLR appeared to be much longer than the response of flower increase (at least 10 days after starting the treatments) (Fig. 4.8 and 4.9).

There is other evidence to support the idea that flowers and young leaves are in competition for photoassimilates. Heitholt and Egli (1985) found that floral removal in soybean during the early reproductive phase increased leaf number, although these new leaves were quite small and did not result in a significant change in leaf area. Conversely, Gehrigler and Keller (1980) studied the distribution

of ^{14}C -labelled assimilates into flowers and young pods in faba bean (Vicia faba) and revealed that topping which reduced the level of intraplant competition and increased pod set, increased the incorporation of label into young flowers.

It is interesting that plant responses to 50% YLR at growth stage R1 differed from those at R3. R1-50 did not significantly increase flower number, pod set (Tables 4.2 and 4.3) or the number of leaves produced (Table 4.1). This suggests that at this stage of development in Amsoy, the reproductive sink was limiting. Extra source availability caused by this treatment went to increase only the seed weight of early setting pods (Table 4.5), because there was no alternative additional sink (e.g. new flower number or increased pod set) for assimilate to flow into.

100% YLR at growth stages R1 and R3 did not significantly change flower number and pod number per plant in Amsoy. In fact, plants given these treatments reinitiated more young leaves resulting in a significantly higher numbers of leaves produced per plant (Table 4.1). Pate and Farrington (1981) studied assimilate distribution of ^{14}C during flowering in Lupinus angustifolius and found that the inflorescence was a minor sink for assimilates compared with root, main stem and developing lateral shoots. Similar results were found by Ho (1984) for tomato. These data support the result of the present study where YLR had an effect on new leaf initiation rather than on flower production at this stage. Removal of active sinks during vegetative growth before flowering is also reported to stimulate more vegetative growth in some plant species (Hussey, 1963; Rojonen and Virtanen, 1968; Aung and Byrne, 1978).

YLR at the growth stage R5 appears to be too late to stimulate flower production : the pattern of cumulative flower production per plant was not altered (data not shown) and total flower numbers were not significantly increased. Growth stage R5 was the late flowering period for both varieties (Fig. 4.3) and flower production activity was low. Plants may have already been preprogrammed to determine flower numbers that the plants are going to produce after the R5 stage (see subsequent discussion).

4.5.2 Effects of YLR on Yield and yield components

In both varieties, pod number per plant was the component most affected by YLR, whereas seeds per pod and seed weight were not affected (Table 4.4).

4.5.2.1 Responses of Matara plants

The significant reduction in seed yield by R1-100 and R3-100 in Matara was due to the small numbers of pods per plant. Yield loss as a result of mature leaf removal during reproductive development causing a shortage in assimilate supply during late stages in soybean is common (Johnston and Pendleton, 1968; Mesa and Fehr, 1984; Bhattacharjee and Ghude, 1985). Determinate soybean cultivars have been shown to be more affected in this respect than indeterminate soybeans (Fehr *et al.*, 1981). This may be due to the ability of indeterminate soybeans to form new leaves during the reproductive phase. However, 50% YLR at all stages and 100% YLR at R5 in Matara did not significantly reduce seed yield, although these treatments caused a significant reduction in the number of leaves remaining on the plants (Table 4.1).

4.5.2.2 Responses of Amsoy plants

In many plant species such as Phaseolus vulgaris (Bennie and Clifford, 1980), Vicia faba (Gehriger and Keller, 1980), tomato (Wien and Minotti, 1988) and soybean (Amuti, 1983), it was found that crop manipulation which reduces intraplant competition (e.g. decapitation) increases fruit numbers per plant.

In Amsoy, although R3-50 significantly increased mature pod number by 43.6%, seed yield per plant was not significantly different from the control (Table 4.4). An increase in pod numbers per plant without an increase in seed yield is not uncommon in soybean research (Burton and Curley, 1966; Boize, 1982; Noodén and Noodén, 1985). However, in most of these cases, yield compensation was due to a reduction in seed weight which was not found in the present study. One explanation is

that the coefficient of variation of yield was high (38.0%), possibly because variations of seed number per pod and seed weight were pooled with the variation of pods per plant. The high variation in seed yield therefore masked the effects of YLR. However, when correlation coefficients which were statistically significant were taken into account, it can be concluded that R3-50 is a promising treatment in increasing pod number per plant and possibly seed yield in the Amsoy cultivar.

Data on the partitioning of yield and yield components into early and late groups showed the flexibility of yield component compensation in Amsoy soybean (Table 4.5). Among the yield components, seed number per pod was the most stable variable.

YLR changed late pod number and early seed weight significantly, but did not alter early pod number or late seed weight (Table 4.5). R3-50 significantly increased late pod set which appeared to be statistically significant after 74 DAP, 33 days after starting YLR (Fig. 4.9). Early seed weight was significantly increased in R1-50 and R3-100 treatments (Table 4.5). These treatments did not increase flower number and pod set, but R3-100 stimulated more new leaf initiation. This suggests that high concentrations of assimilates in conducting tissues caused by YLR during the early stages was not all used for leaf initiation activity, allowing some source assimilate to be available to flow into seeds of setting pods.

4.5.3 Reproductive abortion

It is evident in this experiment that flower abortion was far more important than young pod abortion or large pod abortion (Fig. 4.12). The same findings have also been reported by Van Schaik and Probst (1958b) and Wiebold et al. (1981). Van Schaik and Probst (1958b) found that the percentage of pod abortion (from the young pod stage to the mature pod stage) was relatively constant (ranging from 17 to 29%) while most of the variation in total abortion was due to varietal differences in flower abortion. Wiebold et al. (1981) also reported in 9 determinate soybean cultivars that 19-30% of young pods (or 6-12% of the total flowers) subsequently aborted, mostly when pods were very small.

The rates of reproductive abortion on branches and on the main stem were about the same. On the main stem, the percentage of reproductive abortion was highest in the lower part of the plant in both varieties. Moreover, evidence from plants in treatment R3-50 in the Amsoy cultivar showed that the increase in flower number on branches and on the main stem particularly on nodes 2-4 was a wasteful production, because the increase in pod set was found mainly on nodes 5-8. This increase in flower number with high rate of flower loss on nodes 2-4 on the main stem reflects the time when leaves on the lower nodes (2-4) were photosynthetically active. During the early reproductive stage, they were active enough to increase flower number in response to YLR but during pod development, these leaves became older and were less able to supply enough photoassimilates to retain high pod set in this area.

Many researchers have also reported a high abortion rate in the lower region of the soybean canopy (Hansen and Shibles, 1978; Wiebold et al., 1981; Antos and Wiebold, 1984). Wiebold et al. (1981) suggested that in normal conditions, a localized decrease in photosynthesis can cause an increase in localized abortion because of a reduction in available carbohydrate. Antos and Wiebold (1984) showed that high abortion rates in the lower one-third of the canopy was associated with the low concentrations of total soluble sugar and starch in the stem and petioles. Heitholt et al. (1986b) disagreed with this hypothesis because they found that the concentrations of carbohydrates did not change in fully open flowers although the percentages of reproductive abortion were altered by source-sink manipulations. Moreover, the fact is that reproductive abortion occurred mainly at the flowering stage when plant photosynthetic rate was relatively high, and during the first days after flower opening, flowers are small sinks relative to the size of the whole plant as indicated by a slow absolute dry matter accumulation rate ($<5 \text{ mg.flower}^{-1}.\text{day}^{-1}$) (Heitholt et al., 1986a). Therefore, it seems that while flower abortion may not to be limited by the available supply of photoassimilate present during flower growth, the hormonally controlled sink strength of the flowers may be crucially important (see Chapter 5).

When the rates of reproductive abortion were partitioned into early and late flower categories, differences were found only in Matara (Table 4.7). 100% YLR at growth stage R1 and R3 caused higher

percentages of reproductive abortion for early flowers and late flowers, respectively. These may be because total YLR at these stages increased intraplant competition through new leaf initiation activity and caused a shortage in photoassimilates available to flowers resulting in higher rates of flower abortion. Limiting assimilates at the flowering stage in tomato has also been found to cause young leaves to develop more for sustaining growth and to cause increased floral abortion (Kinet, 1977).

However, YLR by 100% at growth stage R5 reduced the rate of early reproductive abortion. In other words, severe reduction in competitive sinks at this stage in Matara soybean increased pod set of early flowers. This result agrees with that reported in tomato by Ho (1984) who suggested that during the fruiting stage, the priority between sinks for assimilates occurs in the order of fruit > young leaves > flowers. However, because of plant plasticity, the effect of R5-100 was harmful to late-formed reproductive structures as can be seen by the increase in the rate of large pod abortion (Table 4.6). Therefore, no overall change in total combined abortion occurred as can be seen in the same Table. In the indeterminate Amsoy, levels of reproductive abortion remained the same both in early and late groups (Table 4.7). This consistency in abortion rate is also found in highly productive growing conditions. Morandi *et al.* (1988) have reported that short days with light-interrupted nights during the reproductive phase significantly increased pod numbers per plant because it lengthened the duration of the vegetative and reproductive periods, but did not reduce percentages of reproductive abortion. In other words, yield potential (flower number and young pod numbers) can be increased when source capacity is increased, without affecting percent pod set.

The consistency of combined reproductive abortion in both varieties suggests that high reproductive abortion in soybean may be a species characteristic and that plants have been preprogrammed to produce a large number of flowers and then drop a certain proportion of them. This mechanism in soybean plants may be set up as a survival mechanism.

4.5.4 A model for explaining assimilate flows

The objectives of proposing this model are as follows.

- To facilitate the explanation of plant responses to YLR.
- To test the hypothesis of nutrient deficiency in pod set.

The model is shown in Fig. 4.13. The suggestion is that assimilates from a tank produced by current photosynthetically active leaves (PAL) are flowing in a pipe with openings representing growth of different organs. During the early reproductive phase (or flowering period), assimilates normally flow into young leaves (YL) and reproductive growth (RG). The YL (represented by T-joints) were arranged prior to RG (represented by an L-joint) because during this period, YL are reported to be stronger sinks than flowers and pods (Pate and Farrington, 1981; Ho, 1984). At the reproductive site, assimilates flow into two containers of early and late formed reproductive structures. Each container is composed of three sub-containers which are numbers of flowers produced, numbers of pods set and mean seed weight (mg.seed^{-1}). These three components were found to be significantly different between treatments. Seed number per pod was excluded because it was consistent among the treatments for both early and late reproductive structures. Within each container, assimilates can gravitationally flow from the top sub-container (flowers) to the sub-containers underneath (pods and seeds).

The amount of assimilate flowing into each component depends on current assimilate availability (PAL), intensity of YLR and time of YLR (days after planting, DAP). In control plants, PAL increased with time and produced assimilate which was available for both early and late formed reproductive structures throughout the season. Conversely, new leaves were rapidly initiated during early flowering but the rate then decreased with time in normal plants. This new leaf initiation (NLI) was affected by YLR which was presented by blank joints in the diagram. Closing T-joints (or replacing with joints as seen in the diagram) can increase pressure in the pipe and cause leakages. These leakages can be used to explain extra new leaf initiation caused by YLR (data were

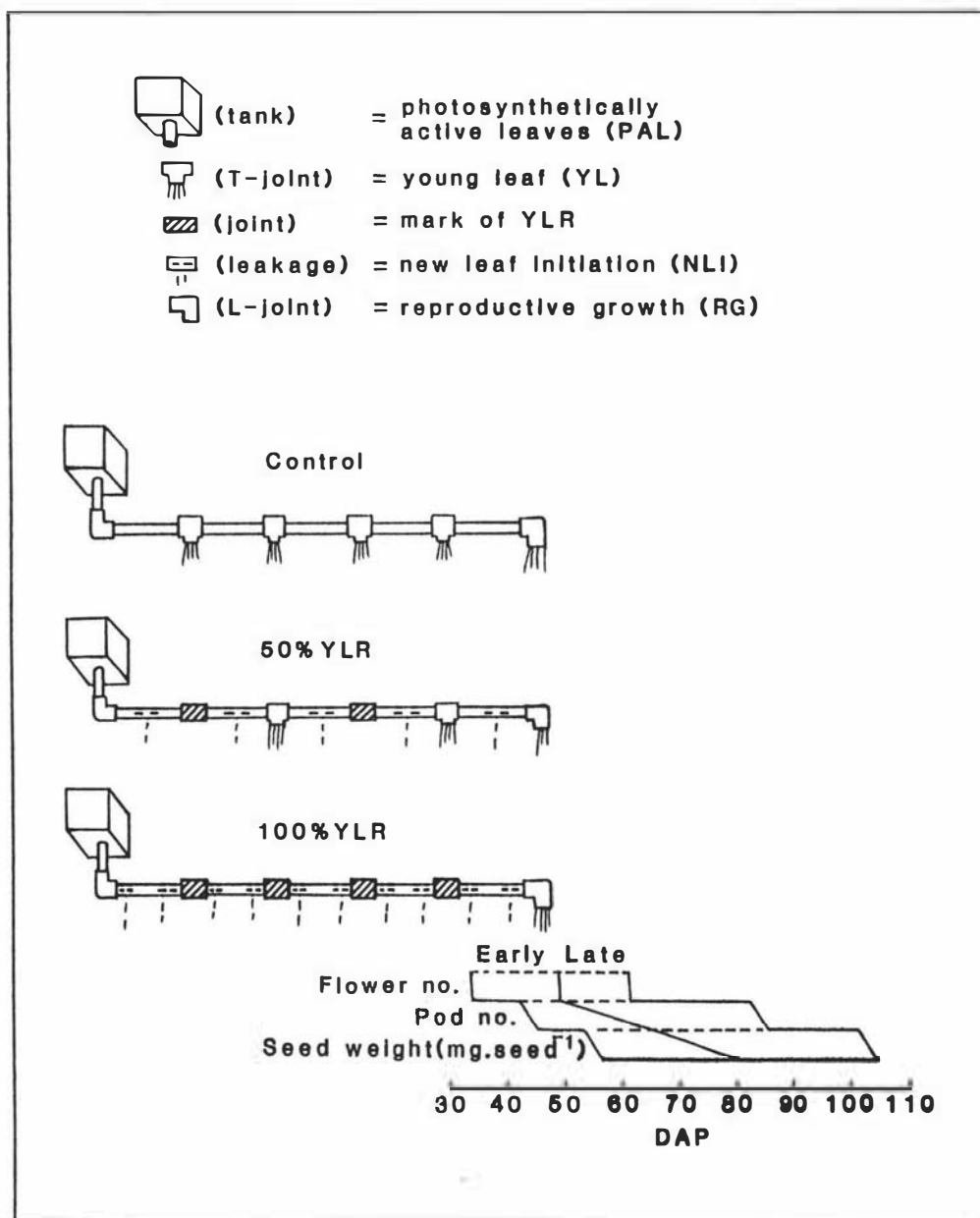


Fig. 4.13 A model of assimilate flow

drawn from the differences between the total number of leaves produced in each treatment and in the control in Table 4.1). The number of leakages depends largely on intensity of YLR, but can also be affected by time of YLR.

This model was used to explain and summarize the results for the Amsoy variety as shown in Fig. 4.14. Time (days after planting) was also drawn from the results except time of seed growth which was approximately marked by growth stages R5 to R8. To interpret this figure, the value of each parameter as affected by YLR has to be compared with value of the same parameter for the control. An asterisk following a value or values (in the case of the combined number of early and late flowers for R3-50) marks the significant differences from the control at probability 0.10. In the case of extra NLI, the asterisks represent the significance of the total number of leaves produced per plant from Table 4.1.

Thus, from Fig. 4.14, source-sink relationships can be linked and discussed together more clearly. At the source level, PAL was really important for the growth of reproductive structures. Basically, the growth of sink organs is affected by assimilate availability. Numbers of leaves, leaf position and light interception are factors that affect the photosynthetic capacity and consequently affect sink growth. At the sink level, pod set and seed weight can be increased by crop manipulation. The capacity of dry-matter production in leaves may be, at any given time, either higher or lower than the capacity of dry-matter accumulation in other parts of the plant (Ho, 1988). There is a dynamic relationship between these two factors. Therefore, at different times, either source- or sink-limiting situations may exist in crop production. The interpretation is divided into 3 cases as follows.

- i) When plants were in stage R1, closing T-joints (or replacing with blank joints = YLR) did not instantly increase assimilate flow into the first two sub-containers (early flowers and early pod number). Closing half of the T-joints (R1-50) did not cause leakage (new leaf initiation), but increased the flow into the third sub-container (early seed weight), whereas closing all the T-joints (R1-100) caused high

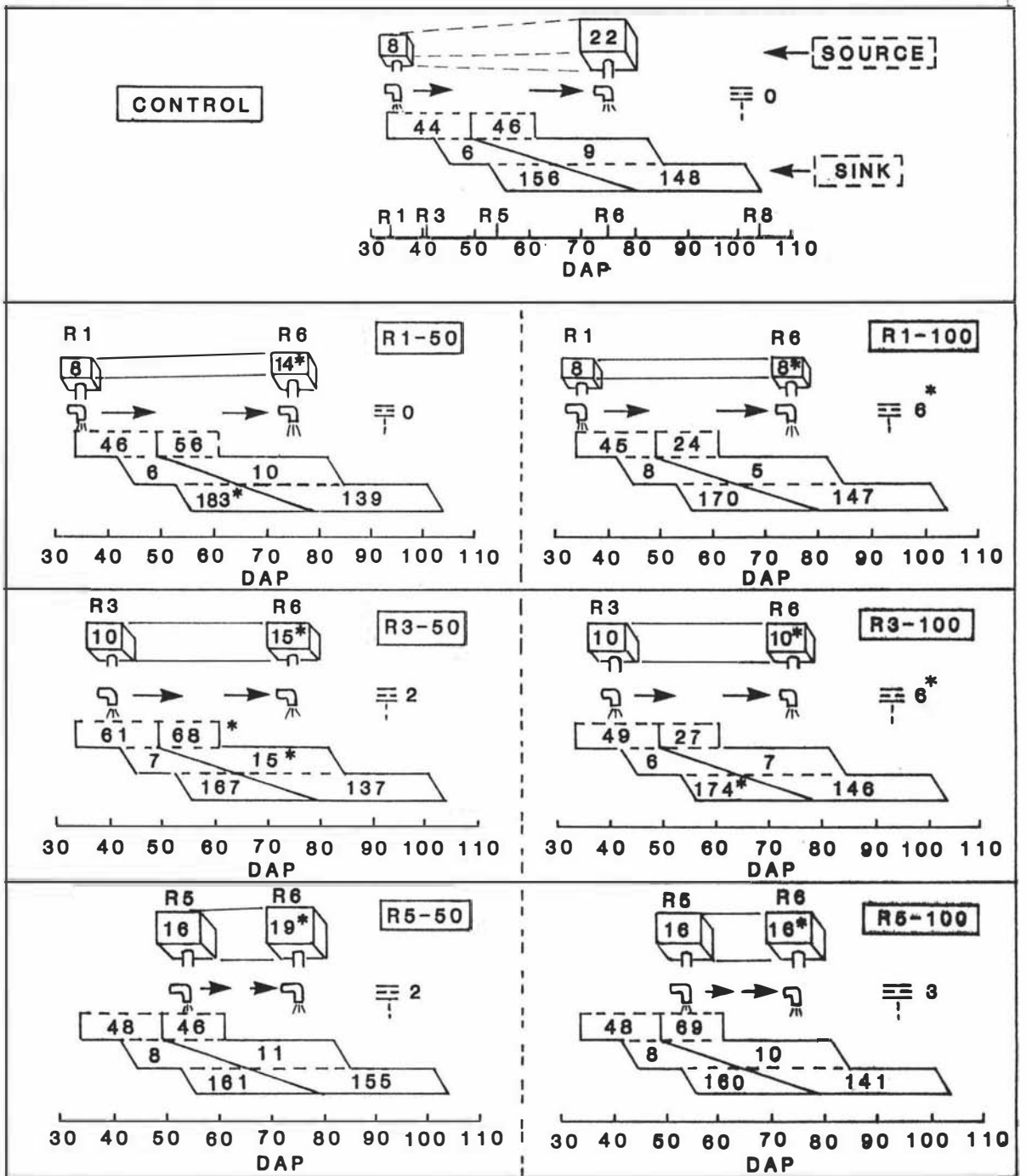


Fig. 4.14 A model of assimilate flow used to summarize the results of Amsoy variety

leakage (NLI). This means that yield limitation was at the level of the first and second sub-containers (early flower production and pod set). At R1, these plants appear to be sink limited, suggesting that the hypothesis of nutrient deficiency always controlling pod set in soybean is not totally true. Plants may have already been preprogrammed from the R1 stage to produce a certain number of early flowers and early pods. Changes in hormonal balances by YLR may also be responsible for new leaf initiation in the R1-100 treated plants, but not in R1-50 plants.

ii) When the flow of assimilates was manipulated at R3, closing half of the T-joints (R3-50) increased the size of late sub-containers (significantly increasing the total number of flowers and late pod set). This indicates that during this stage source-limitation plays a role in controlling seed yield, because increasing source availability by reducing sink competition can now increase pod set. However, closing all the T-joints at this stage (R3-100) caused leakages (NLI) without increasing the output to the sub-containers except the third one of the early group (early seed weight). This suggests that severe removal of young leaves stimulated a high NLI, rapidly increasing sink competition. Therefore, although a small amount of surplus assimilate was left to increase early seed weight, sink demand from young initiating leaves prevented any subsequent improvement in reproductive yield.

iii) When PAL was reduced to 19 or 16 at growth stage R6 as seen in R5-50 and R5-100, respectively, sink output (in the containers) was about the same as in the control. It is now too late for a significant increase in potential yield, sink activity is once again limiting reproductive development.

