COMPETITION AND PRODUCTIVITY IN ASSOCIATIONS OF BEANS (*PHASEOLUS VULGARIS* L.) AND BEETS (*BETA VULGARIS* L.) GROWN AT TWO LEVELS OF SOIL FERTILITY

by

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A THESIS SUBMITTED IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR

THE DEGREE OF DOCTOR OF PHILOSOPHY

in

THE FACULTY OF GRADUATE STUDIES

(Department of Plant Science)

We accept this thesis as conforming

to the required standard

THE UNIVERSITY OF BRITISH COLUMBIA

October, 1998

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Vancouver, Canada

Date _OCTOBER 20, 1998_

DE-6 (2/88)

Abstract

Plant competition for resources is a major component of plant interference. Field experiments were conducted in the summers of 1994 and 1995 to study competition at two soil fertility levels. Mixtures and pure stands of beans (*Phaseolus vulgaris* L.) and beets (*Beta vulgaris* L.) were established, involving nine population density combinations and three pure stand densities per species. Density treatments were assigned to sub-plots, with two soil fertility levels as the main plots in a split plot randomized complete block design. Treatment effects were evaluated using several analytical procedures. Analysis of variance showed that mean yield per plant significantly responded to population density of each species. Interactions between species, and species and fertilizer, were occasionally significant. Inverse yield-density regressions indicated that beans were the stronger competitor in 1994, but beets were the stronger competitor in 1995. In both species, competition for soil resources seemed to be more important than competition for light, and competitive responses were stronger in the fertilized treatment. Plant proportions were affected by experimental treatments. In beans, dry matter allocation to pods predominated in 1994, but allocation to stems was larger in 1995. In beets, dry matter allocation was dominated by storage root formation in both years. Allometric analysis detected adjustments in plant allometry, although direct, *i. e.* non-allometric, experimental influences on dry mass per plant also occurred. Yield component analysis indicated that for both species leaf area index was the most important direct contributor to yield variation, while for beans pod filling was also important. In both years and at the higher soil fertility level, the relative productivity of mixtures per unit land area slightly exceeded that of pure stands, as indicated by relative yield total (RYT) and relative land output (RLO) exceeding 1.0. The combined total productivity of the associations (i. e. total land output, TLO) was strongly influenced by the performance of beets, the more productive of the two species. Relative indices of mixture productivity (RYT or RLO) are poor indicators of total productivity (TLO). Overall, these investigations provide some connections among the competitive responses of the associated species, their growth, and their complementary productive performance.

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SYMBOLS AND ABBREVIATIONS

Symbols and abbreviations	Page (First appearance)	Description
α	17	Allometric coefficient (or constant after ln-transformation)
A	25	Area of land (m^2)
a_{i0} or a_{j0}	12	Intercept in yield-density models. Inverse of mean yield per plant in the absence of neighbours
a_{ii} or a_{jj}	12	Within-species regression coefficient in yield-density models
a_{ij} or a_{ji}	12	Between-species regression coefficient in yield-density models
ANOVA	39	Analysis of variance
β	17	Allometric exponent (or coefficient after ln-transformation)
Ca	60	Calcium
Ca^{2+}	7	Calcium cation
CO_2	10	Carbon dioxide
CP	83	Mallows CP statistic
df	42	Degrees of freedom
ε'	18	Residual variation in yield in allometric models
FWMSR	39	Fresh mass of marketable beet storage roots (g)
FWMP	39	Fresh mass of marketable bean pods (g)
γ	18	Non-allometric coefficient
H or HI	16	Harvest index = Wy/W
K	36	Potassium
K^+	7	Potassium cation
k	18	Subscript indicating k^{th} allometric or non-allometric term
LA	39	Leaf area per plant (m^2)
LA/A	82	Leaf area index = LA/A
LAI	82	Leaf area index = LA/A
LAR	80	Leaf area ratio = LA/W
LER	23	Land equivalent ratio
LIN	60	Fraction of light (PAR) intercepted by the shoot canopy
ln	17	Natural logarithm
LWR	82	Leaf weight ratio = WL/W
Mg	36	Magnesium

Symbols and abbreviations	Page (First appearance)	Definition
N	36	Nitrogen
NAR	80	Net assimilation rate (see ULR)
n/A	25	Number of plants per land area
NH_4^+	7	Ammonium cation
P	36	Phosphorous
PAR	57	Photosynthetically active radiation
PN	39	Number of pods
R^2	13	Multiple coefficient of determination
RLO	24	Relative land output
RYT	23	Relative yield totals
S	36	Sulphur
SLA	82	Specific leaf area = LA/WL
TDP	15	Two dimensional partitioning
TLO	25	Total land output
ULR	80	Unit leaf rate (same as net assimilation rate) = $(1/LA)(dW/dt)$
W	39	Total dry weight (total shoot dry weight for beans, and total shoot plus storage root for beets) (g)
WL	39	Leaf dry weight (g)
WMP	39	Dry weight of marketable pods (g)
WMSR	39	Dry weight of marketable storage roots (g)
WP	39	Pod dry weight (g)
WS	39	Stem dry weight for beans (g)
WSR	39	Storage root dry weight (g)
X	11	Species population density (plants per land area)
X_i	12	Population density (plants per land area) of species denoted by subscript i
X_j	12	Population density (plants per land area) of species denoted by subscript j
y	11	Mean yield per plant
Y	11	Yield per unit land area
z	17	Yield of a secondary measure in allometric relationships

ACKNOWLEDGEMENTS

1.0 General Introduction

Plants growing together in close proximity tend to interfere with each other, and the occurrence of interference is evident from the responses that neighbouring plants elicit from one another (Harper 1961, Harper 1977). Interference can be caused by several processes, including competition for required environmental resources, such as light and mineral nutrients, and by allelochemical influences (Rice 1974, Harper 1977). Other forms of interference include: the alteration of pest and disease relationships, the attraction of pollinators, nitrogen transfer in legume/non legume associations, and microclimate modification such as sheltering from wind (Steiner 1984, Vandermeer 1989, Fukai and Trenbath 1993). In natural plant communities, mixed associations may provide some protection from herbivory (Hjalten and Price 1997). Hence, interference may include both beneficial and harmful influences on target individuals.

In practice, it is often difficult to identify what modes of interference are occurring in a plant association, or to isolate and quantify their contributions to plant responses. It is likely, however, that competition for resources is often an important component of interference, as is suggested by the extensive body of literature concerning the resource-dependence of densely populated agricultural crops. Indeed, some definitions of plant competition (Aspinall and Milthorpe 1959, Welden and Slauson 1986) correspond closely to the definition of interference (Harper 1961). Also, compared with other major influences on the performance of plant associations, such as pests, diseases and environmental stresses, the nature of plant competition is poorly understood. In large part, this can be attributed to inherent difficulties in studying competition, due to the potential complexity of competitive relationships among associated plants.

The subject of plant competition has broad significance in biology, and this is reflected in various perspectives and definitions. According to Harper (1961), an agronomist looks at competition as the response of plants to density-induced resource shortages; an ecologist looks at it as implying those forces by which one organism succeeds at the expense of another; a geneticist looks at competition as the interactions operating among individuals of different genotypes; while a plant physiologist looks at competition in terms of differences

in the efficiency with which different individuals secure limited environmental factors necessary to plant growth and reproduction. Several definitions of plant competition are found in literature. For example, Grime (1977) defines plant competition as the tendency of neighbouring plants to utilize the same quantum of light, ion of a mineral nutrient, molecule of water, or volume of space. Tilman (1980) defines plant competition as the capacity of a species to reduce a resource to a level too low to support the growth of the associated species. Plant competition has also been taken to mean the restrictions in growth of a plant which arise from its association with other plants (Aspinall and Milthorpe 1959, Welden and Slauson 1986). It is this usage for the phrase plant competition that will be adopted throughout this thesis, since the different forms of interference will not be distinguished.

Questions as to whether or not competition occurs among plants, and its magnitude in time and space, are by far the most commonly addressed questions in field experiments on competition (Goldberg and Barton 1992). Competition is of interest to plant community ecologists because it may be an important determinant of community composition and dynamics (Harper 1977, Tilman 1982, Sivertown 1987, Wilson 1988, Keddy 1989, Goldberg 1990, Tilman 1990a). Plant competition may contribute to mortality in dense plant stands, and this has important implications for stand density management decisions *e. g.* in silviculture (Newton and Smith 1989). A substantial number of studies have investigated competitive balances in mixed species associations (Jolliffe 1997), and some efforts have been made to determine whether competitive responses are modified by secondary factors, such as by environmental conditions (*e. g.* Suehiro and Ogawa 1980), other circumstances of an association (*e. g.* Turkington and Jolliffe 1996), and genotype (*e. g.* Tollenaar 1992, Tollenaar *et al.* 1997).