This model shows that most, but not all, events can be explained on the basis of a nutrient model. In particular, the sink limitation in cases i) and iii) cannot be explained on a nutrient hypothesis. At these stages (R1 and R5) the plants seem unable to respond to increased

nutrient supply. This gap in the model and the consistency of high abortion rates point to the fact that other mechanism(s) such as hormonal control may be involved.

Van Schaik and Probst (1958a) stated that 'while shedding of reproductive organs generally is considered to be affected largely by environment, there are strong indications that considerable genetic control is present also'. In the present study, the imposition of YLR effects was based on the idea of competitive sink reduction. Although YLR could increase pod numbers per plant in Amsoy which proved the basic idea of assimilate diversion, the reproductive abortion rates between treatments were still consistent. The adverse effects of YLR in Matara plants also did not alter the percentages of combined reproductive abortion even though the plants produced fewer flowers. Therefore, the expectation that YLR could reduce intraplant competition was correct, but the suggestion that YLR might change the percentage of combined reproductive abortion was untrue. YLR could only change the percentages of components of the combined abortion rates, such as the percentage of early or late reproductive abortion in Matara or the percentages of young pod and large pod abortion in Amsoy. This suggests that the total extent of reproductive abortion for the whole plant is likely to be strongly genetically controlled, possibly through hormone action.

4.6 CONCLUSION

The idea that young leaf removal (YLR) may reduce intraplant competition is proved to be correct in both Matara and Amsoy soybeans since YLR was shown to divert assimilates to cause an increase in flowers or pods at least for a short period during development. The difference between these two varieties seems to be the degree of intraplant competition and possibly the level of plasticity of growth responses. In Matara, severe YLR at the early reproductive stages (R1 and R3) caused a reduction in both pod number and seed yield. Evidence from the results for Amsoy at R1 stage suggests that high reproductive abortion in soybean seems not to be dependent on assimilate availability, because manipulation to reduce intraplant competition during the early flowering period did not increase pod set. In Amsoy, however, YLR by 50% starting at growth stage R3 increased flower and

pod numbers per plant by 44.1% and 43.6%, respectively. YLR too late (R5) caused no increase in yield components but did not significantly reduce seed yield or yield components either.

Flower production was high in the bottom half of the main stem in both varieties, whereas pod set was slightly different between Matara and Amsoy. In Matara, pod set on the main stem was high in the middle region, but in Amsoy, pod set was more equally distributed amongst the main stem nodes. YLR changed the patterns of vertical flower production and pod set. 50% YLR at R3 in Amsoy plants increased flower production by 49.4% on the main stem and by 38.2% on branches, and increased pod set by 83.3% on the main stem but by only 9.5% on branches. The increase in pod set on the main stem occurred mainly in the middle part of the plants (nodes 5 to 8).

The most interesting result was that YLR did not change rate of combined reproductive abortion in both varieties. Matara exhibited only a slightly lower percentage of reproductive abortion than Amsoy (mean values over all treatments 79.2 vs 81.6%). Reproductive abortion occurred at all stages during development but particularly and dramatically during the flowering stage (mean values over all treatments 68.1% and 73.1%). This effect was consistent in all treatments. Young pod abortion was 9.4% for Matara and 11.0% for Amsoy. Both varieties showed very low large pod abortion (mean values over all treatments less than 1%).

Fitting these data into a model describing nutrient flows into reproductive components (section 4.5.4) confirms that this data cannot be fully explained on the basis of assimilate partitioning alone.

CHAPTER 5

GENERAL DISCUSSION AND SCOPE FOR FURTHER STUDY

5.1 GENERAL DISCUSSION

The dominant theme of this study has been the role of reproductive abortion in affecting soybean seed yield. This high rate of reproductive abortion is found in many crop plants and particularly in legumes (see also section 4.2.2.2) and is considered to be a major agronomic disadvantage limiting the expression of seed yield potential.

In the field study (Chapter 2), it was clear that the rates of reproductive abortion in Matara and Amsoy soybean were both consistent and high, despite the 10-fold difference in planting densities employed (5.8 to 61.2 plants.m⁻²). In the field, flower abortion and young pod abortion (<2 cm-long pods) was much more pronounced than large pod abortion (≥2 cm-long pods). This effect was supported by the results in Chapter 4. Failure in fertilization of soybean flowers was proved to be a negligible cause of their abortion (Chapter 3). Abortion occurs as a result of the curtailment of subsequent development.

Intraplant competition was suspected to be a key factor influencing the high level of reproductive abortion in plants grown under low interplant competitive stress, especially in the Amsoy variety (section 2.5.5). Results from the final experiment (Chapter 4) reveal that competition between vegetative and reproductive growth in each cultivar certainly occurs. YLR could alter early or late flower abortion in Matara depending upon plant growth stage and rate of removal. In Amsoy, YLR increased large pod abortion possibly via the increase in sink load (increased in flower number, see Table 4.2). However, competitive effects do not appear to be the sole factor involved in reproductive abortion. Despite the fact that reduced intraplant competition by young leaf removal (YLR) should result in the redirection of photoassimilate towards reproductive growth, this did

not reduce the level of combined reproductive abortion. The consistency of reproductive abortion both in the field and in the glasshouse suggests that this reproductive abortion is not totally regulated by assimilate availability.

It is well known that soybean cultivars differ in their levels of reproductive abortion (section 4.2.1). Matara has less plastic growth, less competition between vegetative and reproductive growth, higher seed growth rate, shorter leaf duration and lower rate of reproductive abortion compared with Amsoy. However, it may be worthwhile noting here that Matara which is suggested as a good cultivar because of its reproductive efficiency (see section 2.5.8) may not perform as well as Amsoy if unfavourable conditions occur during reproductive development. As found in Chapter 4 (Table 4.7), adverse conditions that affect source availability may increase rates of reproductive abortion at certain stages and may reduce pod numbers per plant (Table 4.3), because Matara has less plasticity in vegetative growth to compensate during later stages. Amsoy may be a better cultivar to be grown in uncertain environmental conditions as its longer leaf duration is a key factor in maintaining yield. However, in areas where normal growth with less stress is expected, Matara still has a higher potential in terms of its reproductive efficiency with less input consumption for vegetative growth.

From the literature, however, it is unclear whether there is a relationship between the type of stem termination and abortion levels. No published papers appear to have emphasized this aspect either by studying near iso-genic lines or related varieties. In this study, results showed that differences in the type of stem termination and the level of intraplant competition between the semideterminate cultivar Matara and the indeterminate cultivar Amsoy are associated with differences in reproductive efficiency. Matara showed a lower percentage of reproductive abortion in the field study than Amsoy (65 vs 82%) and a slightly lower level (78 vs 82%) in the glasshouse experiment. However, Matara produced similar pod numbers per plant and seed yield as Amsoy (section 2.4.1.2). One factor which needs to be considered in this particular study is that Matara shares a similar genetic background with Amsoy ('Matara' = 'Amsoy' x 'Portage', Anderson, 1987). The main differences between these two varieties

occur in vegetative growth parameters, (e.g. shoot dry weight, leaf area), type of stem termination and plant maturity date. These differences are evident in the vegetative growth occurring during the late flowering period (Phase III in Figs. 2.19 and 2.20). Such data suggest there may be a relationship between type of stem termination and reproductive abortion in soybean.

Despite conclusions from the field study, reproductive abortion can occur at any stage of development as shown in sections 3.4.5 and 4.4.5. Moreover, it was found that competition is also exerted between ovules and young seeds at different positions within a pod (Chapter 3). It is evident that the basal ovule which should have priority in growth and development by being nearest to the pedicel shows a lower efficiency of fertilization and higher proportion of subsequent seed abortion. This again supports the suggestion that the hypothesis of nutrient deficiency cannot totally explain reproductive behaviour in soybean plants. Growth and development of ovules at the middle position or at the apical end may be triggered and advanced by fertilization which may occur prior to the basal position because they are near to the stigma. This may enhance their higher competitive ability which may also be mediated through hormonal action.

The rate of abortion at each stage may be affected by environmental conditions. Results from the third experiment clearly show that although reproductive abortion is altered according to the availability of assimilate supply at certain stages, plants of both cultivars show their flexibility in adjusting abortion rates at other stages. This compensation capacity results in combined reproductive abortion rates being constant. As discussed in section 4.5.4, the idea that assimilate supply completely controls reproductive abortion cannot be sustained, and other possibilities, including hormonal control, may be suggested to explain the control mechanisms involved.

5.2 SCOPE FOR FURTHER STUDY

Further studies aimed at improving soybean seed yield through a reduction in reproductive abortion might be directed to two main areas :

- i) Mechanical removal of competitive sinks
- ii) Growth regulator application

Although investigations into these areas of soybean research have been actively conducted for the past few decades [e.g. McAlister and Krobe, 1958; Hicks and Pendleton, 1969; Amuti, 1983 for (i) : and Hume et al., 1972; McCormick and Poll, 1979; Noodén and Noodén, 1985 for (ii)], there are still no satisfactory results in terms of soybean yield improvement. This may partly be because of the diversity of soybean growth habit and different cultivar responses to the environment. The results from the present study suggest that plant growth stage and the extent of crop manipulation are both extremely important and may well be specific in their response within a given soybean variety. Future studies thus need to be based on a clear understanding of growth morphology.

5.2.1 Mechanical manipulation

Plant growth stage is absolutely crucial in mechanical manipulation in soybean. Evidence from the present study clearly shows that partial reduction in competitive sinks by young leaf removal starting at growth stage R3 is most effective in enhancing pod set in the indeterminate Amsoy cultivar, but not in the semideterminate Matara. Further work might place emphasis on studies on mechanical manipulation at this growth stage both in the glasshouse and in the field. Results from this study also show that although the level of reproductive abortion occurring at some stages can be altered, the rate of combined reproductive abortion is remarkably constant between treatments. In Matara, for example, the percentage of reproductive abortion in early formed flowers (before growth stage R4) can be reduced by young leaf removal starting from growth stage R5 (Table 4.7). Therefore, it may be worth experimenting by completely reducing competitive sinks after growth stage R5. This may be done by mechanically removing young leaves and perhaps flowers produced after growth stage R5 to encourage photoassimilates to flow into reproductive structures formed before this stage.

Evidence also shows that leaves produced after growth stage R5 contribute very little to seed yield, especially in Amsoy plants. Mechanical alteration of plant structure, including topping (both the main stem and branches) of plants once this stage is reached may also be considered useful in determining the 'source-sink' relationship effects on reproductive growth in the field situation.

As the further studies suggested above employ fewer treatments, they should be done with more plant samples in each replicate (may be 5 to 10 plants per replicate). Young leaf removal experiments in the present study employed only one plant in each of 5 replicates because of the restriction in experimental area and labour, therefore, high variations as indicated by percentages of coefficient of variation were obtained and the level of probability <0.10 was used. Although the probability 0.10 is acceptable by statisticians in agricultural research, the results may be more obvious in terms of yield components and, in particular, yield if more plant samples were employed. Therefore, further studies might emphasize only one or two stages of development (R3 and perhaps R5) and, if needed, only one rate of YLR, i.e. 50%.

5.2.2 Chemical manipulation

As noted in section 5.1, it is very likely that hormones play an important role in controlling reproductive abortion. The roles of hormones in influencing reproductive development in soybean have been discussed by Noodén (1984), Noodén and Letham (1986) and Brenner *et al.* (1986). Hormonal balances in the whole plant system rather than changes in any single hormone probably control reproductive abortion in soybean (see section 4.2.3.2). In the following section, the role of hormones from different plant organs in relation to flower abortion is briefly discussed. Two basic approaches to the study of hormonal effect may be as follows :

- i) Pure research on hormone levels as affected by plant manipulation
- ii) Applied research on plant growth regulator application and crop management.

5.2.2.1 Hormonal changes as influenced by young leaf removal

Results from this study shows that reproductive development can be stimulated by young leaf removal (YLR). It is believed that the influence exerted by the young leaves is mediated by hormones. Aung and Byrne (1978) reported that either TIBA (an inhibitor of auxin transport) application to stem, petiole or hypocotyl or a direct application of cytokinin onto axillary buds gave the same result as young leaf removal in tomato seedlings in stimulating bud development. Moreover, there is some evidence that leaf removal increases cytokinin activity in the buds of Xanthium (Henson and Wareing, 1977) and aborting flowers have low levels of cytokinin activity and high levels of gibberellin activity (Leonard and Kinet, 1982). In soybean, it has been found that exogenous applications of cytokinins can promote flower development and pod set (Crosby et al., 1981; Carlson et al., 1987; Dyer et al., 1987).

Young leaves may be sources of auxins or gibberellins and perhaps other compounds (Sachs and Hackett, 1983) which promote their own sink activity and may possibly be detrimental to reproductive growth. Abdul and Harris (1978) found that a reduced number of flowers formed in the first inflorescence of tomato are associated with high GA-like activity in diffusates from young leaves. There is also some evidence that gibberellins may inhibit phloem unloading and sucrose accumulation in storage sink tissues in carrot in competition with shoot growth (Thomas, 1986). Further, auxins may inhibit leaf abscission depending on the timing and position of the auxin source (Davies, 1987). These effects of gibberellins and auxins produced by vegetative sinks seem to be detrimental to reproductive growth in soybean. This is supported by evidence that exogenous treatment of soybean leaves with gibberellins causes lower pod set (Birnberg and Brenner, 1987) and exogenous applications of auxin-transport inhibitors such as TIBA and morphactin can increase pod set (Noodén and Noodén, 1985), possibly through the diversion of photoassimilates between leaf growth and reproductive growth. The increase in pod set by YLR beginning at growth stage R3 in Amsoy in the present study may thus be a result of reduced endogenous levels of gibberellins and/or auxins and increased cytokinins during subsequent development. A study on changes in these hormone levels in

treated and untreated Amsoy would be most interesting. Comparisons using Matara where YLR at growth stage R3 was ineffective might prove a valuable reference. Results from this research may be helpful in understanding hormonal control in soybean reproductive development and also in supporting further applied research on the use of exogenous plant growth regulators in soybean production.

5.2.2.2 Further work in chemical manipulation

From the above discussion, it therefore seems likely that two groups of plant growth regulators have potential for enhancing reproductive development, i.e. auxin-transport inhibitors and cytokinins. TIBA was once considered promising in soybean yield improvement. However, its lack of consistent effectiveness under field conditions has resulted in it now not being used commercially (Peat and Jeffcoat, 1982). Other auxin-transport inhibitors have also been investigated (e.g. Dybing and Lay, 1981; Noodén and Noodén, 1985). Stutte and Davis (1983) reviewed the effects of 26 plant growth regulators (mostly growth retardants) on soybean seed yield and noted a wide range of yield response from negligible amounts (below 100 kg.ha^{-1}) to occasionally very impressive increases of over 800 kg.ha^{-1} . Once again, this reinforces the suggestion that future success with plant growth regulators in soybean depends on recognizing differences in the environmental conditions under which soybeans are grown, differences between growth types and varieties grown in different areas and even in the rates and times for applying given compounds.

Results from the present study suggest that further research should investigate the interaction between growth retardant application and planting density. McCormick and Poll (1979) studied TIBA application and plant density in soybean in New Zealand and found that yield response was related to environmental conditions especially water supply. In years when water supply was not limiting, yields were improved 16 to 20% with TIBA applied at the flowering stage at rate of 19 g.ha^{-1} . When crop growth was limited by water supply, yield was similar or reduced depending upon the stage of water deficit and the rate of TIBA application. The importance of plant density and planting pattern in the yield response to TIBA was not well defined because of inconsistent results between years. However, they found that Amsoy

soybean, in a highly productive year, gave a yield increase due to TIBA application at the beginning of flowering stage (10% flowering) only in low density (20 plants.m⁻²). In lower productive years, yield was increased only in high density (40 plants.m⁻²) plantings. However, they did not vary the stage of plant growth at which TIBA was applied. Based on the results of the present study, TIBA may be effective in low density (20 plants.m⁻²), if it was applied at later stages when intraplant competition is higher.

It is likely, again from the results of the present study, that soybean seed yield from plant densities ranging from 5.8 to 23.8 plants.m⁻² may be increased by growth retardants and/or cytokinins because at these densities, plants exhibit intraplant competition during the mid-flowering to late-flowering periods (Phases II and III in Figs. 2.19 and 2.20). Time of application may be expected to be at the beginning of Phase II; and at the beginning of Phase III in medium (23.8 plants.m⁻²) and low (5.8 plants.m⁻²) densities, respectively. Application may even be extended to plants at higher densities (e.g. 40 plants.m⁻²), but at very high plant densities (i.e. 61.2 plants.m⁻²), yield might not be significantly increased by the use of growth retardants because in this study, soybean plants showed very low intraplant competition.

Further study might also concentrate on the potential of auxin-transport inhibitors or topping (or young leaf removal) combined with subsequent exogenous cytokinin application, especially at growth stage R3 in Amsoy soybean, because auxin-transport inhibitors at this stage might reduce the competitive impact of new vegetative growth due to new leaf initiation and subsequent cytokinin application may enhance pod set (Crosby, et al., 1981; Carlson et al., 1987; Dyer et al., 1987) and prolong leaf duration (Noodén and Letham, 1986). This might enhance soybean seed yields as a result of reduced reproductive abortion, and take advantage of the longer leaf duration of Amsoy. Once again, in both this study and the one suggested in the previous paragraph, a comparison between Amsoy and the responses of the semideterminate Matara may be a valuable approach.