A significant debate exists as to whether the intensity of plant competition changes along a productivity gradient (Grime 1973, 1979, Wilson and Keddy 1986) or stays similar (Newman 1973, Tilman 1988). Some connections between competition and productivity have been investigated in ecological field experiments (*e. g.* Mack and Harper 1977, Turkington and Harper 1979, Turkington 1989, Turkington *et al.* 1993, Wedin and Tilman 1993, Tilman *et al.* 1996,). A very extensive literature on competition and productivity, however, has been generated in agricultural contexts. For example, influences of weed species on crop

productivity are often interpreted as competitive influences (Cousens 1985a, b, Radosevich 1987, Roush *et al.* 1989, Singh *et al.* 1991, Wilson *et al.* 1995, Tollenaar *et al.* 1997). Since competition implies resource-dependence, the large body of literature concerning the influences of light, carbon dioxide and soil fertility on crop yields is also pertinent. Finally, competitive balances between associated species are thought to be an important determinant of productivity in agricultural intercrops (Vandermeer 1989, Fukai 1993) although the quantitative links between competition and intercrop productivity need to be clarified.

My own interests and educational background lie in areas of soil fertility and plant nutrition. This has led me to focus on the main theme of this thesis: plant competition in intercrops grown at different soil fertility levels. Working in this subject area has advanced my knowledge on issues pertaining to the agronomy of intercropping, and it has helped to prepare me for future research and teaching of agriculture which will be useful to the Kenyan farming community.

1.1 Research Objectives

If interference is defined as plant responses to their neighbours (Harper 1961), then knowledge of this subject should be advanced through studies of competitive influences on plant performance. The research reported in this thesis was intended to characterize competition, productivity and their relationships when common beans (*Phaseolus vulgaris* L.) and table beets (*Beta vulgaris* L.) are intercropped at two soil fertility levels. These species were selected for use because they are a legume/non-legume association, analogous to the legume/non-legume intercrops commonly grown in the tropics and sub-tropics (Vandermeer 1989). In addition, the two crops can be grown in a contemporary fashion, co-existing between emergence and harvest, and they have similar recommended monoculture population densities (Anonymous 1994). Finally, they offer the contrast of forming above-ground (bean pods) or below-ground (beet storage root) yield components. Experiments were repeated during two seasonss, 1994 and 1995.

Specific objectives of this research were:

(1) to evaluate within- and between-species components of interference in associations of bean and beet, in order to determine if interference is consistent for a number of different measures of plant growth, at different soil fertility levels, and for different seasonss (Chapter 3),

(2) to evaluate within- and between-species components of interference in associations of bean and beet, focusing on foliar nutrient accumulation and shoot canopy light interception, in order to determine if competition for nutrients and/or light is consistent for different soil fertility levels and for different seasonss (Chapter 4),

(3) to further detail the impacts of interference, soil fertility and seasons on plant growth, using methods of plant growth analysis, allometric analysis and yield component analysis (Chapter 5),

(4) to evaluate the productivity and mineral nutrient uptake of intercropped beans and beets. Several issues to be addressed in this evaluation are: whether the mixed associations are more productive than their corresponding pure stands, whether there is more mineral nutrient uptake in mixed associations than in their corresponding pure stands, and whether these assessments of productivity are influenced by soil fertility and seasons (Chapter 6).

It should be noted that each objective can be stated in the form of a null hypothesis. For example, objective number 4 can be re-stated as null hypotheses as: mixtures do not significantly produce more than their corresponding pure stands, and that there is no significant difference in nutrient uptake, when beans and beets are grown in mixtures, compared to their uptake in pure stands. In addition, each statistical analysis carried out in this thesis involves the assessment of one or more null hypotheses.

2.0 Literature Review

Like beetles in the biosphere, the literature on competition is vast and diverse. It is suitable to begin, then, with a quotation from the preface from Crowson's (1981) volume on the Coleoptera, as cited by Keddy (1989):

> "To deal with so vast a group as the Coleoptera...is doubtless an over-ambitious aim for any single author; it is inevitable that my attempt to do so will not satisfy any specialists in their own particular fields. I hope, however, that such specialists, once they have overcome their initial dissatisfaction, may gain from this book by coming to see their particular interests in wider contexts, and perhaps even by picking up ideas which might suggest new and fruitful directions for their investigations."

This chapter will mainly focus on literature that pertains to plant competition and mixed cropping systems. Within the large subject area of plant competition, this review will consider some aspects of below-ground and above-ground competition, particularly in connection with soil fertility and light interception. It will consider how inverse yield-density relationships and methods of plant growth analysis can be used to quantify and detail competitive responses. Some aspects of evaluating the productivity of mixed cropping systems will also be introduced. Finally, this chapter will describe the plant species chosen for use in these investigations.

2.1 Plant competition for resources

2.1.1 General background

The subject of competition by plants, for environmental resources essential to their growth, is of broad interest. Ecologists have long been interested in competition because of its roles in shaping patterns of plant abundance and distribution and its effects on the traits of competing species (Goldberg and Barton 1992). Competition is taken into account by community ecologists in their efforts to elucidate the structure and dynamics of natural plant communities. Plant competition is also important in agriculture and silviculture, since it bears upon issues of appropriate planting density, thinning, intercropping, and weed management. A broad literature on plant competition, for both natural and agricultural associations, now exists. Some monographs, textbooks and symposium proceedings are: Harper (1977), Grime

(1979), Tilman (1982), Milthorpe (1961a), Silvertown (1987), Keddy (1989), and Grace and Tilman (1990).

Agricultural settings, although they seldom have the diversity and complexity of natural plant associations, offer opportunities to explore competition under well-defined situations, especially because they allow the constituents and structures of associations to be closely regulated. In addition, the use of annual crops allows the rapid turnover of experiments. Within-species competition can be investigated in crop monocultures, *i. e.* single species or sole crop associations. Crop species mixtures, however, also allow between-species competition and its consequences to be evaluated. Studies in plant competition have shown that between-species competition is more complex than within-species competition, probably due to the modification of such traits as canopy structure and root proliferation (Fukai and Trenbath 1993, Trenbath 1976, Wilson 1988) and the modification of microclimate such as sheltering from wind (Steiner 1984, Vandermeer 1989, Fukai and Trenbath 1993). Hence, studies on crop mixtures offer the possibility to investigate some questions of interest to both ecology and agronomy. For example, studies on crop mixtures may help to address questions concerning the intensity of plant competition at different levels of productivity (Grime 1977, 1979, Tilman 1982, 1988). Also, it has been argued (Willey 1972, 1979) that intercrops should be most productive when the associated species do not fully compete, but instead when they use resources in some complementary fashion, and that advantages of using intercrops can be made possible through maximizing such complementarity. In this context, it was found by Natarajan and Willey (1980) and Reddy and Willey (1981) that crops may absorb mineral nutrients more effectively when grown in mixtures than when grown as pure stands.

2.1.2 Competition for mineral nutrients and other soil factors

Soil resources for which plants can compete include water, mineral nutrients and possibly oxygen in some cases (Greenwood 1969, Vandermeer 1989). Clement, Weaver and Hanson (1929), cited by Wilson (1988), considered the mechanisms that might operate in plant competition and concluded that competition occurred for light, soil nutrients and water. They attempted to separate these factors, but this was first accomplished by Donald (1958)

who partitioned shoot and root competition between two grasses. Donald (1958) found that root competition was greater than shoot competition, but there was a positive interaction between the two. However, he could not entirely separate competition for mineral nutrients from competition for water. Snaydon (1971) also found that root competition had a greater effect than shoot competition, and probably began sooner after mixtures were established. Although evidence distinguishing between shoot and root competition is available (Wilson 1988), it is difficult to study below-ground competition under field conditions; effects of below-ground competition are usually evident through changes in aboveground plant components.