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APPENDICES

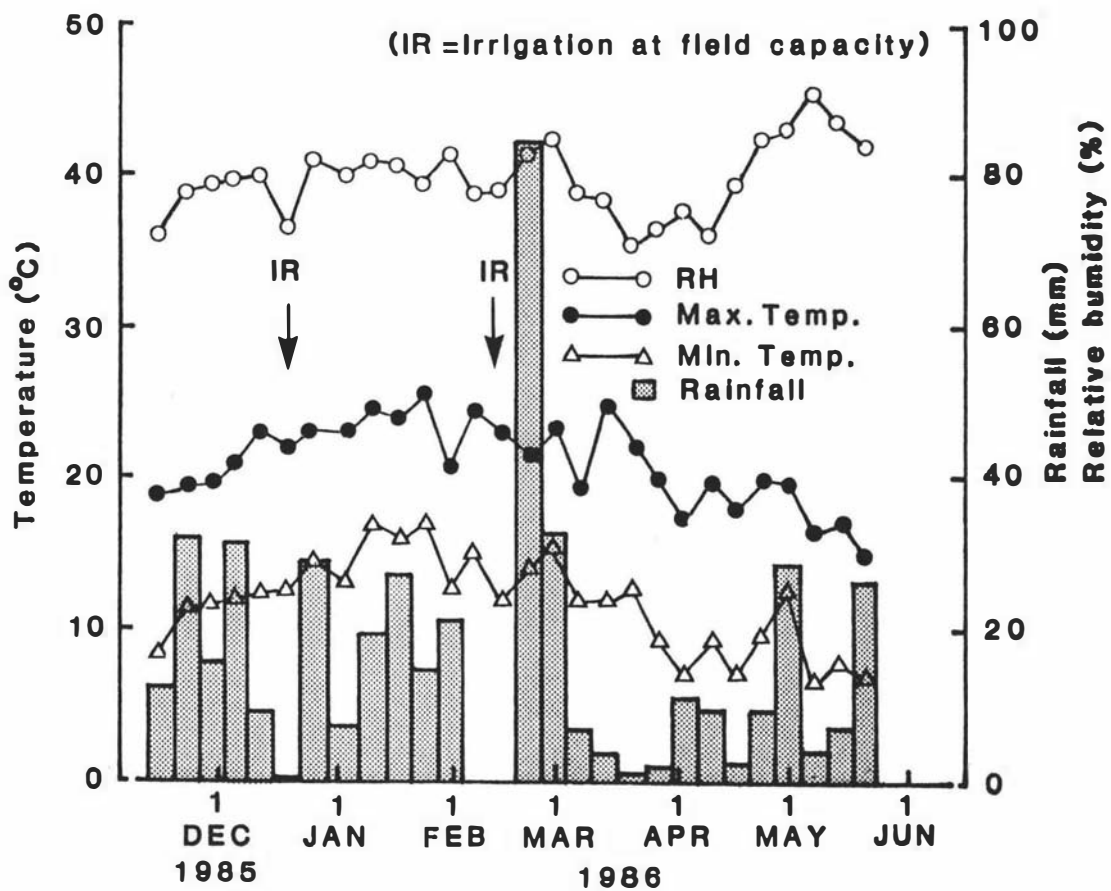
APPENDIX 1 SOIL ANALYSIS OF THE EXPERIMENTAL FIELD (M AND H LABORATORIES LIMITED AND NEW ZEALAND SOIL TESTING SERVICE 1980 LIMITED)

| Element | Figure Obtained | Element | Figure Obtained |
|-----------|-----------------|--------------|-----------------|
| pH | 5.4 | Nitrate | 15.0 |
| Calcium | 515.0 | Phosphorus A | 14.3 |
| Magnesium | 3.4 | Phosphorus B | 20.0 |
| Potassium | 36.0 | Iron | 5.0 |
| Ammonium | 0.5 | Manganese | 5.0 |

Explanation of figures : pH....measured in water, Magnesium, Potassium, Ammonia, Nitrate, Iron, Manganese ... parts per million measured in the soil extract determined according to the improved method of Morgan-Venema.

Phosphorus A.....parts per million measured in Sodium Bicarbonate solution of pH 8.5 (half hour Olsen method)

Phosphorus B.....parts per million soluble in diluted Sulphuric Acid (method Beater)



APPENDIX 2 CLIMATIC CONDITIONS AT DSIR RESEARCH STATION
 PALMERSTON NORTH, NEW ZEALAND
 (1.5 KM FROM THE FIELD SITE)

APPENDIX 3

NELDER'S SPACING RADIAL DESIGN

According to Bleasdale (1967), it was taken as an axiom that the nature of a response to a variable is best established by determining the effect of a large number of wide-ranging values of the variables, even though some of these values may seem to be ridiculous when viewed in the light of current practice. Thus, it was required to study the effect on yield of a large range of plant densities, each grown at a large range of patterns of arrangement. Based on this background, Nelder (1962) subsequently developed a series of designs for spacing experiments, using grids which could be defined by the intersections of sets of parallel or concurrent straight lines and the arcs of concentric circles. Plants are grown in rows which radiate from a point, with the distance between plants along a radius approximately equal to the distance between radii at that point, allowing a large range of plant densities to be grown in a small area (see Fig. A3.1). Further, guard plants are only needed around the outer edge and inner edge of a group of plants arranged in this systematic manner.

Bleasdale (1967) presented an expanded form of calculations to enable an experimenter to layout the design in the field. The following information is used to determine the distance between each plant along the radii and the distance required between each radius.

- a. Number of plant densities used
- b. Area per plant at the lowest density
- c. Area per plant at the highest density

The parameters used in these calculations are presented diagrammatically in Fig. A3.2. There is also a constant, α which takes a values of less than 1.111, if α should exceed this value, then the deviation of squareness of the plant spacing will exceed the 5% allowed by Nelder (1962) and the range of spacings should be decreased, or the number of densities increased so that the value of α is made less than 1.111 again.

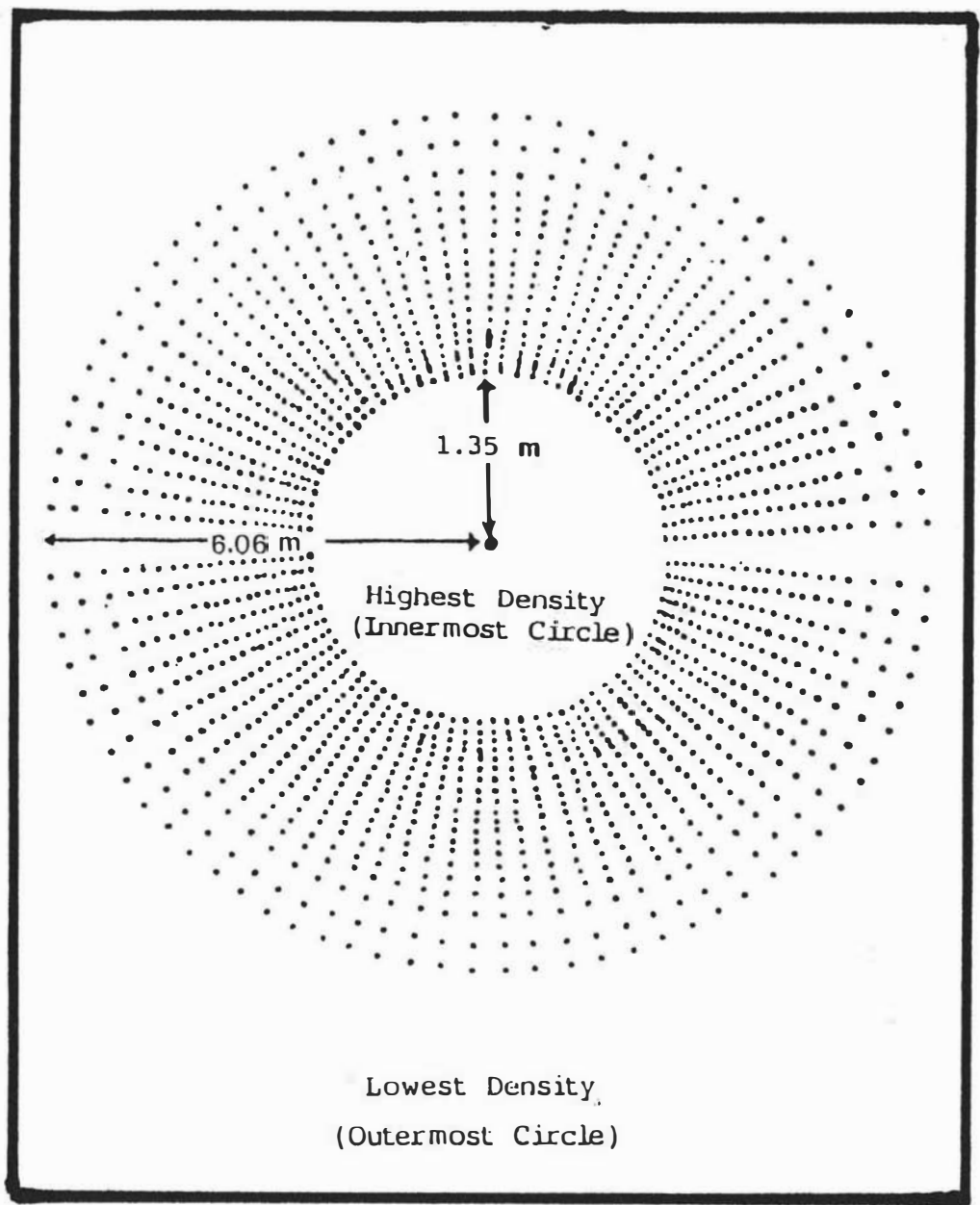


Fig. A3.1 The layout of the Nelder radial spacing design

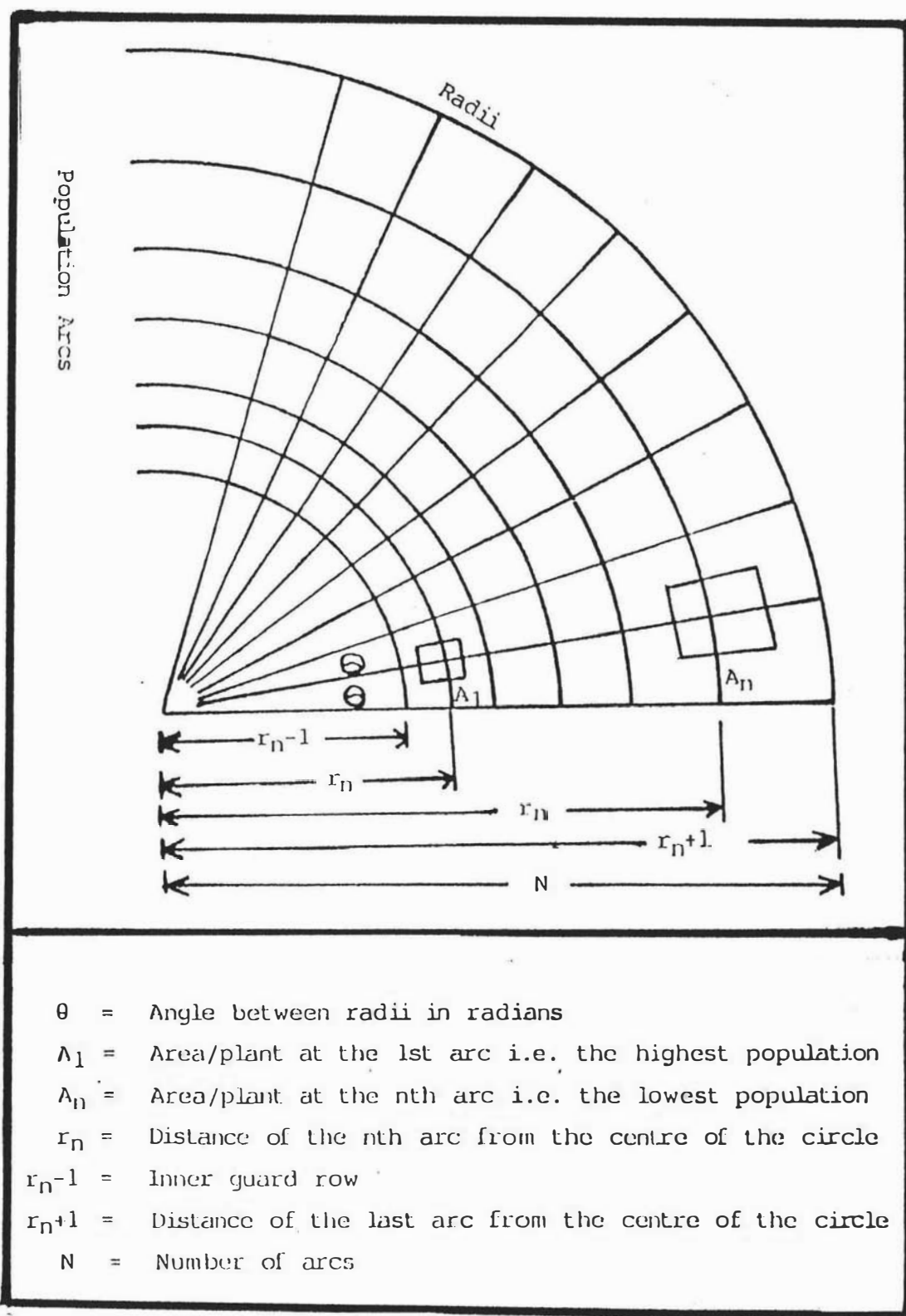


Fig. A3.2 A diagrammatic representation of Nelder's radial design (Type 1a)

The sequential steps in calculating dimensions for the radial design are as follows :

- a) Calculate the value of the constant α which governs the rate of change of spacing.

In this experiment the constant α was derived using the equation :

$$(2N - 2) \log \alpha = \log A_n - \log A_1$$

- b) Calculate the angle between radii (θ) using the equation below :

$$\theta = r(\alpha - 1)/\sqrt{\alpha}$$

r is the rectangularity of plant arrangement so that in a 'square' arrangement, $r = 1$

The value of θ is converted from radians to degrees using a standard mathematical table. The angle between radii determines the number of radii in a circle.

- c) Calculate spacings of the plants along a radius measured from the centre of the circle using the equations for r_0 . This measures the distance of the first plants from the centre of the circle.

$$r_0 = \sqrt{2A/(\theta(\alpha^3 - \alpha))}$$

r_0 is the distance of the first plant from the centre of the circle. This is a row of guard plants, and the experimental plants are in row r_1 .

Thereafter, the distance of the second plant from the centre is calculated using the formula :

$$r_1 = r_0 \times \alpha$$

The formula for the third plant is

$$r_2 = r_1 \times \alpha$$

and so on until the distance of the last plant is calculated $r_n + 1$. (Note that the value r_0 refers to the distance from the centre of the circle to the first actual plants in the circle. These are guard plants and are not experimental plants).

- d) Calculate the population densities per hectare per arc of the lowest and highest densities. This can be done by calculating the area per plant using the formula :

$$A_n = r_n^2 \theta (\alpha^2 - 1) / 2\alpha$$

Lastly, calculate the area of the experimental plot. The experimental plot is laid out depending on the number of arcs and the spacing between them which is equivalent to the length of the radii.

The data calculated for the experiment are given in Table A3.1. An α value of 1.111 was used which means that each successive plant population was 14.6% higher the last population.

The rectangularity was maintained at 1.0 and the angle between successive radii was 4.5 degrees.

Table A3.1 Numerical data for 4.5 degree radial layout

| | Arcs | | Areas | | |
|----|---------------------------------|-------------------|---------------------------------|---------------------------------|-----------------------------|
| | Distance along radii (metre) | Increment (cm) | Per plant (cm ²) | Increment (cm ²) | Plant per m ² |
| 1 | 1.35 | | 119.22 | | 83.88 |
| 2 | 1.47 | 11.13 | 139.61 | 20.3 | 71.63 |
| 3 | 1.59 | 12.04 | 163.48 | 23.87 | 61.17 |
| 4 | 1.71 | 13.03 | 191.29 | 27.81 | 52.28 |
| 5 | 1.86 | 14.09 | 223.87 | 32.58 | 44.67 |
| 6 | 2.01 | 15.24 | 262.06 | 38.19 | 38.16 |
| 7 | 2.18 | 16.49 | 306.90 | 44.34 | 32.58 |
| 8 | 2.35 | 17.85 | 359.35 | 52.45 | 27.83 |
| 9 | 2.55 | 19.31 | 420.70 | 61.35 | 23.77 |
| 10 | 2.76 | 20.90 | 492.51 | 71.81 | 20.30 |
| 11 | 2.98 | 22.61 | 577.51 | 84.00 | 17.34 |
| 12 | 3.23 | 24.46 | 674.89 | 98.39 | 14.82 |
| 13 | 3.49 | 26.46 | 790.05 | 115.16 | 12.66 |
| 14 | 3.78 | 28.63 | 925.02 | 134.97 | 10.81 |
| 15 | 4.09 | 30.99 | 1083.01 | 158.00 | 9.24 |
| 16 | 4.42 | 35.53 | 1267.78 | 184.77 | 7.89 |
| 17 | 4.79 | 36.27 | 1484.30 | 216.51 | 6.74 |
| 18 | 5.18 | 39.24 | 1737.65 | 253.35 | 5.75 |
| 19 | 5.60 | 42.47 | 2034.22 | 296.58 | 4.92 |
| 20 | 6.06 | 45.95 | 2381.51 | 347.28 | 4.20 |

APPENDIX 4

CURVE FITTING TECHNIQUE

Several equations were used to test their fitness for explaining the relationship between vegetative growth and plant density of field grown soybeans in the first experiment. Some of the equations are shown below :

$$\begin{array}{ll} y = 1/(a+bx) & \dots\dots\dots 1 \\ y = a+bx+cx^2 & \dots\dots\dots 2 \\ y = a+b(\log x) & \dots\dots\dots 3 \\ y = a+b(\log x)+c(\log x)^2 & \dots\dots\dots 4 \\ \log y = a+bx & \dots\dots\dots 5 \\ \text{and } \ln y = a+bx+cx^2 & \dots\dots\dots 6 \end{array}$$

The criteria used to select the best relationship were R^2 values and visual examination of curve in relation to the plotted data. Residuals are also plotted against variable x to test the fitness of the equations examined.

Data on changes in shoot dry weight with density for Amsoy are presented as an example. Table A4.1 shows R^2 values of each equation.

Table A4.1 R² values of equations examined the fitness for explaining the response of shoot dry weight of field grown Amsoy soybean to planting densities

| Equation | R ² values | | | |
|-----------------------------------|-----------------------|--------|--------|--------|
| | 30 DAE | 50 DAE | 70 DAE | 90 DAE |
| (1) $y = 1/(a+bx)$ | 64.9 | 86.5 | 74.2 | 88.2 |
| (2) $y = a+bx+cx^2$ | 48.4 | 92.0 | 83.8 | 72.3 |
| (3) $y = a+b(\log x)$ | 43.2 | 92.4 | 83.7 | 75.1 |
| (4) $y = a+b(\log x)+c(\log x)^2$ | 47.7 | 92.6 | 89.0 | 77.6 |
| (5) $\log y = a+bx$ | 57.4 | 85.0 | 74.2 | 78.2 |
| (6) $\ln y = a+bx+cx^2$ | 57.6 | 91.7 | 90.9 | 82.2 |

There are many equations where R^2 values are considerably high in all growth stages in Table A4.1. Although, equation (1) has been previously used to explain the response of plant growth to plant density in birdsfoot trefoil (Lotus corniculatus L.), using a radial spacing design by McGraw et al. (1986), this equation was not the best to explain the response in this experiment. This equation is a asymptotic model and may be used successfully in radial spacing trials with enough border arcs. In the study presented in Chapter 2, the equations that showed higher R^2 values, especially after plants reached 50 DAE are parabolic models, such as equations (2), (4), and (6).