Competition for soil factors may occur earlier than for light because root systems often develop faster than the shoot. However, this may be more applicable in even-aged plant associations than in situations where some plants emerge later than others. Root morphology may be an important factor in competition for soil resources. For example in grass/clover mixtures, Evans (1977) found that grasses had longer, thinner and more finely branched roots than clover. Evans (1977) postulated that in a grass/clover pasture, most of the clover roots would be competing with grass roots for available nutrients, but only a small portion of grass roots would be in competition with those of clover; i. e. competition for soil resources is believed to take place when plants share common depletion zones. As roots of the component species absorb nutrients and water, areas around the absorbing roots, the depletion zones, are formed. This is the first of two processes thought to characterize plant competition for soil resources - the effects of plants on the soil (Goldberg and Werner 1983, Goldberg 1990). The second process is the response of the plants to soil depletion. Depletion zones can differ for different soil resources. Water and nitrates are more mobile, and are usually taken up at higher rates than, for example, phosphates. Hence, depletion zones for water and nitrates are expected to be more extensive than for phosphates.

In addition to gradual diffusion, mobile nutrients such as nitrates are carried by bulk flow in moving water. Their depletion zones, therefore, are similar to those for water, provided that the nutrients are absorbed rapidly when they arrive at the roots. Nutrients like phosphates, NH_4^+, Ca^{2+} and K^+ are often largely adsorbed onto ion exchange sites in the soil, which limits their mobility. Their concentration in soil water is low and their flow is

dominated by diffusion, a relatively slow process. Hence, competition for soil nutrients is influenced by their mobility in the soil as well as by the extension of roots into the soil and by plant demand. The uptake of nutrients and water by roots takes place simultaneously, so it is difficult to separate competition for these resources. It would be expected, however, that competition for water would predominate under moisture stress when the availability of nutrients is adequate, and competition for nutrients would predominate when water is adequate, but availability of nutrients is low.

Compared with monocultures, there is evidence that there is greater uptake of macronutrients by intercrops (Natarajan and Willey 1980, Reddy and Willey 1981). This may reflect increased demand, if the intercrops are innately more productive than the monocultures. It may also be the consequence of more extensive occupation of the soil by the different root morphologies possessed by multiple species. In addition, functional diversity may be greater in mixtures, which may have more complex mycorrhizal associations and N-fixing components. For example in a grass/legume mixture, the uptake of nitrogen by the grass can be influenced by the legume in two opposing processes (Haynes 1980). The legume may increase the supply of available nitrogen in the root medium by biological N-fixation, but it may also compete for mineral soil nitrogen. The balance between competition and transfer is not constant with time but changes with growth cycles of the species in the sward (Vallis 1978, cited by Haynes 1980). The mechanism of nitrogen transfer is not well understood, but is thought to be through several processes: secretion of nitrogenous compounds into the soil, thereby making them available to the non-legume, the decay of nodules and roots of the legume, and sloughage of the roots of the legume (Agboola and Fayemi 1972, Natarajan and Willey 1980, Bandyopadhyay and De 1986, Elmore and Jackobs 1986, Gliessman 1986, Patra *et al.* 1986, Vandermeer 1989, Senaratne and Ratnasinghe 1993, Bulson *et al.* 1997).

Biologically fixed nitrogen transfer has also been demonstrated to be mediated through mycorrhizae (Haystead 1983, van Kesse *et al.* 1985). Mycorrhizal infestation of the grass/clover associations can confer a competitive advantage on the clover (Haynes 1980). Cush (1974), cited by Haynes (1980), showed that when ryegrass and clover were grown together, mycorrhizally associated clover competed more effectively for P than non-

mycorrhizal clover. Hall (1978) showed that at low soil P levels mycorrhizal association produced a 5-fold increase in total clover dry mass in monoculture, and a 40-fold increase when clover was grown with ryegrass. The clover appeared to be infested in preference to the grass, and apparent mycorrhizal-induced depressions in yield were observed in the grass (Haynes 1980). However, use of mycorrhizae with clovers requires caution since the fungi can be parasitic to clover, thereby reducing its growth which may give grasses a competitive advantage over the clover. It is suggested that the host-endophyte relationship in the mycorrhizal symbiosis may change from mutualism to parasitism as soil P availability increases (Cush 1974, cited by Haynes 1980).

2.1.3 Above-ground competition

Photosynthetically active radiation is also an essential environmental resource for crop growth. It must be intercepted and utilized immediately by plants; it cannot be stored as radiant energy for later use (Keating and Carberry 1993). Solar radiation becomes a limiting factor in crops where fertilizers and irrigation are applied, and neighbouring plants compete for solar radiation by direct interception. In the field, radiation is more difficult to manipulate than some other resources, such as water and nutrients (Steiner 1984). The interception and utilization of solar radiation by plants, in sole crops and in mixtures, have been reviewed in several publications, including: Donald (1963), Black (1971), Harper (1977), Monteith (1981), Caldwell (1987), and Keating and Carberry (1993).

Research on sole crops (monocultures) has frequently considered temporal and spatial aspects of the capture and use of solar radiation, e. g. by manipulating plant population or canopy structure architecture. Peak values of light interception can be achieved by establishing sole crops with optimum plant population (Steiner 1984); higher populations can result in excessive shading of lower parts of the shoot canopy which in turn can reduce crop growth rate.

Research on mixtures has, on the other hand, tended to concentrate on the differential abilities of associated species to compete for radiation (Keating and Carberry 1993). Over time, two major components of light interception are: the duration of the crop cycle, and the rate of leaf area development between crop emergence and the attainment of an optimal leaf area index. Associated with the temporal distribution of the leaf area is the spatial distribution

of photosynthetic structures. Better spatial arrangement of mixed species canopies can enhance light interception through a modification of the canopy extinction coefficient. For example, Keating and Carberry (1993) argued that addition of an under-story intercrop with high extinction coefficient, would increase the whole-canopy extinction coefficient, thus increasing light interception at a given value of leaf area index. Several approaches used in intercropping aim at reducing the competition for light, and possibly competition for other factors. These include: relay intercropping in which species are not entirely contemporary, planting dominant crops in double rows (plant grouping), orientation of rows in an east-west direction, increasing the leaf inclination of the dominant crops (resulting in a lower canopy extinction coefficient), and growing of shade tolerant plants in the sub-story.

Carbon dioxide (CO_2) is the other aboveground environmental resource for which plants can compete. Research has shown that competitive outcome in several simple temperate communities can change substantially with different CO_2 concentrations (Bazzaz *et al.* 1985). CO_2 has been shown to influence plant competition through its modification of relative growth rate and change in plant phenology. For example Reekie and Bazzaz (1989), working with seedlings of five tropical trees grown at ambient and elevated CO_2 levels, found that CO_2 increased canopy height of the seedlings. Their results suggested that competition for light was the major factor determining community composition, and that elevated CO_2 concentration affected competitive outcome through its effect upon canopy architecture. In another experiment, Reekie and Bazzaz (1991), using four annuals grown at ambient and elevated CO_2 levels, observed that elevated CO_2 concentration affected competitive outcome more through its effect on growth than its effect on phenology.

Finally, it should be noted that competition is not necessarily for one resource. It may start with soil resources at early stages of plant growth, but as time goes on, plants grow and the environment varies. Hence, depending on prevailing conditions, competition processes should change, e. g. from below-ground to above-ground, particularly with the closing up of the plant canopy. Also competition in the soil may affect competition above-ground, and vice-versa. For example mutual shading of a legume by a non-legume may lower the rate of N-fixation in the soil, or even lower the rate of photosynthate transfer to the roots, thereby reducing the rate of uptake of essential nutrients, hence altering the competitive relationships.

2.2 Competition and yield-density relationships

Competitive interference ought to be intensified when plants are crowded, compared to sparse associations. Accordingly, density-dependence offers one way to explore competition, and experiments on plant competition have often involved variations in this factor.

Early work on yield-density relationships was reviewed by Willey and Heath (1969). For monocultures on a per unit land area basis, crop yield initially increases with increase in population density. Progressively smaller increases in crop yield per unit land area are observed at higher population densities until yield shows no further increase (asymptotic pattern) or eventually starts to decline (parabolic pattern). The asymptotic relationship between population density and yield per unit land area is referred to as the law of constant final yield (Shinozaki and Kira 1956, Harper 1977, Silvertown 1987), and it is characteristic for yield measures such as total or above-ground biomass. The asymptotic behaviour may reflect both density-dependent mortality and plastic reduction in size of individual plants in dense populations (Weiner 1988). The asymptote represents the limit on total biomass formation given the total amount of available resources for crop growth. However, as population densities change, the partitioning of biomass to the various organs of the plants may change. Seed output often suffers in this reallocation (Harper 1961), and such changes in partitioning account for the parabolic patterns exhibited by yields of certain plant components (Willey and Heath 1969, Hutchings and Budd 1981, Weiner 1988).