In most cases, unusual observations indicated by regression analysis were found for plants grown at 71.6 plants.m⁻² (see also figures in Appendix 5). Agronomically, this can be explained in that plants grown at this density were subjected to border effects and had an advantage in competition for light and growth factors by being near to the innermost area. It was decided that the equation with best fitness for all data should be used, but predicted values of plants grown at 71.6 plants.m⁻² must not be used in interpretation.

All the equations were further plotted with observed data to examine their fitness. Plots of residuals from every equation were also considered. To illustrate this, the plotted curves of predicted and observed values and the plots of residuals from equations (1), (2), and (6) for shoot dry weight of Amsoy at 70 DAE are shown here for comparison (Figs. A4.1 and A4.2). It can be seen that equation (6) is the best fit to the observed data (Fig. A4.1c) and also shows no systematic variations in the plot of residuals (Fig. A4.2c).

It was found that equation (6) is the best equation for explaining the relationship between every parameter of vegetative growth and plant density for every sampling date in both Matara and Amsoy cultivars.

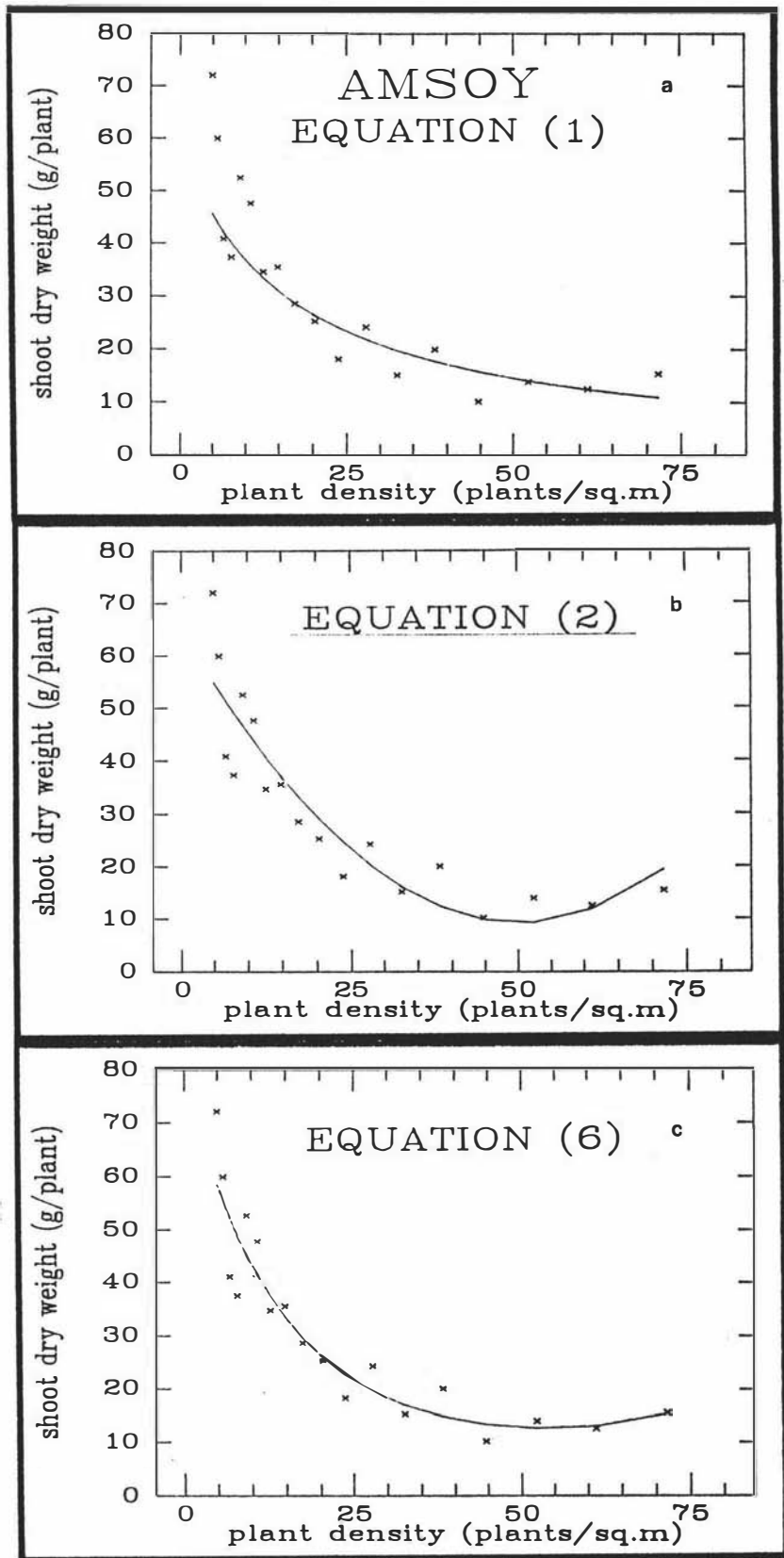


Fig. A4.1 Plotted curves of predicted and observed values from : (a) equation (1), (b) equation (2), and (c) equation (6); data are shoot dry weight of Amsoy at 70 DAE

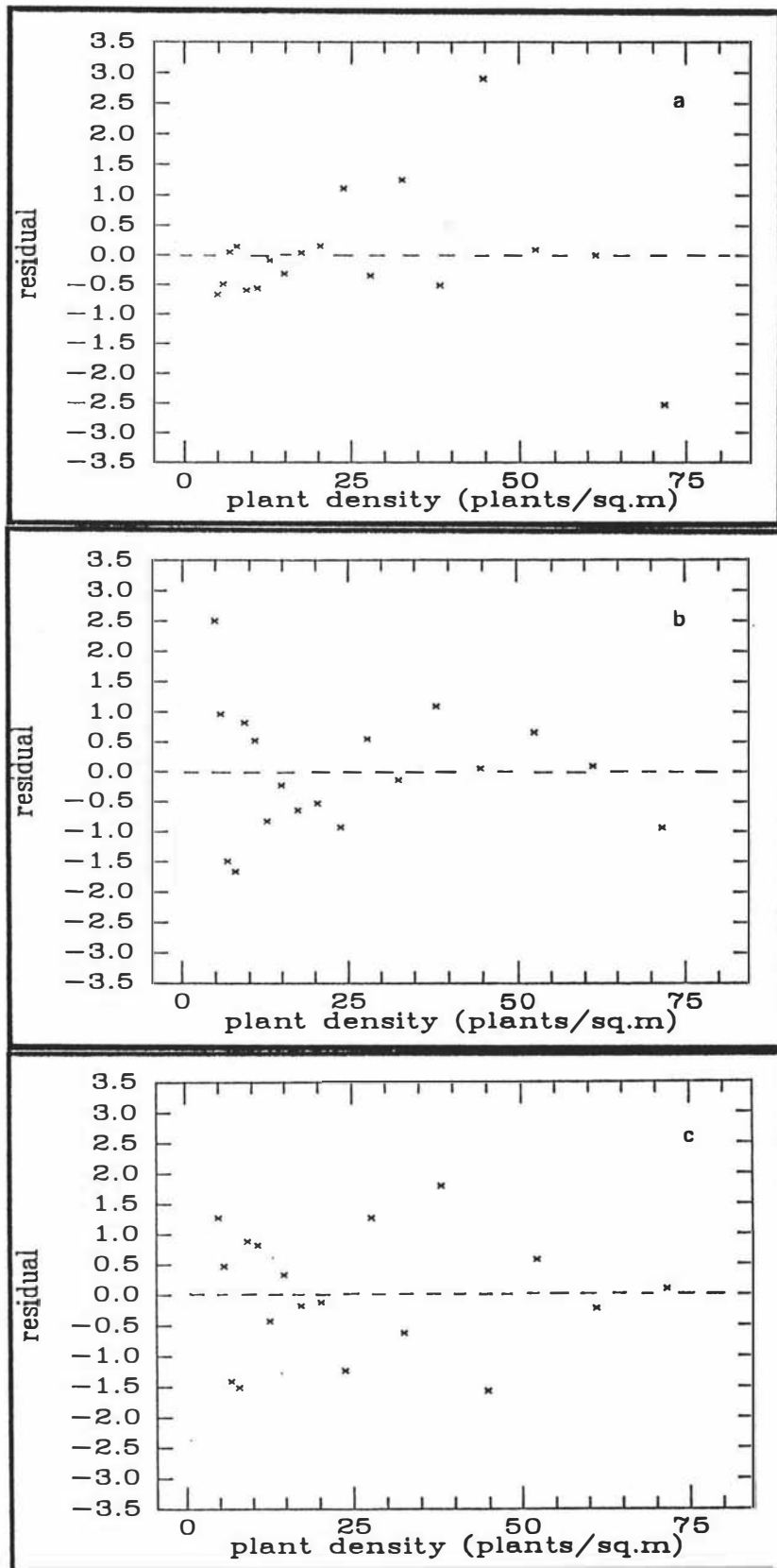


Fig. A4.2 Plots of residuals from : (a) equation (1), (b) equation (2), and (c) equation (6); data are shoot dry weight of Amsoy at 70 DAE

APPENDIX 5

GRAPHS SHOWING MODELS, R^2 VALUES AND THE RESPONSE OF VEGETATIVE GROWTH OF MATARA AND AMSOY SOYBEAN AS AFFECTED BY A WIDE RANGE OF PLANT DENSITIES

The chosen relationship is equation (6), the quadratic exponential equation. Data presented in Figs. 2.2-2.3 and Figs. 2.6-2.10 in Chapter 2 are the values predicted from the curves.

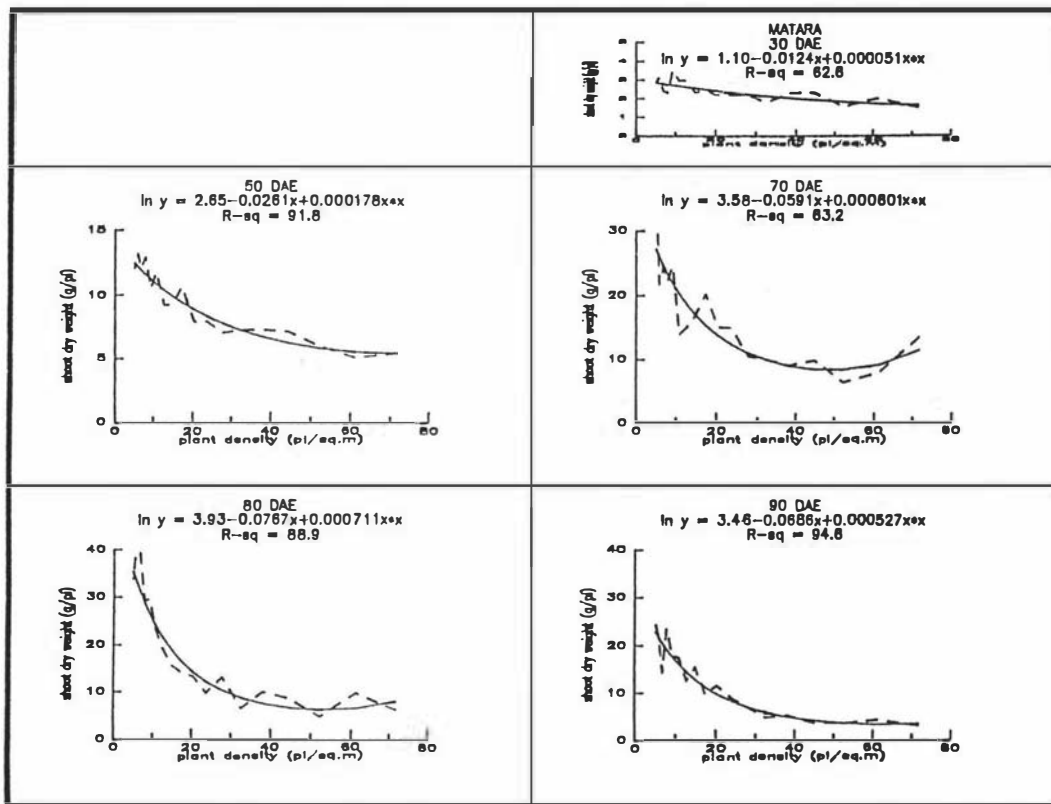


Fig. A5.1 Predicted values derived from quadratic exponential equations and observed values of shoot dry weight of Matara soybean at the five sampling dates

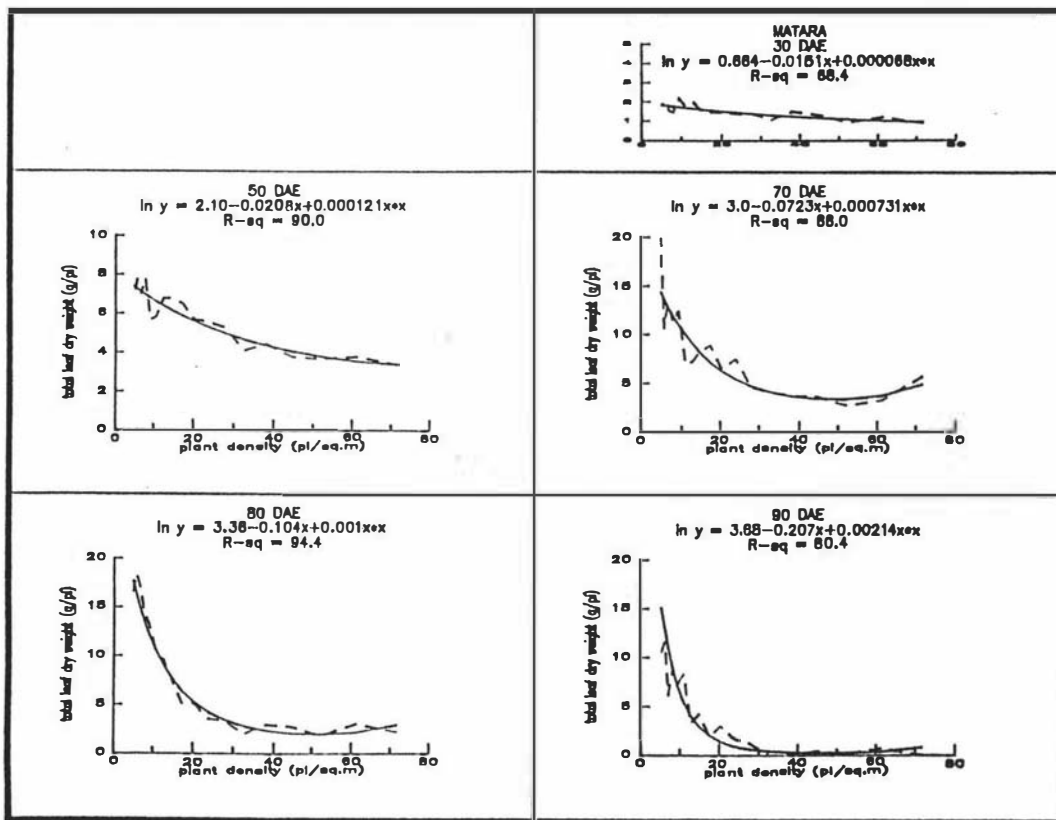


Fig. A5.2 Predicted values derived from quadratic exponential equations and observed values of total leaf dry weight of Matara soybean at the five sampling dates

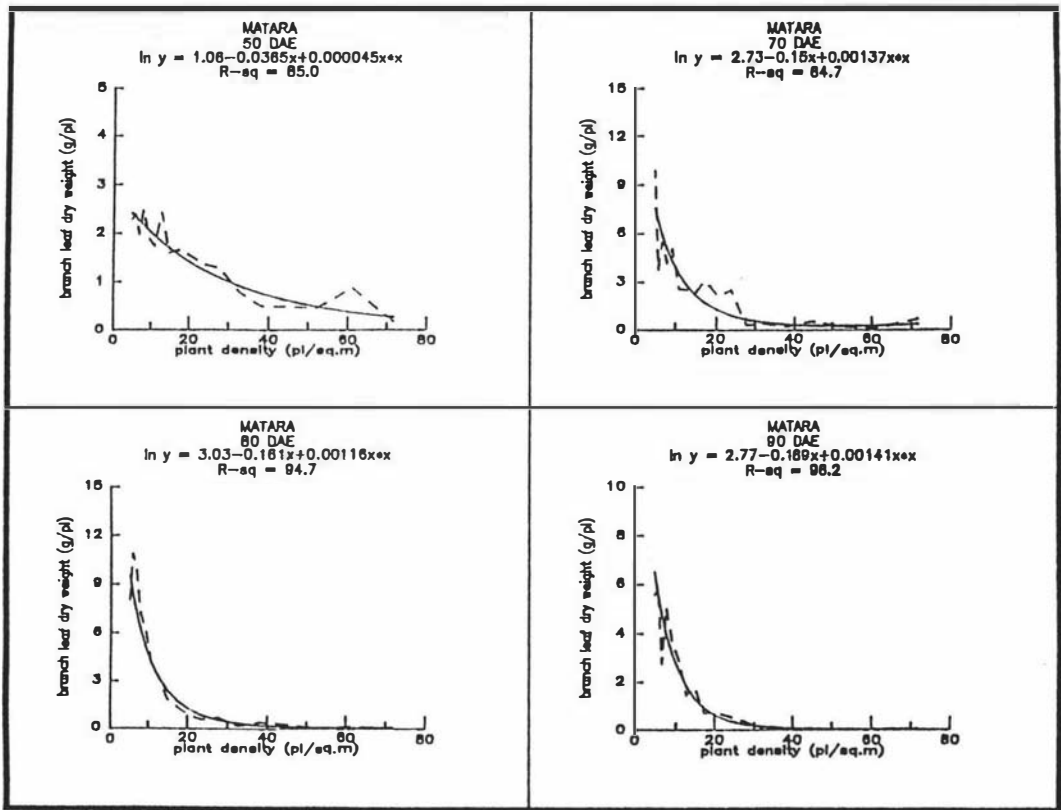


Fig. A5.3 Predicted values derived from quadratic exponential equations and observed values of branch leaf dry weight of Matara soybean at the four sampling dates