Yield of a population per unit land area (Y) is the product of mean yield per plant (y) and plant population density (X). Exploring yield-density relationships on a per unit land area basis is not ideal (Willey and Heath 1969), because population density is not a potential independent variable in relation to yield per land area: $Y = yX$. Yield-density relationships, therefore, have more often been explored on a per plant basis. In that frame of reference, increasing plant population density has been shown to reduce almost every aspect of individual plant yield (Weiner 1988). A variety of mathematical forms have been used to describe that reduction, including inverse (*e. g.* Shinozaki and Kira 1956), inverse exponential (Willey and Heath 1969), negatively logarithmic (Shainsky and Radosevich 1991), negatively linear (Chan and Walstad 1987, White and Newton 1989,), and negatively hyperbolic (Oliver 1984, Brand 1986, Wagner *et al.* 1989).

Of these forms, inverse relationships have been used most extensively, starting with the work of Kira *et al.* (1953) and continuing until the present (Shinozaki and Kira 1956, Holliday 1960, Bleasdale and Nelder 1960, Bleasdale and Thompson 1966, Mead 1966, Gillis and Ratskowsky 1978, Wright 1981, Spitters 1983, Vandermeer 1984, Jolliffe 1988, Jolliffe 1997). The initial choice of inverse models was based on empirical observations on the form of decline of yield per plant as population density is increased. Such models are to be expected, however, if plant performance is being controlled by competition for resources (Jolliffe 1988). Relatively simple inverse yield-density relationships have been found to provide consistently good descriptions of yield-density responses (*i. e.* high coefficients of determination) with many plant associations (Jolliffe 1997), and they have biologically meaningful parameters. The "reciprocal yield equation" was introduced by Shinozaki and Kira (1956) to describe the density dependence of monoculture yield per plant:

$$y_i^{-1} = a_{io} + a_{ii} X_i \qquad (2.1)$$

where y_i is the mean yield per plant of species i, and X_i is species population density. Parameter a_{io} is the reciprocal mean yield per plant in the absence of competitors, and hence it quantifies the (inverse of) growth potential of plants unrestricted by competition. Parameter a_{ii} measures the strength of within-species competition. If transformed to a per unit land area basis, by multiplying by X_i, equation (2.1) expresses an asymptotic yield-density relationship.

Such models have been amended to include the effects of additional species (*e. g.* Wright 1981, Spitters 1983). For example, in a binary mixture of species denoted by subscripts i and j:

$$y_i^{-1} = a_{io} + a_{ii} X_i + a_{ij} X_j \qquad (2.2a)$$

$$y_j^{-1} = a_{jo} + a_{jj} X_j + a_{ji} X_i \qquad (2.2b)$$

In addition to plant growth potentials ($1/a_{io}$ and $1/a_{jo}$) and within-species influences (a_{ii} and a_{jj}), these models take into account between-species influences, as expressed by coefficients a_{ij} and a_{ji}.

Similarly, such models might be extended to describe more complex associations, involving more than two species. However controlled experiments on multi-species associations, where such an extension might be used, have seldom been done (Minjas 1981). For binary mixtures, another extension of the simple inverse models includes the use of an

exponent other than -1.0 (*e. g.* Jolliffe 1988) to allow greater flexibility in expressing the yield decline. In addition, population density interaction terms (X_iX_j) might be added to equation (2.2) if the presence of a companion species changes the competitive influences of the target or companion species (Jolliffe 1988, Shainsky and Randosevich 1991). Interactions, however, are frequently weak or insignificant (Jolliffe 1997). For 66 cases when yield-density regressions were developed using eqn. 2.2 (Table 2 in Jolliffe 1997), the average multiple coefficient of determination obtained was 0.93. Given this effectiveness, and the simplicity of interpreting competitive balances using equation (2.2), such models have usually been applied without extensions.

Welden and Slauson (1986) and Shainsky and Randosevich (1991) identified two aspects of plant competition, intensity and importance, which can be differentiated using such yield-density models. The *intensity* of competition is the amount of yield loss due to increased density or proximity of competitors. This can be measured from the slopes of the yield-density responses given by the values of the regression coefficients, a_{ii}, a_{ij}, a_{jj} and a_{ji}. The *importance* of competition is the degree to which competition explains variation in plant yield, relative to other factors such as diseases, genetics, microclimate, site-specific variations etc. This can be inferred from the multiple coefficient of determination for a yield-density regression, while the relative importance of each species' density can be inferred from partial coefficients of determination for each density component (Shainsky and Randosevich 1991).

It should be noted that such yield-density relationships provide population-level assessments, since they describe mean plant performance. They do not describe the behaviour of the specific targets of competitive influences: the individual plants (Weiner 1985). Another important branch of this subject area, often referred to as neighbourhood analysis, explores competition at the target plant level, often by measuring the size-dependence of plant performance (*e. g.* Weiner 1990). Neighbourhood approaches can provide distinctive insights into processes of plant competition, such as the occurrence of competition by resource depletion or resource pre-emption (Weiner 1990, Newton and Jolliffe 1998). Neighbourhood and population-level approaches, however, are not mutually exclusive; they offer useful and different ways of interpreting plant competition. Neighbourhood approaches were not used in

the present investigations, since my main goals concerned competition and its relationships to population performance.

2.3 Analyzing the impacts of competition on plant growth

Since interference involves plant responses to their neighbours (Harper 1961), our understanding of competition and other modes of interference may be advanced by detailing such responses. Analytical models of plant growth provide ways in which we can measure and interpret interference as a source of variation in plant growth. Three main branches of plant growth analysis have been developed: conventional plant growth analysis; yield component analysis and sub-organismal demographic analysis. All three begin with simple observations of the sizes of plants or plant parts, transform these observations to indices of growth, and then use these indices to interpret the data.

Conventional plant growth analysis is, in essence, a time-based analytical model of growth (Jolliffe *et al.* 1982). There are several comprehensive reviews of conventional plant growth analysis (Evans 1972, Causton and Venus 1981, Hunt 1982). The subject originated in early works by Gregory (1918), Blackman (1919), Briggs *et al.* (1920a, 1920b) and Fisher (1921). Central aspects of growth addressed by conventional plant growth analysis include: the efficiency and extent of assimilatory systems, and the duration and partitioning of growth (Jolliffe *et al.* 1982). These issues are evaluated using characteristic indices of growth, such as crop growth rate, relative growth rate, net assimilation rate, leaf area ratio and leaf area index (Warren Wilson 1981). Compared with other methods of plant growth analysis, conventional plant growth analysis contains indices that are more closely connected to ordinary physiological assessments of performance. For example net assimilation rate is a reflection of whole-plant net photosynthesis integrated over time. Determining the rate indices requires measurements to be taken as time proceeds, but some indices used in conventional plant growth analysis are ratios (leaf area index, leaf area ratio, specific leaf area, leaf weight ratio and harvest index), and these can be determined from observations taken at a single harvest. At the population level, population density and biomass density are included as indices in conventional plant growth analysis (Warren Wilson 1981).

Demography explores the structure and condition of populations. Sub-organismal demographic analysis of plant growth was introduced by Bazzaz and Harper (1977). In this procedure, the individual plant is viewed as an additive population of structures, and the demography of that population is assessed. The procedure is most effective for plants containing a rich and repetitive population of structures, such as leaf population in flax plants (*Linum usitatissimum*) which was evaluated in the original study by Bazzaz and Harper (1977). Other examples of sub-organismal demographic analysis include Hunt and Bazzaz (1980) and Gaye and Jolliffe (1993). In a study on bean, sub-organismal demographic analysis was used to determine which flowers were most important in pod production (Lovett Doust and Eaton 1981). Sub-organismal demographic analysis can be performed on data from a single harvest, although information from a sequence of harvests will aid in the understanding of population changes.

Yield component analysis, dating from Engeldow and Wadham (1923), analyzes variation in yield as the mathematical product of yield components, each component being a ratio of plant measures (Fraser and Eaton 1983). (The term "yield" is used here, as it is used most frequently in this thesis, to denote a particular output of plant growth, such as pods or seeds, and not in the statistical sense, where "yield" denotes an dependent variable.) Yield component analysis has contributed to the improvement of plant productivity (Yoshida 1972). A wide variety of statistical techniques have been utilized to explore relationships between yield component variations and yield variations (Fraser and Eaton 1983). One procedure (Eaton *et al.* 1986, Jolliffe *et al.* 1989, Jolliffe and Gaye 1995), analyzes yield variations by two dimensional partitioning which combines multiple regression with the analysis of variance. This procedure allows yield variation to be broken down into contributions by yield components and experimental sources of variation. As with the other methods of plant growth analysis, yield component analysis can be performed on data from a single harvest, although information from a sequence of harvests will aid in interpreting plant behavior.

These three branches of growth analysis provide somewhat different perspectives on plant performance, but they are not mutually exclusive. For example, there are several studies where more than one of these approaches has been used (Jolliffe *et al.* 1982, Hunt and Bazzaz 1982, Jolliffe and Courtney 1984, Jolliffe *et al.* 1989, Gaye and Jolliffe 1995). Also, some

measures have been used in more than one form of plant growth analysis. This is true for harvest index, which is an important index within conventional plant growth analysis (Jolliffe *et al.* 1982), but which has also been used in sub-organismal demographic analysis (*e. g.* Lovett Doust and Eaton 1981, where it was called reproductive effort) and yield component analysis (Gaye and Jolliffe 1995). The research described in this thesis will exploit yield component analysis, and a limited form of conventional plant growth analysis, but sub-organismal demographic analysis will not be used.

These three branches of plant growth analysis have been formally interconnected, using concepts of allometry (Jolliffe and Courtney 1984). Allometry has been defined in various ways (Gould 1966, Smith 1980, Causton and Venus 1981, Morris and Myerscough 1986, Weiner and Thomas 1992, Weiner and Fishman 1993, Bonser and Aarssen 1994, Niklas 1994, McLachlan *et al.* 1995). Here, it will be used to denote quantitative relationships that exist among different parts of an organism (Jolliffe *et al.* 1988), a definition which reflects the linguistic roots of the term ("other measures").

Since the classic works of Thompson (1917, 1942) and Huxley (1932) the importance of allometry in biological organisms has been widely recognized. However, the significance of size in understanding the shape and functions of an organism has been given more emphasis in animals than in plants. With a few notable exceptions, remarkably little work has been done on the allometry of plant growth and reproduction (Reiss, 1989). The importance of allometry in many branches of biology can be exemplified by its use in Taxonomy; if the allometry of some groups of organisms overlaps, they may fall within the same taxonomic group, but if their allometry differs, they may need to be placed in different taxonomic groups. Allometry is also used to reconstruct animals from their partial fossil remains. In plants, allometry is useful in formulating testable hypotheses about the adaptive value of traits (Le Maitre and Midgley 1991).

It is important to realize, however, that variation in allometry occurs among individuals within a taxonomic group, due to adjustments as individuals age and respond to environmental influences. For example, nutrient- and water-limited plants may become more 'rooty' and shaded plants more 'shooty' (Hunt 1988, Morris and Myerscough 1986). Such adjustments have connections with functional processes and plant acclimatization to their

environment. For example, Geiger *et al.* (1996) stated that the responses of dry matter partitioning to environmental factors establishes allometric growth among plant parts and maintains the functional balance between the supply and use of carbon. They further suggested that a key mechanism contributing to the regulation of carbon partitioning is an expression of genes that control the activity of the enzymes that initiate sucrose metabolism at specific sites and stages of ontogeny.

Much of the literature on the allometry in plants has focussed on forest trees (*e. g.* Gower *et al.* 1987, Weller 1987, Clough and Scott 1989, Cromer and Jarvis 1990, Johnson 1990, Kolb and Steiner 1990a, Kolb and Steiner 1990b, Le Maitre and Midgley 1991, Makela and Albrektson 1992, Shainsky *et al.* 1992, Elliott and Clinton 1993, Gower *et al.* 1993, Harrington and Fownes 1993, Scatena *et al.* 1993, Newton and Jolliffe 1993, Bonser and Aarssen 1994, Weiner and Fishman 1994, Niklas 1995). Less work seems to have been done on allometry in herbaceous annuals (Stanhill 1977a, Stanhill 1977b, Weiner *et al.* 1990, Weiner and Thomas 1992, McLachlan *et al.* 1995, Nagashima and Terashima 1995, Gedroc, *et al.* 1996), in grasses (Jolliffe *et. al.* 1988) and in agronomic crops (Mchaina 1991, Stutzel and Aufhammer 1991).

As competitive influences vary, plants may undergo differential responses among different measures of plant size. *i. e.* there may be allometric changes. Allometric relations are commonly studied using regression models based on the bivariate power function (Huxley 1932):

$$y = \alpha z^{\beta} \tag{2.3a}$$

where y and z are two measures of an organism, or part of an organism, parameter α is the allometric coefficient and parameter β is the allometric exponent. Note that this model expresses bivariate proportionality, since:

$$y/z = \alpha z^{\beta-1} \tag{2.3b}$$

For two main reasons, it is usual to apply a ln-transformation to eqn. 2.3a: (1) the resulting linear relationship (eqn. 2.4) is more convenient for interpretation, and (2) a ln-transformation can be an effective means of transforming biological data so that it meets statistical assumptions of normality and homoscedasicity. After ln-transformation, equation (2.3a) becomes:

$$\ln(y) = \ln(\alpha) + \beta\ln(z) + \ln(\varepsilon) \tag{2.4}$$

where $\ln(\varepsilon)$ has been included to account for residual variation in $\ln(y)$ not accounted for by $\ln(\alpha)$, β and $\ln(z)$. Equation (2.4) is a straight-line relation with $\ln(\alpha)$ as the y-intercept and β as the slope of the line. If both sides of equation (2.4) are differentiated with respect to time (t), and assuming $\ln(\alpha)$ and β to be constants, it can be shown that the slope β is the ratio of the relative growth rates of y and z (Whitehead and Myerscough 1962, Jolliffe and Courtney 1984). Hence β is of physiological interest, and it connects allometry to other fields of plant growth analysis (Jolliffe and Courtney 1984). Parameter α is dependent on the arbitrary choice of the scale of measurement for z since it is the value of y when z equals 1.0. The slope of the double-logarithmic regression between $\ln(y)$ and $\ln(z)$ (*i. e.* parameter β) measures proportional changes, and is scale-independent, being unaffected by the unit of measurement (Smith, 1980). Various methods for estimating β have been used *e. g.* least squares regression (Jolliffe *et al.* 1988), major axis and reduced axis procedures (Riska, 1991, Niklas, 1994) and maximum likelihood regression (Causton and Venus 1981).

Jolliffe *et al.* (1988) expanded equation (2.4) to allow the direct assessment of allometric responses to experimental treatments. Inspection of eqn. (2.4) indicates that experimental treatments might affect $\ln(y)$ through allometric adjustments (*via* changes in α and/or β), through change in scale (*via* change in $\ln(z)$), and/or through non-allometric adjustments (*via* changes in $\ln(\varepsilon)$). For example, for an experiment involving three treatment factors, *e. g.* plant population densities X_i and X_j and mineral nutrient regime N, the allometric relationship expands to (Jolliffe *et al.* 1988):

$$\ln(y) = \ln(\alpha') + \beta_0\ln(z) + \beta_1 N\ln(z) + \beta_2 X_i\ln(z) + \beta_3 X_j\ln(z) + \beta_4 N X_i\ln(z) + \beta_5 N X_j\ln(z)$$
$$+ \beta_6 X_i X_j\ln(z) + \beta_7 N X_i X_j\ln(z) + \gamma_1\ln(N) + \gamma_2\ln(X_i) + \gamma_3\ln(X_j) + \gamma_4\ln(N X_i)$$
$$+ \gamma_5\ln(N X_j) + \gamma_6\ln(X_i X_j) + \gamma_7\ln(N X_i X_j) + \ln(\varepsilon') \tag{2.5}$$

In this model, terms involving β explain allometic responses to treatments while terms involving γ explain non-allometric effects of treatments on y. The constant of the expanded model ($\ln(\alpha')$) is the result of grouping of terms and arises from both allometric and non-allometric sources. Using such an expansion, Jolliffe *et al.* (1988) found that plant population density affected allometry in orchardgrass and timothy plants grown in mixtures at different population densities.

2.4 Crop mixtures

In agricultural cropping systems, plants are often restricted to single-species populations, referred to in the literature as pure stands, sole crops, or monocultures. In natural communities and some agricultural systems (*e. g.* mixed pastures, intercrops), plant species are not isolated but exist in association with members of different species. Agricultural associations of two or more different species are referred to as multiple cropping (Willey 1979) or mixtures (Mead 1979, Mead and Willey 1980, Nnko and Doto 1980, Vandermeer 1989). Trenbath (1974) suggested that associations of different genotypes of the same species, or different age classes of the same cultivar could also be considered to be mixtures.