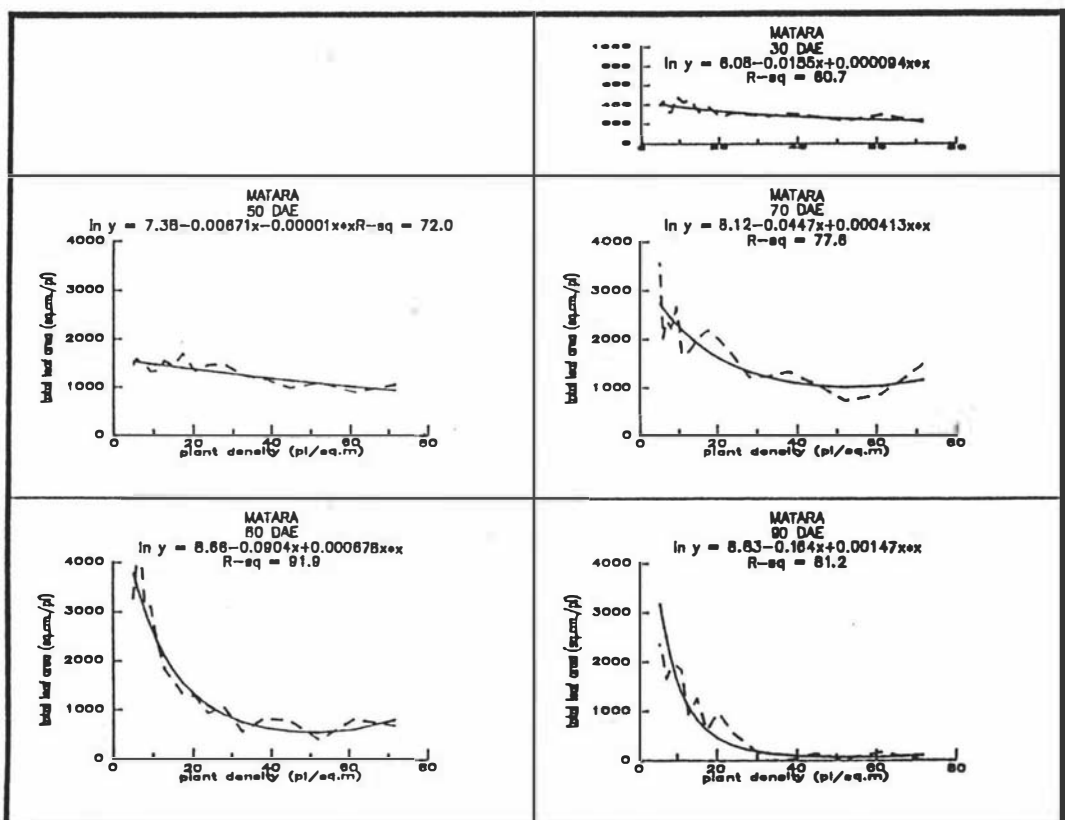


Fig. A5.4 Predicted values derived from quadratic exponential equations and observed values of total leaf area of Matara soybean at the five sampling dates

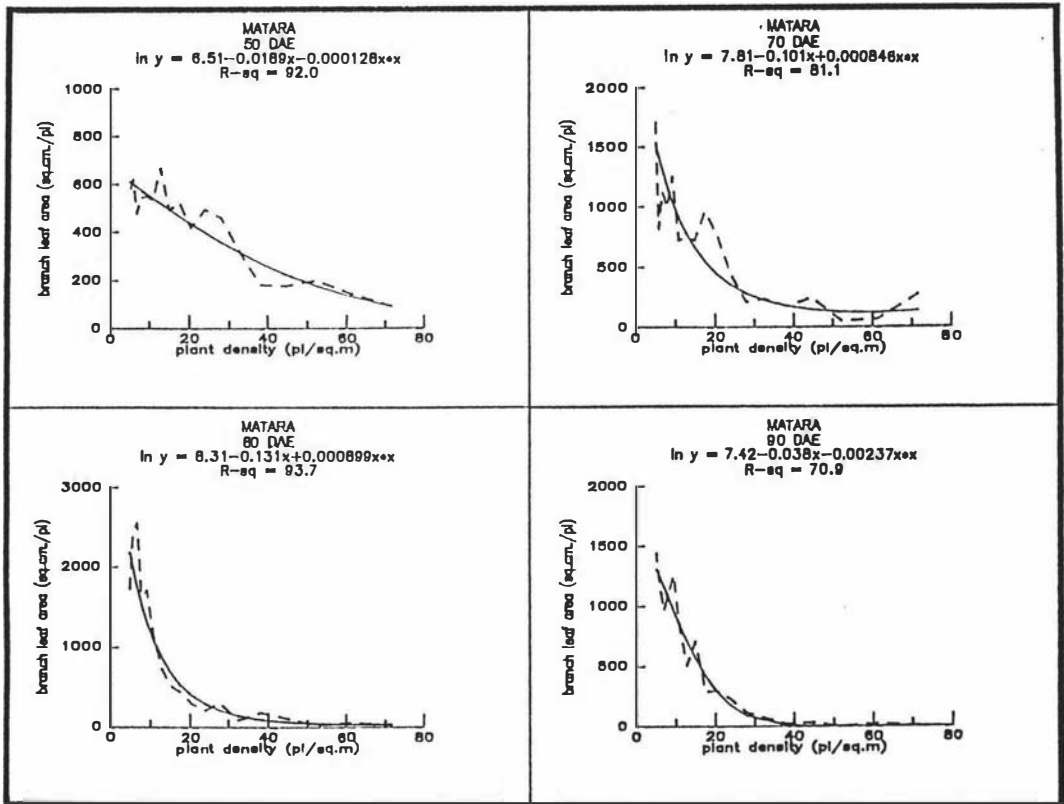


Fig. A5.5 Predicted values derived from quadratic exponential equations and observed values of branch leaf area of Matara soybean at the four sampling dates

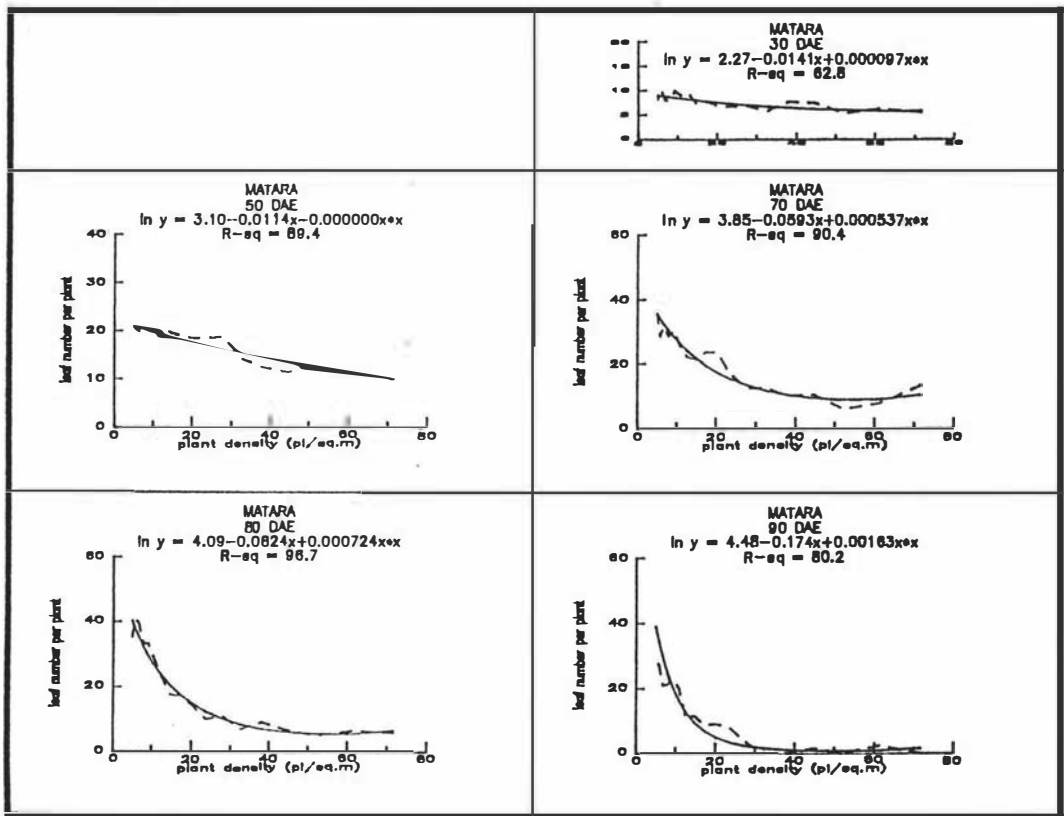


Fig. A5.6 Predicted values derived from quadratic exponential equations and observed values of leaf number per plant of Matara soybean at the five sampling dates

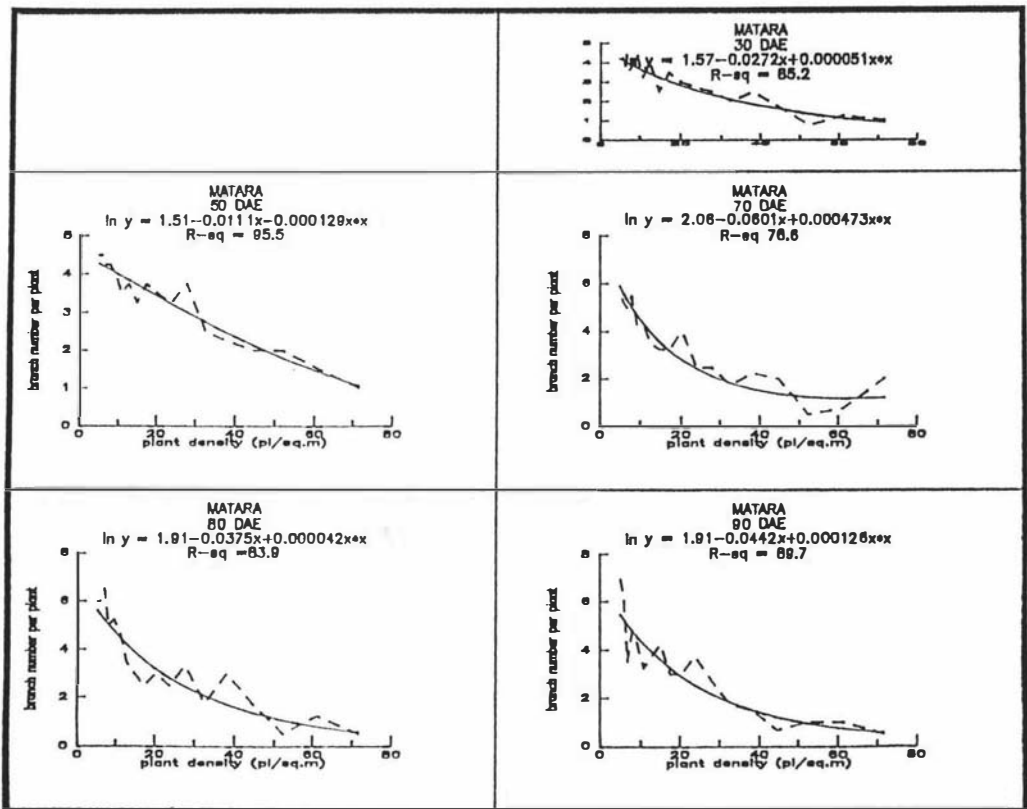


Fig. A5.7 Predicted values derived from quadratic exponential equations and observed values of branch number per plant of Matara soybean at the five sampling dates

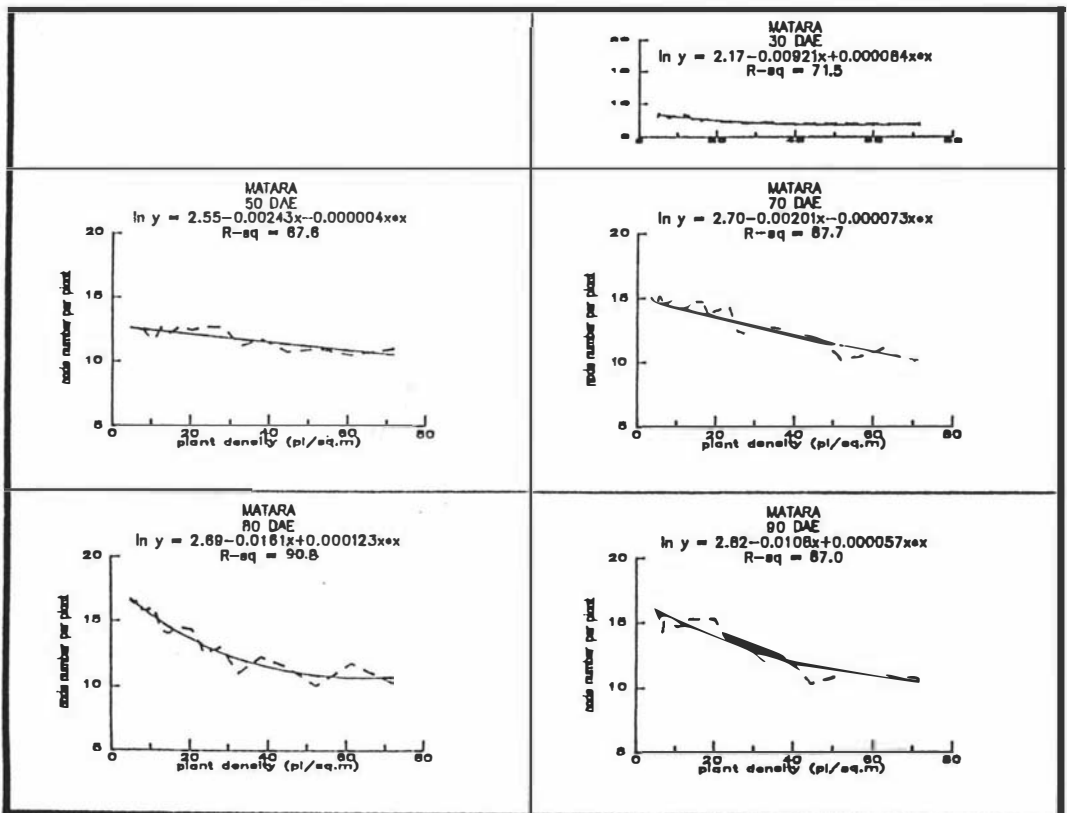


Fig. A5.8 Predicted values derived from quadratic exponential equations and observed values of node number per plant of Matara soybean at the five sampling dates

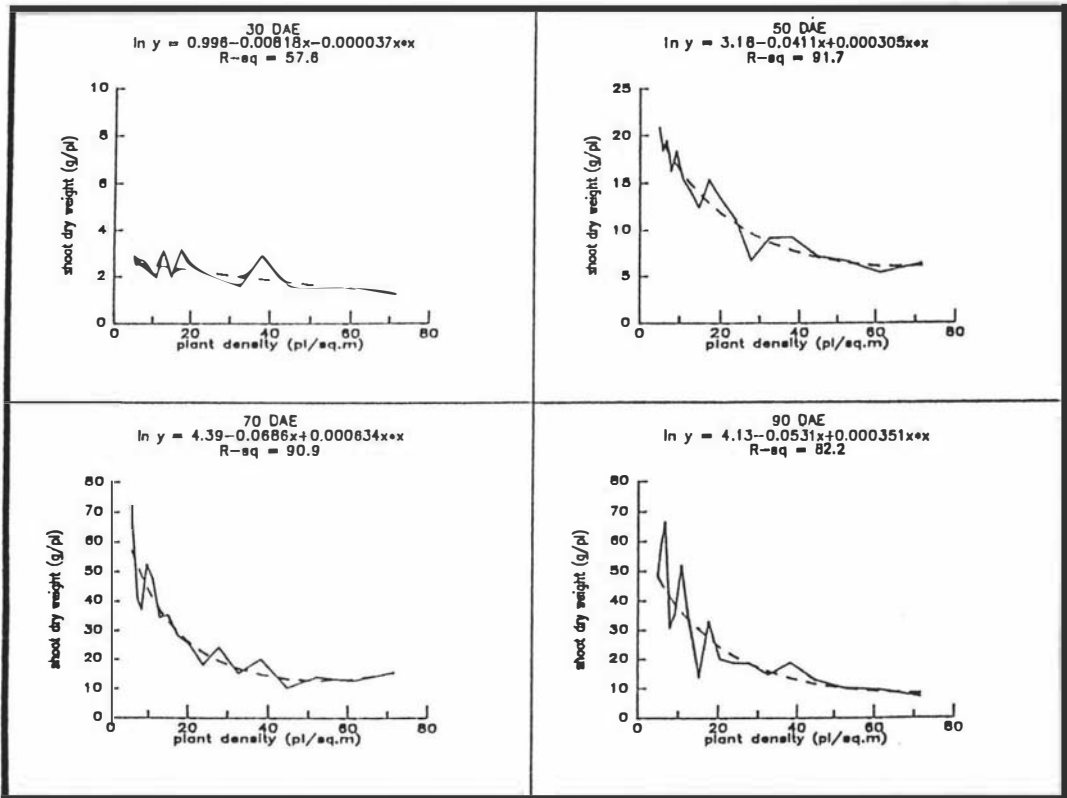


Fig. A5.9 Predicted values derived from quadratic exponential equations and observed values of shoot dry weight per plant of Amsoy soybean at the four sampling dates

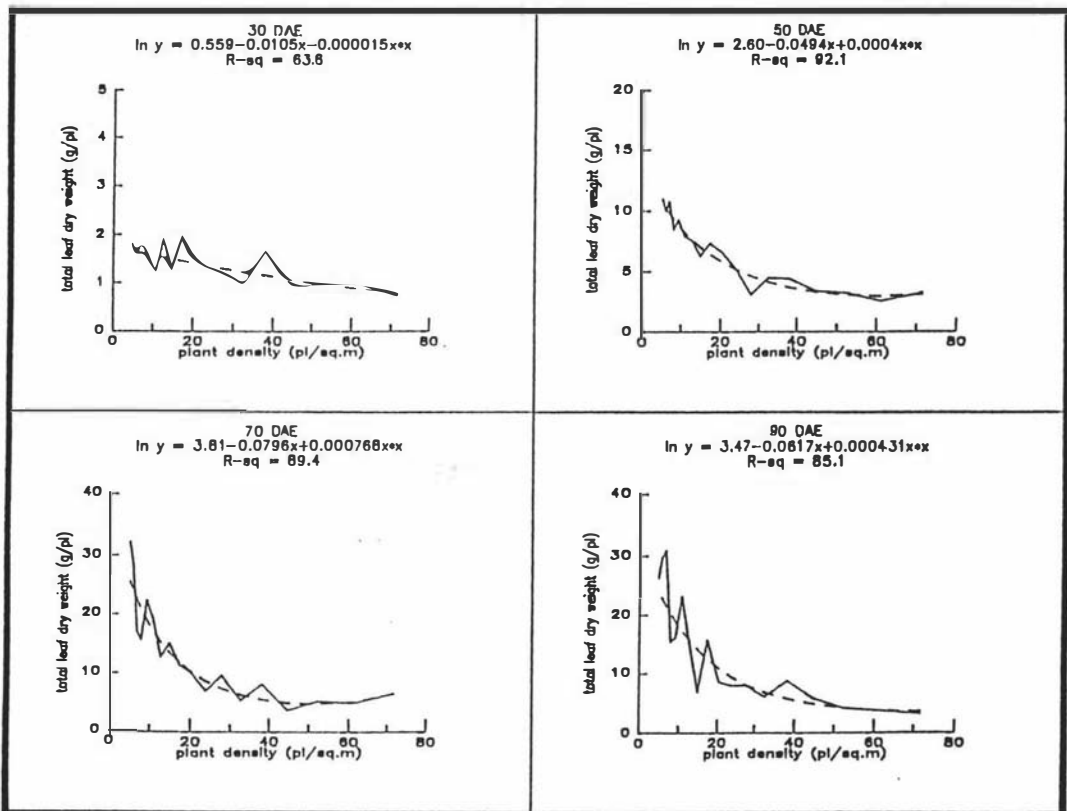


Fig. A5.10 Predicted values derived from quadratic exponential equations and observed values of total leaf dry weight per plant of Amsoy soybean at the four sampling dates