Two terms widely used in connection with multiple cropping systems are intercropping and mixed cropping. In intercropping, plants are grown in organized patterns, including rows, strips and/or various arrangements within and between rows. Mixed cropping involves a more random distribution of the associated species (Mead 1979, FAO 1991). Both systems involve some simultaneous presence of two or more crop species on the territory. In some cases the two terms have been used interchangeably (*e. g.* Willey 1979). The distinction between the two terms may be useful, however, since the spatial arrangement of coexisting species within mixtures is important in determining mixture performances (Andrews 1972, Mead 1979, Willey 1979, Yunusa 1989). Intercropping is also considered to be space-dependent form of multiple cropping, (Pearce and Gilliver 1978, Mead 1979, Mead and Willey 1980, Nnko and Doto 1980, Vandermeer 1989). In both the mixed cropping and intercropping systems, the component species are not necessarily sown at exactly the same time. Also, harvesting time may be different, but the crops usually co-exist for a significant part of their growing periods.

Spatial and temporal arrangement of the intercropped species may also vary, resulting in various intercropping patterns (Andrews and Kassam 1976). Intercropping is further categorized into: (1) row intercropping, which involves growing two or more crops simultaneously, where one or more crop species are planted in rows. This pattern is gaining prominence in the tropics, particularly where ploughs have replaced machetes and fire as the main tool of land preparation. (2) strip intercropping in which two or more crops are grown simultaneously in different (alternating) strips, wide enough to permit independent

cultivation, but narrow enough for the crops to interact agronomically. This system is more common in societies in the tropics and subtropics, where machinery is used for tilling and planting. (3) relay intercropping, which involves coexistence of two or more crops during only part of their life cycles, but in the remainder of their life cycles they do not overlap. This form of intercropping may actually include the other three, since its primary categorization variable is time (Vandermeer 1989). (4) alley intercropping (or hedgerow intercropping), is a low input crop production system in which crops are grown in the spaces between rows of planted woody shrub or tree species, usually legumes. Here, the woody species are periodically pruned to: prevent shading, provide green manure (*in situ*) and mulch for the companion crops, minimize intercrop competition for moisture and nutrients, and provide fuelwood or stakes (Jama 1993, Ssekabembe 1984, Mugendi 1991).

Multiple cropping is popular among small-scale farmers in the tropics and subtropics (Wahua and Miller 1978, Willey 1979). It is so deeply established among peasant farmers that a complete change of the system to sole cropping may not be acceptable to many (Nnko and Doto 1980). In most of sub-Saharan African agriculture, Kenya included, the system is characterized by low, or no, use of inputs such as fertilizers, herbicides and pesticides (Nyambo *et al.* 1980). Such inputs are costly and there is limited technical know-how among the farmers (Vandermeer 1989). Subsistence farming in Kenya, which comprises about 80% of the Kenyan agriculture, is almost entirely intercropping. For example, only 6% of beans, the most important pulse and second to maize in importance as a food crop, is produced from pure stands (Njuguna *et al.* 1981). The remaining 94% of bean production occurs in mixtures, mainly with maize and other cereals, *e. g.* sorghum and millet.

In the past, particularly in the tropics, intercropping has sometimes been looked upon as a backward and disadvantageous system as compared with monocropping (Willey 1979, Nyambo *et al.* 1980). As a result, relatively little research on intercropping; was carried out. But since about 1970, there has been a growing interest in intercropping, as it has been recognized as a complex and potentially beneficial system of crop production. A number of institutions are prominently engaged in research on intercropping in the tropics and sub-tropics, including research institutes such as International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), International Center for Research in Agroforestry (ICRAF),

International Institute of Tropical Agriculture (IITA), Centro Internacional de Agricultura Tropical (CIAT), under their umbrella body Consultative Group on International Agricultural Research (CGIAR), as well as universities and national research institutes, *e. g.* Kenya Agricultural Research Institute (KARI). In developed countries, research on crop mixtures has mainly focussed on pastures and meadows (Stern and Donald 1962, Turkington,*et al.* 1979, Turkington and Harper 1979, Haynes 1980, Snaydon and Howe 1986, Snaydon and Satorre 1989, Duralia and Zimdahl 1991, Goldberg and Barton 1992, Turkington and Chanway 1993, Wedin and Tilman 1993, Tilman *et al.* 1996, Turkington and Jolliffe 1996).

Research on mixed associations has shown that productivity is sometimes enhanced compared with pure stands (Willey and Osiru 1972, Trenbath 1974, Willey 1979, Natarajan and Willey 1980, Ofori and Stern 1987, Snaydon and Satorre 1989, Yunusa 1989, Pilbeam *et al.* 1994, Tilman *et al.* 1996, Bulson *et al.* 1997, Jolliffe 1997). Relay intercrops extend the total production period, allowing more extended exploitation of environmental resources than a single-season crop may accomplish. Yield advantages in contemporary species mixtures have been attributed to the complementary interactions between the component crops, resulting in more complete use of environmental resources than when species are grown separately (Natarajan and Willey 1980, Snaydon and Satorre 1989, Pilbeam *et al.* 1994, Bulson *et al.* 1997). The mechanisms of these complementary interactions are not fully understood, but are thought to be related to: (1) more light interception in an intercrop due to light being more efficiently spread over a greater leaf surface, in time and space (2) better ground cover resulting in less evaporation from the soil, hence better water uptake and more efficient water use, (3) occupation of different soil strata by roots of the associated species, (4) nitrogen transfer from legumes to non-legumes, in legume/non-legume intercrops (Agboola and Fayemi 1972, Natarajan and Willey 1980, Reddy and Willey 1981, Bandyopadhyay and De 1986, Elmore and Jackobs 1986, Gliessman 1986, Patra *et al.* 1986, Senaratne and Ratnasinghe 1993, Bulson *et al.* 1997) and (5) better uptake of nutrients in mixtures than in sole crops (Dalal 1974, Hall 1974, Natarajan and Willey 1980, Reddy and Willey 1981). In addition to increased resource exploitation, altered risks to pests and diseases, and beneficial microclimate changes may contribute to yield advantages in mixed associations (Fukai 1993).

Multiple cropping is also of interest in relation to issues of pollution and the conservation of natural resources (Fageria 1992). The use of cover crops and green manures, which can be considered as forms of relay intercropping, is gaining prominence in developed countries as a means to check nitrate leaching and prevent deterioration of ground water quality (*e. g.* Francis *et al.* 1992, Aweis 1994, Bomke *et al.* 1996, Jannink *et al.* 1996). Intercropping, particularly combinations of N-fixing legumes with non-legumes, may become more important with the increasing importance of organic farming in the developed countries (Bulson *et al.* 1997).

Multiple cropping systems are also significant to farmers because of the economic and nutritional benefits these farming systems can confer. These include: diversity of diet and income source, stability of production, efficient use of family labor, and intensive production with limited land resource (Francis *et al.* 1976, Wahua and Miller 1978, Willey 1979, FAO 1991). Multiple cropping systems, however, are not necessarily superior to sole crops. Crop mixtures are more complex than sole crops and they can be difficult to manage, especially under mechanized agriculture (Willey 1979). Also, yield disadvantages in intercrops have been reported (Willey and Osiru 1972, Trenbath 1974, Fisher 1979, Pilbeam *et al.* 1994), sometimes due to insect pests and diseases in the mixed associations (Ministry of Agriculture, Kenya 1983, Willey 1979).

2.5 Some measures of performance of mixed crop associations

In an emerging area of scientific investigation, it is not unusual for a number of different experimental approaches and assessments to be attempted. This is the case for studies on crop mixtures, where several relative and total measures of mixture performance, such as those described in the following sections, have been used. In addition to the measures detailed here, which include the most commonly used measures of intercrop productivity (RYT and LER), other assessments have been used. Other approaches, not used in this thesis, include the use of relative resource total (Connolly 1987, Turkington and Jolliffe 1996), and bivariate analysis of intercrop yields (Mead 1983, Vandermeer 1989, Snaydon and Satorre 1991).

2.5.1 Relative Yield Total and Land Equivalent Ratio

Some of the early studies on the productivity of crop mixtures used a replacement series structure (de Wit 1961). This is a substitutive design in which component species are mingled in varying proportions, so that as the proportion of one species increases, other species decline. For a two-species replacement series, de Wit and Van den Bergh (1965) used Relative Yield Total (RYT) to compare the productive performances of mixtures with pure stands. In a binary mixture:

$$RYT = (Y_{ij}/Y_{ii}) + (Y_{ji}/Y_{jj}) \qquad (2.6)$$

where, as before, Y represents yield per unit land area, and the subscripts i and j designate the two crop species. Here, the species are either grown together in the same plot as a mixture (ij and ji) or in separate plots as monocultures (ii or jj). This index was used in two major studies that attempted to resolve the question of whether mixtures are more productive than monocultures (Trenbath 1974, Hiebsch and McCollum 1987).

Relative productivity of mixtures and pure stands has also been calculated using land equivalent ratio (LER), defined as the relative land area under pure stands that is required to produce the yields achieved in mixtures of two or more species, under the same level of crop management (Willey 1979, Mead and Willey 1980, Fageria 1992). This index is also calculated from:

$$LER = (Y_{ij}/Y_{ii}) + (Y_{ji}/Y_{jj}) \qquad (2.7)$$

the same formula used to calculate RYT. According to Willey (1979a, 1979b), there are three outcomes that can arise from eqn. (2.6) or (2.7): values of LER or RYT less than 1.00 indicate mutual inhibition, *i. e.* the crops show antagonism in mixture; LER greater than 1.00 indicates cooperation or a complimentary relationship; and LER equal to 1.00 indicates mutual compensation or neither an antagonistic nor complimentary interaction between the two species. The LER concept has also been extended to take into account the persistence of crop production over time and space *e. g.* area-x-time equivalency ratio (Hiebsch and McCollum 1987), area harvest equivalency ratio (Balasubramanian and Sekayange 1990), and effective and staple land equivalent ratios (Riley 1985).

Several different bases have been used for the calculation of LER. In many cases LER is determined in the context of a replacement series experiment and is equivalent to RYT. However, optimum pure stand yields (Huxley and Maingu 1978) and mean pure stand yields (Pilbeam *et al.* 1994) have also been used in the denominators of eqn. (2.7). Over time, the variable standards used in calculating LER may have an unfortunate consequence: different researchers reporting different LER values may, in fact, have similar productive situations, or conversely, different researchers reporting the same LER values may in fact have different productive situations.

It should also be noted that in calculations of RYT and LER the total area and numbers of individuals present in the pure stands do not correspond to those used in the mixture and hence are not precise operational alternatives (Jolliffe 1997). It is generally accepted that the total output from crops depends on the area of land that is under production, and on the plant numbers that populate that land. Hence, it can be argued that a comparison of the relative productive performances of mixtures and pure stands should be based on the same land area and populations, which is not true for either RYT or LER (Jolliffe 1997).

2.5.2 Relative Land Output and Total Land Output

To deal with this problem, Relative Land Output (RLO) was introduced as a measure of the relative yields of mixtures and pure stands involving equal plant populations and land areas (Jolliffe 1997). RLO is a generalization of a measure used by Wilson (1987) for mixtures involving balanced populations. For a set of plant species (suscripts i, j, ...), RLO is given by:

$$RLO = (Y_i+Y_j+...)_m/(Y_i+Y_j+...)_p \qquad (2.8a)$$

where Y again indicates species yield per land area and subscripts m and p designate mixtures and pure stands, respectively. For RLO, the yields are obtained from equal plant populations and land areas allocated to the pure stands and mixtures. For a binary mixture, using the same notation as for RYT and LER, eqn. (2.8) can be re-expressed as:

$$RLO = (Y_{ij}+Y_{ji})/(Y_{ii}+Y_{jj}) \qquad (2.8b)$$

As detailed in Jolliffe (1997), RLO can be calculated directly from experimental observations where pure stands are grown at the same total density as the mixtures, a situation that occurs in constant density replacement series.

However, relative productive performances of mixtures *vs.* pure stands, assessed by RYT, LER or RLO, are not necessarily the issue which is of greatest importance in agronomy. A farmer is likely to be more concerned with the question of what production system offers the greatest sustainable total production than with whether a mixture is more productive than pure stands. Total production is assessed by Total Land Output (TLO), which is simply calculated from the sum of the yields of all species present, and has no implicit constraints concerning relative or total species densities:

$$\text{TLO} = (Y_i + Y_j + \ldots) \tag{2.9}$$

It should be noted that RYT and LER, but not RLO and TLO, can be calculated if measures of yield for the different crops are qualitatively different. To deal with this problem for RLO and TLO, surrogate measures for yield, such as nutritional or economic value, could be used when the original measures of yield are qualitatively different.

2.5.3 Mixture productivity and yield-density relationships

In addition to directly calculating RYT, RLO and TLO from experimental observations of crop yield, these measures could be estimated from yield-density relationships, if adequate relationships are known. This was one approach recently used to assess the general tendency for yield advantages in binary associations (Jolliffe 1997), and in that study a variety of yield-density models were used. Here, the inverse yield-density relationships described earlier will be exploited.

Re-expressing species population density X, as number of plants (n) of a species per unit land area (A), then yields per unit land area may be predicted from mean yields per plant:

$$Y_i = y_i X_i \text{ or } Y_i = y_i n_i / A \tag{2.10a}$$

$$Y_j = y_j X_j \text{ or } Y_j = y_j n_j / A \tag{2.10b}$$

It should be noted that errors in estimating yields (*y*) will be magnified when they are multiplied by n/A. Using the inverse yield-density models described earlier (eqn. (2.2)) mixture yields per unit land area can be predicted from:

$$Y_{ij} = (Y_i)_m = (n_i/A)/(a_{io} + a_{ii} n_i/A + a_{ij} n_j/A) \tag{2.11a}$$

$$Y_{ji} = (Y_j)_m = (n_j/A/(a_{jo} + a_{jj} n_j/A + a_{ji} n_i/A) \tag{2.11b}$$

and these estimates can be substituted in eqn (2.6), (2.8) and (2.9) to predict RYT, RLO and TLO, respectively. The inverse models also allow the prediction of pure stand yields for the RYT and RLO calculations. In the pure stands, the companion species are absent. Also, for both RYT and RLO the pure stands involve the same densities as the total density of the mixtures. Hence:

$$(y_i^{-1})_p = a_{io} + a_{ii}(n_i + n_j)/A \tag{2.12a}$$

$$(y_j^{-1})_p = a_{jo} + a_{jj}(n_i + n_j)/A \tag{2.12b}$$

In calculating RYT for a constant density replacement series, each pure stand will contain the same number of plants as the combined species have in the mixture. Hence for RYT:

$$Y_{ii} = (n_i + n_j)/(a_{io} + a_{ii}(n_i + n_j)/A) \tag{2.13a}$$

$$Y_{jj} = (n_i + n_j)/(a_{jo} + a_{jj}(n_i + n_j)/A) \tag{2.13a}$$

In the case of RLO, each pure stand contains the same number of individuals that the particular species has in mixed population. Hence:

$$(Y_i)_p = (n_i)/(a_{io} + a_{ii}(n_i + n_j)/A) \tag{2.13a}$$

$$(Y_j)_p = (n_j)/(a_{jo} + a_{jj}(n_i + n_j)/A) \tag{2.13a}$$

Finally, combining eqn. (2.11) and (2.12):

$$RYT = [(a_{io} + a_{ii}(n_i + n_j)/A)]/(a_{io} + a_{ii}n_i/A + a_{ij}n_j/A)]$$
$$+ [(a_{jo} + a_{jj}(n_i + n_j)/A)]/[(a_{jo} + a_{jj}n_j/A + a_{ji}n_i/A)] \tag{2.14}$$

and combining eqn. (2.11) and (2.13):

$$RLO = \frac{[n_i/(a_{io} + a_{ii}n_i/A + a_{ij}n_j/A)] + [n_j/(a_{jo} + a_{jj}n_j/A + a_{ji}n_i/A)]}{[n_i/(a_{io} + a_{ii}(n_i + n_j)/A] + [n_j/(a_{jo} + a_{jj}(n_i + n_j)/A)]} \tag{2.15}$$

If the yield-density relationships provide an adequate description of crop performance on a land area basis, they allow the evaluation of how the relative and total measures of mixed crop performance are related to model parameters. For example, note that RYT or RLO must equal 1.0 when $a_{ii} = a_{ij}$ and $a_{jj} = a_{ji}$. They may not equal 1.0 when $a_{ii} \neq a_{ij}$ and/or when $a_{jj} \neq a_{ji}$ although offsetting yield responses of the two species might occur (Jolliffe 1997).