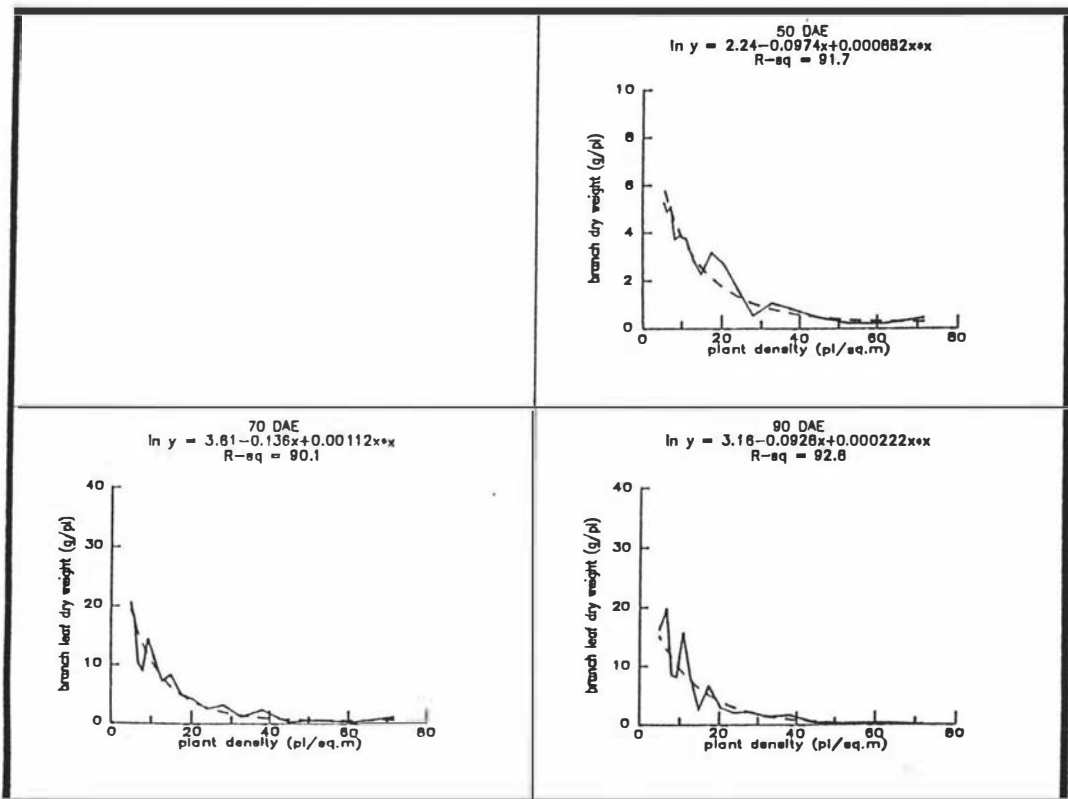


Fig. A5.11 Predicted values derived from quadratic exponential equations and observed values of branch leaf dry weight per plant of Amsoy soybean at the three sampling dates

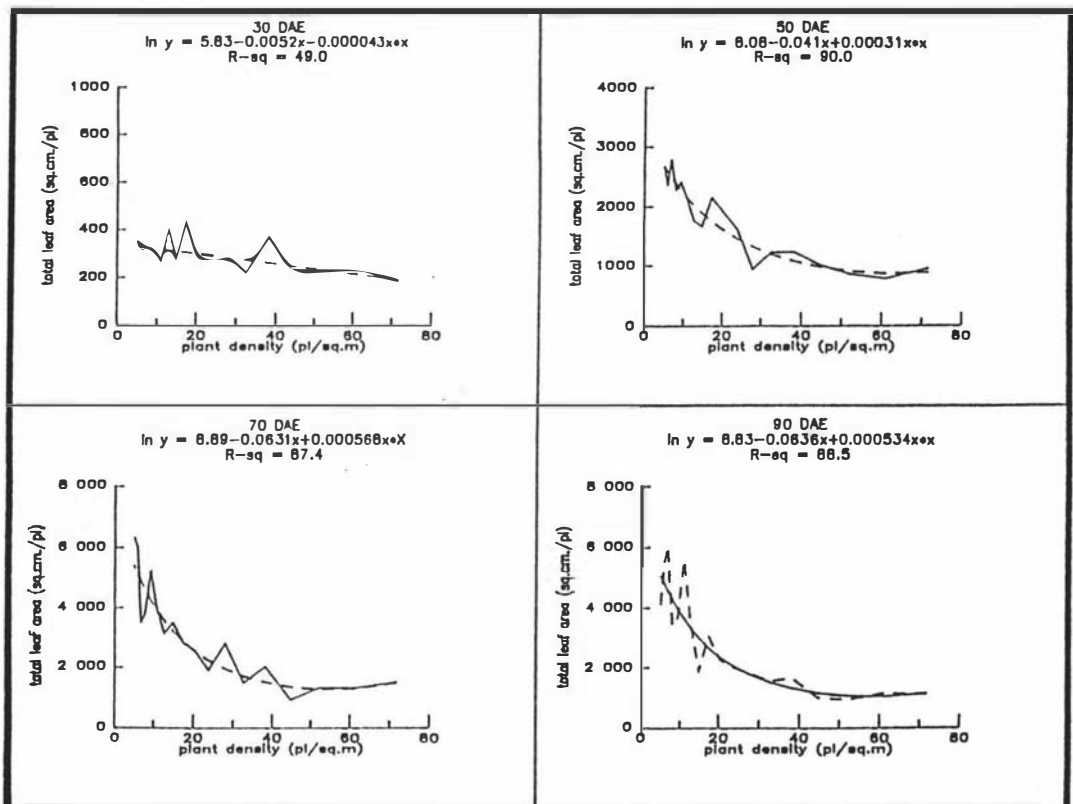


Fig. A5.12 Predicted values derived from quadratic exponential equations and observed values of total leaf area per plant of Amsoy soybean at the four sampling dates

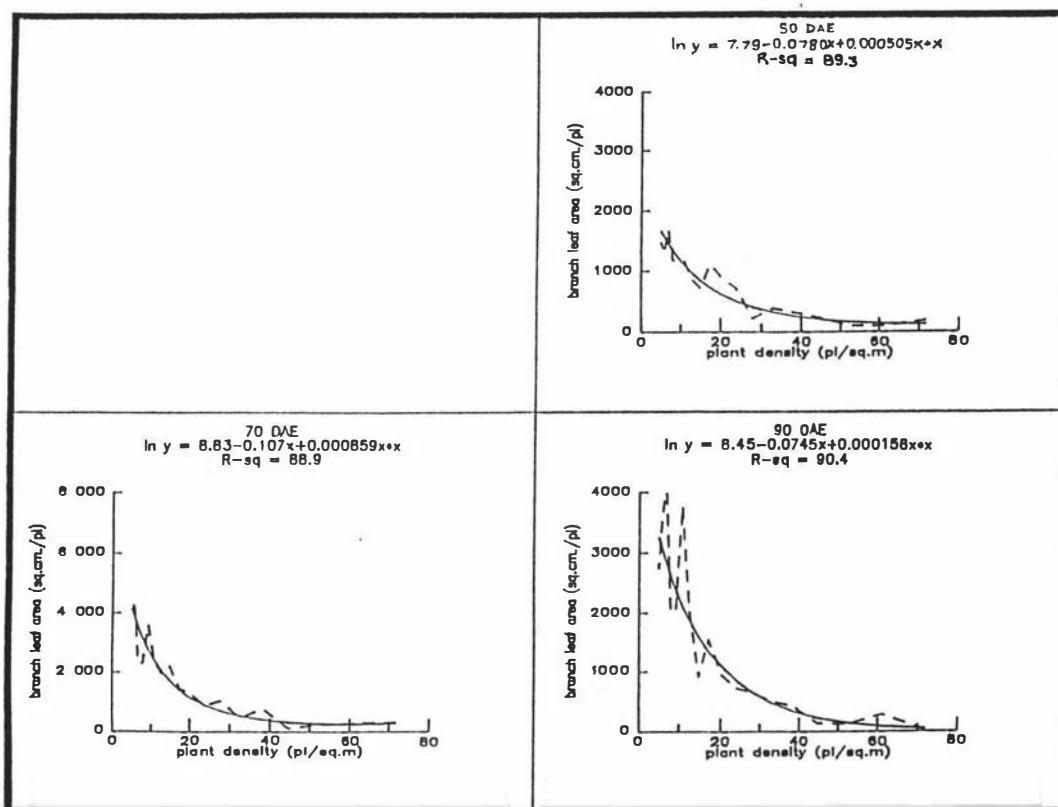


Fig. A5.13 Predicted values derived from quadratic exponential equations and observed values of branch leaf area per plant of Amsoy soybean at the three sampling dates

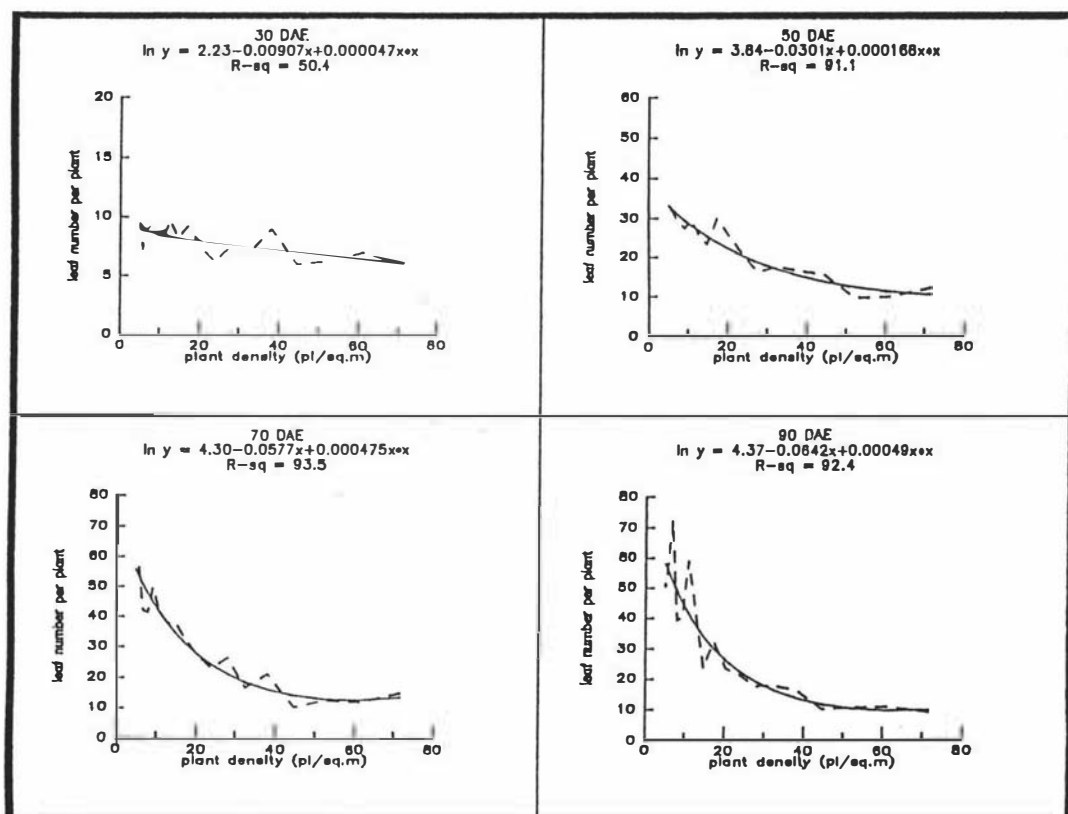


Fig. A5.14 Predicted values derived from quadratic exponential equations and observed values of leaf number per plant of Amsoy soybean at the four sampling dates

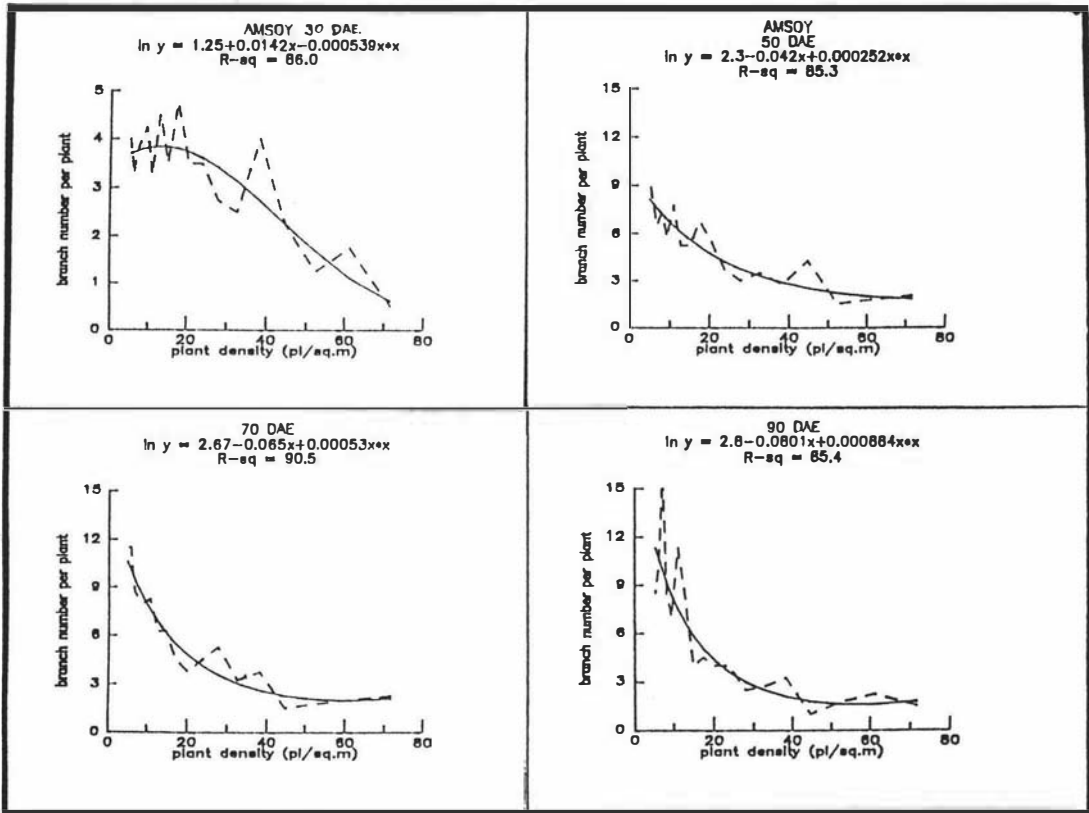


Fig. A5.15 Predicted values derived from quadratic exponential equations and observed values of branch number per plant of Amsoy soybean at the four sampling dates

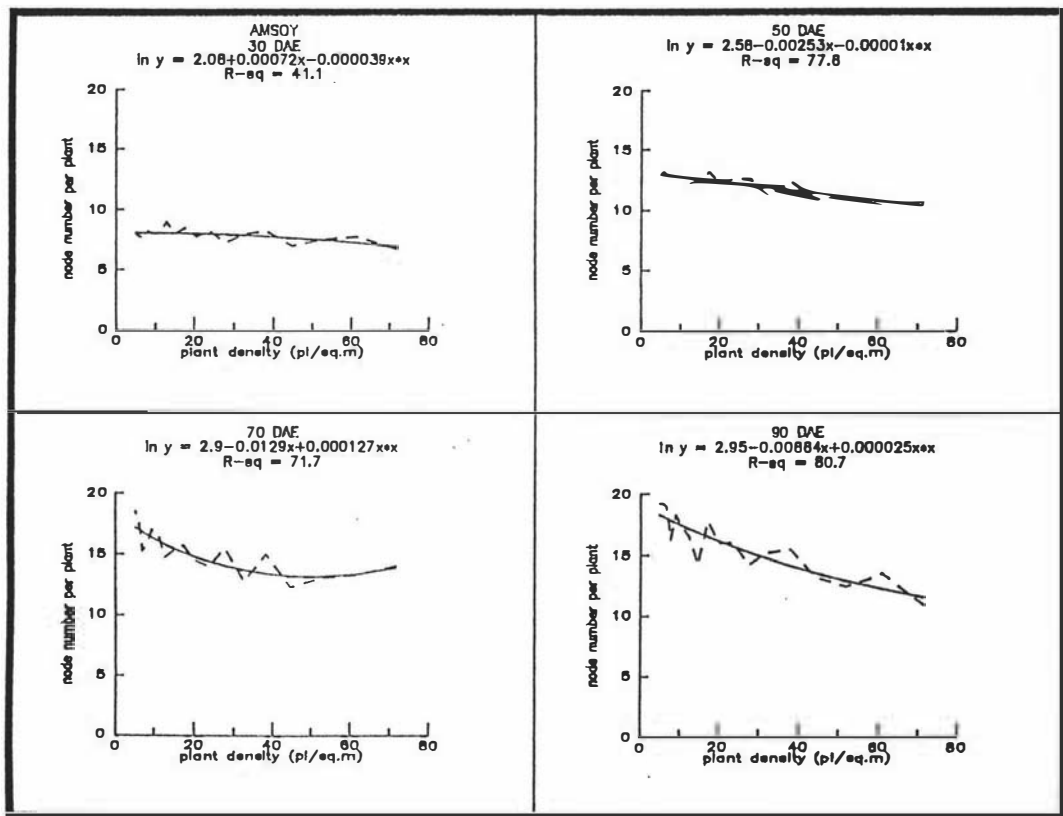
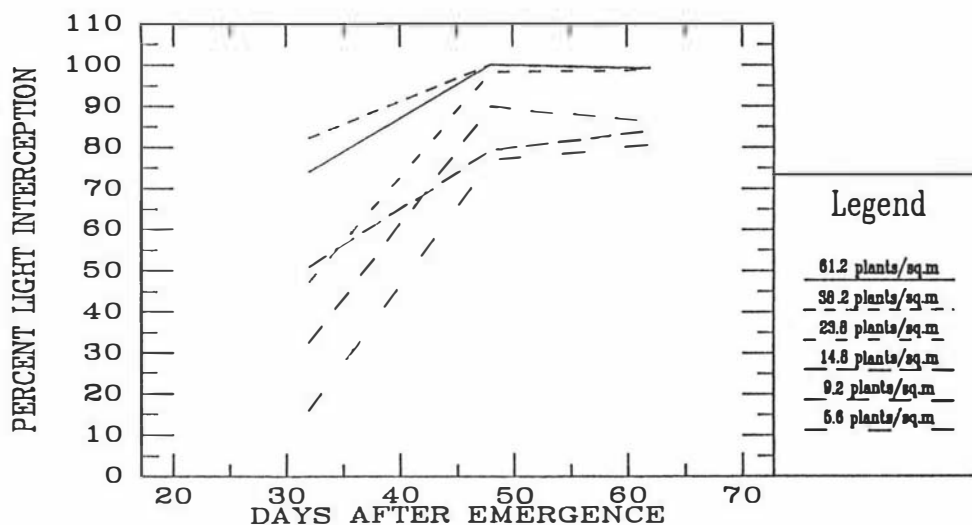
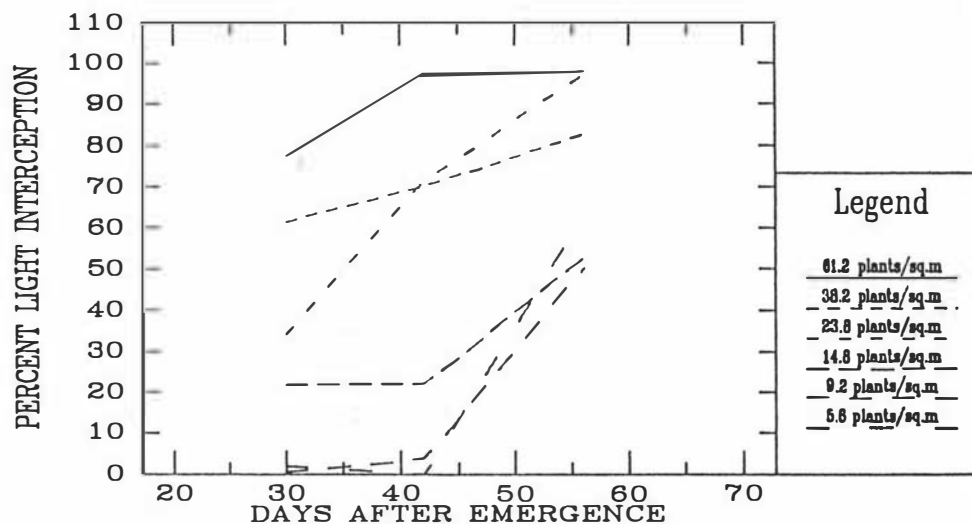


Fig. A5.16 Predicted values derived from quadratic exponential equations and observed values of node number per plant of Amsoy soybean at the four sampling dates

MATARA



AMSOY

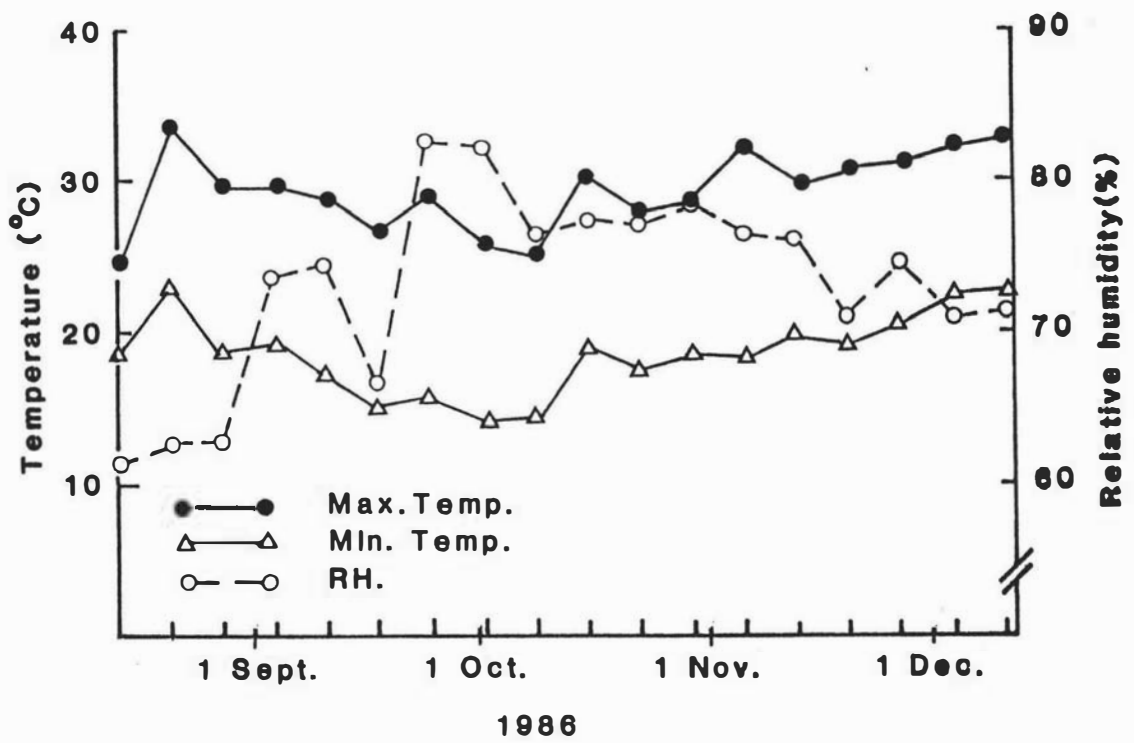


APPENDIX 6 PERCENT LIGHT INTERCEPTION OF PLANTS GROWN AT DIFFERENT PLANT DENSITIES (MEASURED BETWEEN PLANTS OF THE SAME DENSITY BETWEEN 12:00 TO 2 PM) AT 32, 48 AND 62 DAE FOR MATARA AND AT 30, 42 AND 56 DAE FOR AMSOY

APPENDIX 7 POD NUMBER PER NODE AT DIFFERENT PLANT PARTS (TOP, MIDDLE AND BOTTOM) OF PLANTS GROWN AT 61.2, 23.8 AND 5.8 PLANTS.M⁻² (VAR. AMSOY)

| Plant part | Plant density (plants.m ⁻²) | | |
|------------|---|------|------|
| | 61.2 | 23.8 | 5.8 |
| Top | 1.14 | 1.00 | 0.61 |
| Middle | 1.75 | 2.56 | 3.11 |
| Bottom | 0.69 | 1.00 | 1.91 |

Mean values calculated from pod number at each plant part divided by node number of the same part based on plant height (data from Fig. 2.5)



APPENDIX 8 MAXIMUM AND MINIMUM TEMPERATURES AND RELATIVE HUMIDITY IN THE GLASSHOUSE

APPENDIX 9 MODIFIED HALF-STRENGTH HOAGLAND'S NUTRIENT SOLUTION (G/L)

| | Molecular weight (g) | Conc. | Final solution | | ppm |
|---|----------------------|--------|----------------|----------|-----------------|
| STOCK SOLUTION A | | | | | |
| Calcium nitrate $\text{Ca}(\text{NO}_3)_2 \cdot 4\text{H}_2\text{O}$ | 236.15 | 295.19 | .59038 | Ca N | 100.20 70.04 |
| Sequestrene 330 10% DTPA NaFe | 468.20 | 10.4 | .0208 | Fe Na | 2.08 1.02 |
| STOCK SOLUTION B | | | | | |
| Potassium phosphate KH_2PO_4 | 136.08 | 34.02 | .06804 | K P | 19.55 15.49 |
| Potassium nitrate KNO_3 | 101.11 | 126.39 | .25278 | K N | 97.75 35.02 |
| Magnesium sulfate $\text{MgSO}_4 \cdot 7\text{H}_2\text{O}$ | 246.5 | 123.24 | .24648 | Mg S | 24.32 32.06 |
| Boric acid H_3BO_3 | 61.82 | 0.715 | .00143 | B | 0.250 |
| Manganese chloride $\text{MnCl}_2 \cdot 4\text{H}_2\text{O}$ | 197.92 | 0.4525 | .000905 | Mn Cl | 0.251 0.324 |
| Zinc sulfate $\text{ZnSO}_4 \cdot 7\text{H}_2\text{O}$ | 287.55 | 0.055 | .000110 | Zn S | 0.025 0.012 |
| Copper sulfate $\text{CuSO}_4 \cdot 5\text{H}_2\text{O}$ | 249.68 | 0.020 | .00004 | Cu S | 0.010 0.005 |
| Sodium molybdate $\text{Na}_2\text{MoO}_4 \cdot 2\text{H}_2\text{O}$ | 241.93 | 0.0067 | .0000134 | Na Mo | 0.003 0.005 |
| Potassium chloride KCl | 74.56 | 1.575 | .00315 | K Cl | 1.652 1.498 |

| Nutrient | ppm | Nutrient | ppm |
|----------|--------|----------|-------|
| N | 105.06 | B | 0.250 |
| P | 15.49 | Mn | 0.251 |
| K | 118.95 | Cu | 0.010 |
| S | 32.08 | Zn | 0.025 |
| Ca | 100.20 | Mo | 0.005 |
| Fe | 2.08 | Cl | 1.822 |
| Mg | 24.32 | Na | 1.023 |

APPENDIX 10 REPRODUCTIVE DEVELOPMENTAL STAGES AS DESCRIBED BY FEHR AND
CAVINESS (1977)

| Stage No. | Abbreviated stage title | Description |
|-----------|-------------------------|---|
| R1 | Beginning bloom | One open flower at any node on the main stem |
| R2 | Full bloom | One flower at one of the two uppermost nodes on the main stem with a fully developed leaf |
| R3 | Beginning pod | Pod 5 mm (3/16 inch) long at one of the four uppermost nodes on the main stem with a fully developed leaf |
| R4 | Full pod | Pod 2 cm (3/4 inch) long at one of the four uppermost nodes on the main stem with a fully developed leaf |
| R5 | Beginning seed | Seed 3 mm (1/8 inch) long in a pod at one of the four uppermost nodes on the main stem with a fully developed leaf |
| R6 | Full seed | Pod containing a green seed that fills the pod cavity at one of the four uppermost nodes on the main stem with a fully developed leaf |
| R7 | Beginning maturity | One normal pod on the main stem that has reached its mature pod colour |
| R8 | Full maturity | Ninety-five percent of the pods that have reached their mature pod colour. |

APPENDIX 11 PROPORTIONS OF DEVELOPED FLOWERS TO FLOWER BUDS AS AFFECTED
 BY YOUNG LEAF REMOVAL OBSERVED AT 56 DAP FOR MATARA AND 61
 DAP FOR AMSOY

| | Matara | Amsoy |
|---------|---------|--------|
| Control | 0.55 a* | 0.77 a |
| R1-50 | 0.58 a | 0.80 a |
| R1-100 | 0.51 a | 0.68 a |
| R3-50 | 0.51 a | 0.85 a |
| R3-100 | 0.62 a | 0.80 a |
| R5-50 | 0.63 a | 0.81 a |
| R5-100 | 0.63 a | 0.83 a |
| average | 0.58 | 0.79 |
| CV (%) | 12.3 | 11.4 |

* Mean values within a column followed by the same letter are not significantly different at probability .10

APPENDIX 12

ANALYSES OF VARIANCE IN SPLIT BLOCK DESIGN
FOR DATA FROM THE FIELD EXPERIMENT

TABLE A12.1 ANOVA FOR FLOWERING PERIOD (DAYS)

| SOURCE | df | SS | MS | F VALUE | PR>F |
|-------------------|----|---------|-------|---------|--------|
| MODEL | 32 | 1447.17 | 45.22 | 4.35 | 0.002 |
| ERROR | 15 | 155.81 | 10.39 | | |
| CORRECTED TOTAL | 47 | 1602.98 | | | |
| | | | | | |
| BLOCK | 3 | 103.40 | | 3.32 | 0.05 |
| VARIETY | 1 | 553.52 | | 53.29 | 0.0001 |
| BLOCK x VARIETY | 3 | 49.56 | | 1.59 | 0.23 |
| DENSITY | 5 | 531.10 | | 8.61 | 0.0005 |
| BLOCK x DENSITY | 15 | 184.98 | | 1.19 | 0.37 |
| VARIETY x DENSITY | 5 | 24.60 | | 0.49 | 0.79 |

TABLE A12.2 ANOVA FOR FLOWER NUMBER PER PLANT (SQUARE ROOT TRANSFORMED DATA)

| SOURCE | df | SS | MS | F VALUE | PR>F |
|-------------------|----|---------|-------|---------|--------|
| MODEL | 32 | 1064.32 | 33.26 | 25.56 | 0.0001 |
| ERROR | 15 | 19.52 | 1.30 | | |
| CORRECTED TOTAL | 47 | 1083.84 | | | |
| | | | | | |
| BLOCK | 3 | 2.18 | | 0.56 | 0.65 |
| VARIETY | 1 | 345.44 | | 265.43 | 0.0001 |
| BLOCK x VARIETY | 3 | 4.35 | | 1.11 | 0.37 |
| DENSITY | 5 | 691.03 | | 106.19 | 0.0001 |
| BLOCK x DENSITY | 15 | 17.55 | | 0.90 | 0.58 |
| VARIETY x DENSITY | 5 | 3.78 | | 0.58 | 0.71 |

TABLE A12.3 ANOVA FOR REPRODUCTIVE ABORTION PERCENTAGE (ARCSINE TRANSFORMED DATA)

| SOURCE | df | SS | MS | F VALUE | PR>F |
|-------------------|----|-------|--------|---------|--------|
| MODEL | 32 | 1.068 | 0.033 | 5.23 | 0.0007 |
| ERROR | 15 | 0.096 | 0.0064 | | |
| CORRECTED TOTAL | 47 | 1.163 | | | |
| | | | | | |
| BLOCK | 3 | 0.028 | | 0.45 | 0.74 |
| VARIETY | 1 | 0.710 | | 34.12 | 0.010 |
| BLOCK x VARIETY | 3 | 0.062 | | 2.69 | 0.08 |
| DENSITY | 5 | 0.091 | | 2.11 | 0.12 |
| BLOCK x DENSITY | 15 | 0.130 | | 1.36 | 0.28 |
| VARIETY x DENSITY | 5 | 0.046 | | 1.45 | 0.26 |

TABLE A12.4 ANOVA FOR SEED YIELD PER PLANT (G PLANT⁻¹)

| SOURCE | df | SS | MS | F VALUE | PR>F |
|-------------------|----|---------|--------|---------|--------|
| MODEL | 32 | 8896.48 | 278.02 | 13.66 | 0.0001 |
| ERROR | 15 | 305.31 | 20.35 | | |
| CORRECTED TOTAL | 47 | 9201.79 | | | |
| | | | | | |
| BLOCK | 3 | 306.90 | | 1.65 | 0.35 |
| VARIETY | 1 | 178.34 | | 2.87 | 0.19 |
| BLOCK x VARIETY | 3 | 186.19 | | 3.05 | 0.06 |
| DENSITY | 5 | 8015.81 | | 152.17 | 0.0001 |
| BLOCK x DENSITY | 15 | 158.03 | | 0.52 | 0.89 |
| VARIETY x DENSITY | 5 | 51.21 | | 0.50 | 0.77 |

TABLE A12.5 ANOVA FOR SEED YIELD PER UNIT AREA (G M⁻²)

| SOURCE | df | SS | MS | F VALUE | PR>F |
|-------------------|----|-----------|----------|---------|--------|
| MODEL | 32 | 749352.60 | 23417.27 | 4.13 | 0.0026 |
| ERROR | 15 | 85080.41 | 5672.03 | | |
| CORRECTED TOTAL | 47 | 834433.01 | | | |
| | | | | | |
| BLOCK | 3 | 68029.73 | | 1.57 | 0.34 |
| VARIETY | 1 | 111762.15 | | 7.76 | 0.07 |
| BLOCK x VARIETY | 3 | 43211.77 | | 2.54 | 0.10 |
| DENSITY | 5 | 415503.91 | | 29.10 | 0.0001 |
| BLOCK x DENSITY | 15 | 42835.56 | | 0.50 | 0.90 |
| VARIETY x DENSITY | 5 | 68009.48 | | 2.40 | 0.09 |

TABLE A12.6 ANOVA FOR POD NUMBER PER PLANT

| SOURCE | df | SS | MS | F VALUE | PR>F |
|-------------------|----|----------|---------|---------|--------|
| MODEL | 32 | 33363.98 | 1042.62 | 23.97 | 0.0001 |
| ERROR | 15 | 652.39 | 43.49 | | |
| CORRECTED TOTAL | 47 | 34016.37 | | | |
| BLOCK | 3 | 277.18 | | 0.85 | 0.55 |
| VARIETY | 1 | 756.05 | | 6.95 | 0.08 |
| BLOCK x VARIETY | 3 | 326.22 | | 2.50 | 0.10 |
| DENSITY | 5 | 31251.48 | | 195.36 | 0.0001 |
| BLOCK x DENSITY | 15 | 479.90 | | 0.74 | 0.72 |
| VARIETY x DENSITY | 5 | 273.16 | | 1.26 | 0.33 |

TABLE 12.7 ANOVA FOR SEED NUMBER PER POD

| SOURCE | df | SS | MS | F VALUE | PR>F |
|-------------------|----|-------|-------|---------|--------|
| MODEL | 32 | 3.364 | 0.105 | 14.37 | 0.0001 |
| ERROR | 15 | 0.110 | 0.007 | | |
| CORRECTED TOTAL | 47 | 3.474 | | | |
| BLOCK | 3 | 0.698 | | 0.98 | 0.51 |
| VARIETY | 1 | 1.875 | | 7.71 | 0.07 |
| BLOCK x VARIETY | 3 | 0.710 | | 32.37 | 0.0001 |
| DENSITY | 5 | 0.031 | | 1.31 | 0.31 |
| BLOCK x DENSITY | 15 | 0.070 | | 0.64 | 0.80 |
| VARIETY x DENSITY | 5 | 0.030 | | 0.82 | 0.56 |

TABLE A12.8 ANOVA FOR SEED DRY WEIGHT (G 100SEEDS⁻¹)

| SOURCE | df | SS | MS | F VALUE | PR>F |
|-------------------|----|---------|-------|---------|-------|
| MODEL | 32 | 78.733 | 2.460 | 0.62 | 0.88 |
| ERROR | 15 | 59.871 | 3.991 | | |
| CORRECTED TOTAL | 47 | 138.605 | | | |
| BLOCK | 3 | 8.235 | | 0.73 | 0.60 |
| VARIETY | 1 | 16.697 | | 4.47 | 0.12 |
| BLOCK x VARIETY | 3 | 11.213 | | 0.94 | 0.45 |
| DENSITY | 5 | 18.235 | | 5.27 | 0.005 |
| BLOCK x DENSITY | 15 | 10.375 | | 0.17 | 1.00 |
| VARIETY x DENSITY | 5 | 13.978 | | 0.70 | 0.63 |

TABLE 12.9 ANOVA FOR AIR-DRIED SEED GERMINATION PERCENTAGE (ARCSIN TRANSFORMED DATA)

| SOURCE | df | SS | MS | F VALUE | PR>F |
|-------------------|----|-------|-------|---------|-------|
| MODEL | 32 | 0.778 | 0.024 | 2.92 | 0.015 |
| ERROR | 15 | 0.125 | 0.008 | | |
| CORRECTED TOTAL | 47 | 0.902 | | | |
| BLOCK | 3 | 0.061 | | 8.26 | 0.058 |
| VARIETY | 1 | 0.304 | | 123.41 | 0.002 |
| BLOCK x VARIETY | 3 | 0.007 | | 0.30 | 0.828 |
| DENSITY | 5 | 0.236 | | 5.49 | 0.005 |
| BLOCK x DENSITY | 15 | 0.129 | | 1.03 | 0.474 |
| VARIETY x DENSITY | 5 | 0.040 | | 0.96 | 0.470 |

TABLE 12.10 ANOVA FOR SEED MOISTURE CONTENT PERCENTAGE

| SOURCE | df | SS | MS | F VALUE | PR>F |
|-------------------|----|--------|-------|---------|--------|
| MODEL | 32 | 366.78 | 11.46 | 3.21 | 0.010 |
| ERROR | 15 | 53.59 | 3.57 | | |
| CORRECTED TOTAL | 47 | 420.37 | | | |
| BLOCK | 3 | 33.94 | | 3.17 | 0.055 |
| VARIETY | 1 | 18.75 | | 5.25 | 0.037 |
| BLOCK x VARIETY | 3 | 108.84 | | 10.16 | 0.0007 |
| DENSITY | 5 | 109.52 | | 6.13 | 0.003 |
| BLOCK x DENSITY | 15 | 60.17 | | 1.12 | 0.4127 |
| VARIETY x DENSITY | 5 | 35.56 | | 1.99 | 0.139 |

APPENDIX 13

ANALYSES OF VARIANCE IN COMPLETELY RANDOMIZED DESIGN (CRD)
FOR DATA FROM THE YOUNG LEAF REMOVAL EXPERIMENT

TABLE A13.1 ANOVA FOR LEAF NUMBER PER PLANT AT GROWTH STAGE R6 OF MATARA

| SOURCE | DF | SS | MS | F VALUE | PR > F |
|-----------------|----|--------|-------|---------|--------|
| YLR | 6 | 553.14 | 92.19 | 10.58 | 0.0001 |
| ERROR | 28 | 244.00 | 8.71 | | |
| CORRECTED TOTAL | 34 | 797.14 | | | |

TABLE A13.2 ANOVA FOR LEAF NUMBER PER PLANT AT GROWTH STAGE R6 OF AMSOY

| SOURCE | DF | SS | MS | F VALUE | PR > F |
|-----------------|----|--------|--------|---------|--------|
| YLR | 6 | 726.97 | 121.16 | 35.34 | 0.0001 |
| ERROR | 28 | 96.00 | 3.43 | | |
| CORRECTED TOTAL | 34 | 822.97 | | | |

TABLE A13.3 ANOVA FOR NUMBER OF REMOVED LEAVES PER PLANT OF MATARA

| SOURCE | DF | SS | MS | F VALUE | PR > F |
|-----------------|----|---------|--------|---------|--------|
| YLR | 6 | 907.94 | 151.32 | 16.84 | 0.0001 |
| ERROR | 28 | 251.60 | 8.99 | | |
| CORRECTED TOTAL | 34 | 1159.54 | | | |

TABLE A13.4 ANOVA FOR NUMBER OF REMOVED LEAVES PER PLANT OF AMSOY

| SOURCE | DF | SS | MS | F VALUE | PR > F |
|-----------------|----|---------|--------|---------|--------|
| YLR | 6 | 1585.37 | 264.23 | 25.80 | 0.0001 |
| ERROR | 28 | 286.80 | 10.24 | | |
| CORRECTED TOTAL | 34 | 1872.17 | | | |

TABLE A13.5 ANOVA FOR TOTAL NUMBER OF LEAVES PRODUCED PER PLANT IN MATARA

| SOURCE | DF | SS | MS | F VALUE | PR > F |
|-----------------|----|--------|-------|---------|--------|
| YLR | 6 | 159.37 | 26.56 | 1.08 | 0.395 |
| ERROR | 28 | 685.60 | 24.49 | | |
| CORRECTED TOTAL | 34 | 844.97 | | | |

TABLE A13.6 ANOVA FOR TOTAL NUMBER OF LEAVES PRODUCED PER PLANT IN AMSOY

| SOURCE | DF | SS | MS | F VALUE | PR > F |
|-----------------|----|--------|-------|---------|--------|
| YLR | 6 | 233.09 | 38.85 | 2.64 | 0.037 |
| ERROR | 28 | 411.60 | 14.70 | | |
| CORRECTED TOTAL | 34 | 644.69 | | | |

TABLE A13.7 ANOVA FOR NODE NUMBER PER PLANT OF MATARA

| SOURCE | DF | SS | MS | F VALUE | PR > F |
|-----------------|----|-------|-------|---------|--------|
| YLR | 6 | 7.37 | 1.229 | 0.51 | 0.796 |
| ERROR | 28 | 67.60 | 2.414 | | |
| CORRECTED TOTAL | 34 | 74.97 | | | |

TABLE A13.8 ANOVA FOR NODE NUMBER PER PLANT OF AMSOY

| SOURCE | DF | SS | MS | F VALUE | PR > F |
|-----------------|----|--------|------|---------|--------|
| YLR | 6 | 17.54 | 2.92 | 0.60 | 0.72 |
| ERROR | 28 | 136.00 | 4.86 | | |
| CORRECTED TOTAL | 34 | 153.54 | | | |

TABLE A13.9 ANOVA FOR FLOWER NUMBER PER PLANT OF HATARA

| SOURCE | DF | SS | MS | F VALUE | PR > F |
|-----------------|----|----------|--------|---------|--------|
| YLR | 6 | 2140.34 | 356.72 | 0.67 | 0.678 |
| ERROR | 28 | 15018.80 | 536.39 | | |
| CORRECTED TOTAL | 34 | 17159.14 | | | |

TABLE A13.10 ANOVA FOR FLOWER NUMBER PER PLANT OF ANSOY

| SOURCE | DF | SS | MS | F VALUE | PR > F |
|-----------------|----|----------|---------|---------|--------|
| YLR | 6 | 13446.34 | 2241.06 | 3.07 | 0.0195 |
| ERROR | 28 | 20434.40 | 729.80 | | |
| CORRECTED TOTAL | 34 | 33880.74 | | | |

TABLE A13.11 ANOVA FOR PROPORTIONS OF DEVELOPED FLOWERS TO FLOWER BUDS IN HATARA (ARCSIN/TRANSFORMED DATA)

| SOURCE | DF | SS | MS | F VALUE | PR > F |
|-----------------|----|--------|--------|---------|--------|
| YLR | 6 | 0.0930 | 0.0155 | 1.37 | 0.26 |
| ERROR | 28 | 0.3178 | 0.0114 | | |
| CORRECTED TOTAL | 34 | 0.4108 | | | |

TABLE A13.12 ANOVA FOR PROPORTIONS OF DEVELOPED FLOWERS TO FLOWER BUDS IN ANSOY (ARCSIN/TRANSFORMED DATA)

| SOURCE | DF | SS | MS | F VALUE | PR > F |
|-----------------|----|--------|-------|---------|--------|
| YLR | 6 | 0.1629 | 0.027 | 1.68 | 0.16 |
| ERROR | 28 | 0.4512 | 0.016 | | |
| CORRECTED TOTAL | 34 | 0.6141 | | | |

TABLE A13.13 ANOVA FOR YOUNG POD NUMBER PER PLANT OF HATARA

| SOURCE | DF | SS | MS | F VALUE | PR > F |
|-----------------|----|---------|-------|---------|--------|
| YLR | 6 | 396.40 | 66.07 | 0.82 | 0.57 |
| ERROR | 28 | 2266.00 | 80.93 | | |
| CORRECTED TOTAL | 34 | 2662.40 | | | |

TABLE A13.14 ANOVA FOR YOUNG POD NUMBER PER PLANT OF ANSOY

| SOURCE | DF | SS | MS | F VALUE | PR > F |
|-----------------|----|----------|--------|---------|--------|
| YLR | 6 | 3321.09 | 553.51 | 1.85 | 0.125 |
| ERROR | 28 | 8368.80 | 298.89 | | |
| CORRECTED TOTAL | 34 | 11689.89 | | | |

TABLE A13.15 ANOVA FOR LARGE POD NUMBER PER PLANT OF HATARA

| SOURCE | DF | SS | MS | F VALUE | PR > F |
|-----------------|----|--------|-------|---------|--------|
| YLR | 6 | 232.80 | 38.80 | 1.84 | 0.128 |
| ERROR | 28 | 591.60 | 21.13 | | |
| CORRECTED TOTAL | 34 | 824.40 | | | |

TABLE A13.16 ANOVA FOR LARGE POD NUMBER PER PLANT OF ANSOY

| SOURCE | DF | SS | MS | F VALUE | PR > F |
|-----------------|----|---------|-------|---------|--------|
| YLR | 6 | 418.17 | 69.70 | 2.37 | 0.05 |
| ERROR | 28 | 822.40 | 29.37 | | |
| CORRECTED TOTAL | 34 | 1240.57 | | | |

TABLE A13.17 ANOVA FOR MATURE POD NUMBER PER PLANT OF HATARA

| SOURCE | DF | SS | MS | F VALUE | PR > F |
|-----------------|----|--------|-------|---------|--------|
| YLR | 6 | 262.34 | 43.72 | 2.17 | 0.076 |
| ERROR | 28 | 563.20 | 20.11 | | |
| CORRECTED TOTAL | 34 | 825.54 | | | |

TABLE A13.18 ANOVA FOR MATURE POD NUMBER PER PLANT OF AMSOY

| SOURCE | DF | SS | MS | F VALUE | PR > F |
|-----------------|----|---------|-------|---------|--------|
| YLR | 6 | 331.09 | 55.19 | 2.23 | 0.069 |
| ERROR | 28 | 693.20 | 24.76 | | |
| CORRECTED TOTAL | 34 | 1024.29 | | | |

TABLE A13.19 ANOVA FOR SEED WEIGHT (MG. SEED⁻¹) OF HATARA

| SOURCE | DF | SS | MS | F VALUE | PR > F |
|-----------------|----|---------|--------|---------|--------|
| YLR | 6 | 1493.17 | 248.46 | 1.34 | 0.27 |
| ERROR | 28 | 5193.37 | 185.48 | | |
| CORRECTED TOTAL | 34 | 6686.54 | | | |

TABLE A13.20 ANOVA FOR SEED WEIGHT (MG. SEED⁻¹) OF AMSOY

| SOURCE | DF | SS | MS | F VALUE | PR > F |
|-----------------|----|---------|--------|---------|--------|
| YLR | 6 | 607.26 | 101.21 | 0.63 | 0.70 |
| ERROR | 28 | 4462.88 | 159.39 | | |
| CORRECTED TOTAL | 34 | 5070.14 | | | |

TABLE A13.21 ANOVA FOR SEEDS PER POD OF HATARA

| SOURCE | DF | SS | MS | F VALUE | PR > F |
|-----------------|----|-------|-------|---------|--------|
| YLR | 6 | 0.133 | 0.022 | 0.52 | 0.79 |
| ERROR | 28 | 1.185 | 0.042 | | |
| CORRECTED TOTAL | 34 | 1.318 | | | |

TABLE A13.22 ANOVA FOR SEEDS PER POD OF AMSOY

| SOURCE | DF | SS | MS | F VALUE | PR > F |
|-----------------|----|-------|-------|---------|--------|
| YLR | 6 | 0.893 | 0.149 | 0.80 | 0.58 |
| ERROR | 28 | 5.214 | | | |
| CORRECTED TOTAL | 34 | 6.107 | | | |

TABLE A13.23 ANOVA FOR SEED YIELD (G. PLANT⁻¹) OF HATARA

| SOURCE | DF | SS | MS | F VALUE | PR > F |
|-----------------|----|-------|------|---------|--------|
| YLR | 6 | 24.73 | 4.12 | 3.12 | 0.018 |
| ERROR | 28 | 36.94 | 1.32 | | |
| CORRECTED TOTAL | 34 | 61.67 | | | |

TABLE A13.24 ANOVA FOR SEED YIELD (G. PLANT⁻¹) OF AMSOY

| SOURCE | DF | SS | MS | F VALUE | PR > F |
|-----------------|----|--------|------|---------|--------|
| YLR | 6 | 23.89 | 3.98 | 0.90 | 0.51 |
| ERROR | 28 | 123.20 | 4.40 | | |
| CORRECTED TOTAL | 34 | 147.09 | | | |

TABLE A13.25 ANOVA FOR EARLY SEED WEIGHT (G.SEED⁻¹) OF AMSOY

| SOURCE | DF | SS | MS | F VALUE | PR > F |
|-----------------|----|---------|--------|---------|--------|
| YLR | 6 | 2689.00 | 448.17 | 2.55 | 0.043 |
| ERROR | 28 | 4929.26 | 176.04 | | |
| CORRECTED TOTAL | 34 | 7618.26 | | | |

TABLE A13.26 ANOVA FOR LATE SEED WEIGHT (MG.SEED⁻¹) OF AMSOY

| SOURCE | DF | SS | MS | F VALUE | PR > F |
|-----------------|----|---------|--------|---------|--------|
| YLR | 6 | 1190.41 | 198.40 | 1.11 | 0.38 |
| ERROR | 28 | 4988.20 | 178.15 | | |
| CORRECTED TOTAL | 34 | 6178.61 | | | |

TABLE A13.27 ANOVA FOR EARLY SEEDS PER POD OF AMSOY

| SOURCE | DF | SS | MS | F VALUE | PR > F |
|-----------------|----|------|-------|---------|--------|
| YLR | 6 | 1.19 | 0.198 | 1.02 | 0.43 |
| ERROR | 28 | 5.47 | 0.195 | | |
| CORRECTED TOTAL | 34 | 6.66 | | | |

TABLE A13.28 ANOVA FOR LATE SEEDS PER POD OF AMSOY

| SOURCE | DF | SS | MS | F VALUE | PR > F |
|-----------------|----|-------|-------|---------|--------|
| YLR | 6 | 0.921 | 0.154 | 0.71 | 0.65 |
| ERROR | 28 | 6.072 | 0.217 | | |
| CORRECTED TOTAL | 34 | 6.993 | | | |

TABLE A13.29 ANOVA FOR EARLY MATURE PODS PER PLANT OF AMSOY

| SOURCE | DF | SS | MS | F VALUE | PR > F |
|-----------------|----|--------|-------|---------|--------|
| YLR | 6 | 74.97 | 4.16 | 0.37 | 0.89 |
| ERROR | 28 | 316.00 | 11.20 | | |
| CORRECTED TOTAL | 34 | 390.97 | | | |

TABLE A13.30 ANOVA FOR LATE MATURE PODS PER PLANT OF AMSOY

| SOURCE | DF | SS | MS | F VALUE | PR > F |
|-----------------|----|--------|-------|---------|--------|
| YLR | 6 | 314.74 | 52.46 | 2.27 | 0.65 |
| ERROR | 28 | 646.80 | 23.10 | | |
| CORRECTED TOTAL | 34 | 961.54 | | | |

TABLE A13.31 ANOVA FOR EARLY SEED YIELD (G.PLANT⁻¹) OF AMSOY

| SOURCE | DF | SS | MS | F VALUE | PR > F |
|-----------------|----|-------|------|---------|--------|
| YLR | 6 | 7.96 | 1.33 | 0.47 | 0.83 |
| ERROR | 28 | 79.34 | 2.83 | | |
| CORRECTED TOTAL | 34 | 87.30 | | | |

TABLE A13.32 ANOVA FOR LATE SEED YIELD (G.PLANT⁻¹) OF AMSOY

| SOURCE | DF | SS | MS | F VALUE | PR > F |
|-----------------|----|-------|------|---------|--------|
| YLR | 6 | 16.80 | 2.80 | 1.42 | 0.24 |
| ERROR | 28 | 55.17 | 1.97 | | |
| CORRECTED TOTAL | 34 | 71.97 | | | |

TABLE A13.33 ANOVA FOR PERCENT FLOWER ABORTION OF MATARA
(ARCSIN/TRANSFORMED DATA)

| SOURCE | DF | SS | MS | F VALUE | PR > F |
|-----------------|----|-------|-------|---------|--------|
| YLR | 6 | 0.033 | 0.006 | 1.12 | 0.38 |
| ERROR | 28 | 0.141 | 0.005 | | |
| CORRECTED TOTAL | 34 | 0.174 | | | |

TABLE A13.34 ANOVA FOR PERCENT FLOWER ABORTION OF AMSOY
(ARCSIN/TRANSFORMED DATA)

| SOURCE | DF | SS | MS | F VALUE | PR > F |
|-----------------|----|-------|-------|---------|--------|
| YLR | 6 | 0.066 | 0.011 | 0.98 | 0.46 |
| ERROR | 28 | 0.315 | 0.011 | | |
| CORRECTED TOTAL | 34 | 0.381 | | | |

TABLE A13.35 ANOVA FOR PERCENT YOUNG POD ABORTION OF MATARA
(ARCSIN/TRANSFORMED DATA)

| SOURCE | DF | SS | MS | F VALUE | PR > F |
|-----------------|----|-------|-------|---------|--------|
| YLR | 6 | 0.077 | 0.013 | 1.64 | 0.17 |
| ERROR | 28 | 0.218 | 0.008 | | |
| CORRECTED TOTAL | 34 | 0.294 | | | |

TABLE A13.36 ANOVA FOR PERCENT YOUNG POD ABORTION OF AMSOY
(ARCSIN/TRANSFORMED DATA)

| SOURCE | DF | SS | MS | F VALUE | PR > F |
|-----------------|----|-------|-------|---------|--------|
| YLR | 6 | 0.297 | 0.050 | 2.12 | 0.082 |
| ERROR | 28 | 0.653 | 0.023 | | |
| CORRECTED TOTAL | 34 | 0.950 | | | |

TABLE A13.37 ANOVA FOR PERCENT LARGE POD ABORTION OF MATARA
(ARCSIN/TRANSFORMED DATA)

| SOURCE | DF | SS | MS | F VALUE | PR > F |
|-----------------|----|-------|-------|---------|--------|
| YLR | 6 | 0.064 | 0.011 | 3.22 | 0.016 |
| ERROR | 28 | 0.092 | 0.003 | | |
| CORRECTED TOTAL | 34 | 0.156 | | | |

TABLE A13.38 ANOVA FOR PERCENT LARGE POD ABORTION OF AMSOY
(ARCSIN/TRANSFORMED DATA)

| SOURCE | DF | SS | MS | F VALUE | PR > F |
|-----------------|----|-------|-------|---------|--------|
| YLR | 6 | 0.078 | 0.013 | 3.28 | 0.014 |
| ERROR | 28 | 0.111 | 0.004 | | |
| CORRECTED TOTAL | 34 | 0.189 | | | |

TABLE A13.39 ANOVA FOR PERCENT COMBINED ABORTION OF MATARA
(ARCSIN/TRANSFORMED DATA)

| SOURCE | DF | SS | MS | F VALUE | PR > F |
|-----------------|----|-------|-------|---------|--------|
| YLR | 6 | 0.057 | 0.009 | 1.79 | 0.28 |
| ERROR | 28 | 0.148 | 0.005 | | |
| CORRECTED TOTAL | 34 | 0.205 | | | |

TABLE A13.40 ANOVA FOR PERCENT COMBINED ABORTION OF AMSOY
(ARCSIN/TRANSFORMED DATA)

| SOURCE | DF | SS | MS | F VALUE | PR > F |
|-----------------|----|-------|-------|---------|--------|
| YLR | 6 | 0.020 | 0.003 | 0.48 | 0.82 |
| ERROR | 28 | 0.191 | 0.007 | | |
| CORRECTED TOTAL | 34 | 0.211 | | | |

TABLE A13.41 ANOVA FOR PERCENT EARLY REPRODUCTIVE ABORTION OF MATARA
(ARCSIN/TRANSFORMED DATA)

| SOURCE | DF | SS | MS | F VALUE | PR > F |
|-----------------|----|-------|-------|---------|--------|
| YLR | 6 | 0.179 | 0.030 | 5.31 | 0.0009 |
| ERROR | 28 | 0.157 | 0.006 | | |
| CORRECTED TOTAL | 34 | 0.336 | | | |

TABLE A13.42 ANOVA FOR PERCENT EARLY REPRODUCTIVE ABORTION OF AMSOY
(ARCSIN/TRANSFORMED DATA)

| SOURCE | DF | SS | MS | F VALUE | PR > F |
|-----------------|----|-------|-------|---------|--------|
| YLR | 6 | 0.061 | 0.010 | 0.38 | 0.88 |
| ERROR | 28 | 0.740 | 0.026 | | |
| CORRECTED TOTAL | 34 | 0.801 | | | |

TABLE A13.43 ANOVA FOR PERCENT LATE REPRODUCTIVE ABORTION OF MATARA
(ARCSIN/TRANSFORMED DATA)

| SOURCE | DF | SS | MS | F VALUE | PR > F |
|-----------------|----|-------|-------|---------|--------|
| YLR | 6 | 0.426 | 0.071 | 3.51 | 0.010 |
| ERROR | 28 | 0.566 | 0.020 | | |
| CORRECTED TOTAL | 34 | 0.992 | | | |

TABLE A13.44 ANOVA FOR PERCENT LATE REPRODUCTIVE ABORTION OF AMSOY
(ARCSIN/TRANSFORMED DATA)

| SOURCE | DF | SS | MS | F VALUE | PR > F |
|-----------------|----|-------|-------|---------|--------|
| YLR | 6 | 0.160 | 0.027 | 0.58 | 0.75 |
| ERROR | 28 | 1.296 | 0.046 | | |
| CORRECTED TOTAL | 34 | 1.456 | | | |