2.6 Crops used in these investigations

2.6.1 General

Common bush bean (*Phaseolus vulgaris* L.) cv. Contender and table beet (*Beta vulgaris* L.) cv. Ruby Queen, were used in this research. These crops were selected for use for several reasons: (i) both crops are well adapted for growing in British Columbia, (ii) individual plants of the two species have similar growth potentials in that they have approximately the same stature at maturity, (iii) their recommended pure stand population densities, for vegetable crop production, overlap (Anonymous 1994), (vi) both crops may be planted and harvested at about the same time during the time of growth, allowing the effects of continuous coexistence to be assessed, (v) the crops provide a contrast in that bean yields depend on above-ground reproductive development (pods) while beet yields depend on vegetative growth (storage roots), and (vi) one crop is a legume (bean) and the other (beet) a non-legume, analogous to the legume/non-legume combinations often used for intercrops in tropical and sub-tropical regions.

2.6.2 Common bean

Common or kidney bean (*Phaseolus vulgaris* L.), a member of the Leguminosae, is thought to have originated in south and central Americas: large seed types in Peru date from the period 6,000 to 5,000 BC, while small seed types in Mexico and Guatemala date from 500 to 300 BC (Thompson and Kelly 1953, Gepts *et al.* 1988, Yamaguchi 1983, Peirce 1987, Nonnecke 1989). European settlers to North America found native Indians interplanting beans and maize in the 17th century (Peirce 1987). Explorers and traders stocked their ships with beans, and through this trade bean seeds were introduced to Europe, Asia and Africa. Today, beans are mainly grown for pods and immature seeds in developed countries, and for shelled dry beans in subsistence farming in the tropics.

Phaseolus vulgaris is a warm season annual crop and is sensitive to frost. Seeds are planted at a depth ranging from 2 to 5 cm, depending on the soil type and the moisture conditions. Beans germinate in about six days under optimum conditions, and the optimum temperature for germination is 30^0C (Yamaguchi 1983). Germination does not take place below 10^0C or above 35^0C (Yamaguchi 1983, Peirce 1987, Nonnecke 1989). Vegetative

growth of beans requires mean daily temperatures between 15 and 30^0C (Yamaguchi 1983, Peirce 1987, Nonnecke 1989). Temperatures below or above this range can have deleterious effects on the performance of the beans (Nonnecke 1989). As it grows, the bean plant produces a series of trifoliate leaves, following the initial pair of opposite primary leaves. Bean cultivars include both determinate (bush) types and indeterminate (pole) types (Peirce 1987, Ware and McCollum 1980, Nonnecke 1989). Flowers, which are self-fertile, occur in axillary racemes (Ware and McCollum 1980, Nonnecke 1989).

Beans can be harvested as early as seven to nine weeks after seedling emergence. The time of harvesting is usually a compromise between total yield and quality, and regular pod removal can increase yield, compared to a single harvest (Lovett Doust and Eaton 1981). For cultivars grown for pod production, harvesting should be done before seeds are large enough to cause the pod to bulge around the seeds (Thompson and Kelly 1953). The pods are slender, 7.5 to 20 cm long. Pods may be straight or slightly curved, with varying color and number of seeds depending on the cultivar (Adams *et al.* 1985).

Phaseolus vulgaris plants have a shallow root system, forming their main feeder roots in the upper 20 to 30 cm of the soil in a radius of about 45-70 cm from the stem. Due to the shallow roots, even a brief nutrient or moisture deficiency can cause some stress in bean, lowering crop yield (Nonnecke 1989). In areas where rainfall is inadequate for the growth of beans, irrigation is recommended for higher yields (Ware and McCollum 1980, Peirce 1987, Nonnecke 1989). *Phaseolus vulgaris* thrives in fertile, well-drained and well-aerated soils (for optimum nitrogen fixation by the root nodules), having a soil pH just below neutral (Yamaguchi 1983, Peirce 1987, Nonnecke 1989). The optimum soil pH for beans lies between 5.5 and 6.5 (Fageria *et al.* 1991).

Compared with other legumes, beans are usually a poor biological N-fixer, especially in the tropics (Singh 1992); furthermore, increased nitrogen fixation is not necessarily associated with increased seed yield (Buttery *et al.* 1990, cited by Singh 1992). Application of N-fertilizers suppresses nodulation in beans thereby reducing their biological N-fixing capacity, although it has been observed that small "starter" N-applications may be necessary in N-deficient soils, without affecting the symbiotic system (Graham 1981). Symbionts

commonly associated with *P. vulgaris* are: *Rhizobium leguminosarum* bv. *phaseoli*, *Rhizobium tropici*, and *Rhizobium etli* (Martinez-Romero 1994).

When grown in pure stands, beans are usually planted in rows with between-row spacing ranging from 30 to 75 cm, and within-row spacing ranging from 5 to 22.5 cm. (Kay 1979, Lorenz and Maynard 1988). In the tropics and sub-tropics, beans are commonly intercropped with maize (Laing *et al.* 1987), and sometimes with a number of other crops, including sorghum, millet, cassava and coffee. This bean/non-legume intercropping is commonly applied in the hope that bean, being a legume, may not compete for soil N, and may supply the non-legume with biologically fixed nitrogen. In maize/bean intercrops, a between-row spacing of 75 cm and within-row spacing of 30 cm is common (Fisher 1977, Fisher 1979, Chemining'wa and Nyabundi 1994). In different intercrops, however, plant spacing and planting patterns may vary depending on the companion species.

Important bean diseases are: (i) bacterial diseases, including common blight and fuscous blight (*Xanthomonas phaseoli* and *Xanthomonas phaseoli* var. *fuscans*), halo blight (*Pseudomonas phaseolicola*) and bean wilt (*Corynebacterium flaccumfaciens*), (ii) fungal diseases, including anthracnose (*Colletotrichum lindemuthianum*), angular leaf spot (*Isariopsis griseola*), ascochyta leaf spot (*Ascochyta phaseolorum*), gray mold (*Botrytis cinerea*), white mold (*Sclerotinia sclerotiorum*) black root rot (*Chalara elegans*), fusarium root rot (*Fusarium solani* f. sp. *phaseoli*), damping-off, rhizoctonia root rot (*Rhizoctonia solani*), downy mildew (*Erysiphe polygoni*), bean rust (*Uromyces appendiculatus*) and ashy stem blight (*Macrophomina phaseoli*), and (iii) viral diseases, including common bean mosaic, bean yellow mosaic, bean curly top, mottle dwarf, and bean golden mosaic viruses (Peirce 1987, Nonnecke 1989, Howard *et al.* 1994, Anonymous 1994).

Beans are also susceptible to nematodes, the most important of which are: northern root-knot nematode (*Meloidogyne hapla*), root lesion nematode (*Pratylenchus penetrans*) and stubby-root nematodes (*Paratrichodoru* spp.). Important insect pests include: aphids, Mexican bean beetle, European corn borer, seedcorn maggot, European earwig and cutworms (Peirce 1987, Nonnecke 1989, Howard *et al.* 1994, Anonymous 1994).

2.6.3 Table beet

Beet (*Beta vulgaris* L.) is a member of Chenopodiaceae, and is believed to have originated in the Mediterranean region of North Africa, Europe and Middle East. It has been cultivated since at least fourth century BC (Ware and McCollum 1980, Yamaguchi 1983, Nonnecke 1989). The principal beet production areas in North America are New York, Wisconsin, Oregon and Texas in the United States, and Quebec and Ontario in Canada, with Ontario producing the highest yields (Nonnecke 1989). *Beta vulgaris* includes four agricultural types of beets: sugar beet, fodder beet, Swiss sward and table (vegetable) beet. The research described in this thesis involved table beet, the type which is grown mainly for human consumption of its storage roots and tops (Peirce 1987, Nonnecke 1989).

Beta vulgaris is a biennial species that can tolerate cool climates. The beet "seed" for most cultivars is actually a fruit consisting of 2 to 6 true seeds (Ware and McCollum 1980, Salunkhe and Desai 1984, Nonnecke 1989). The true seeds are small, kidney-shaped and brown; they retain their viability for five to six years under ordinary storage conditions (Ware and McCollum 1980). Germination can occur at a wide range of soil temperatures, from 10 to 29^{0}C. Planting depth is shallower than for bean, at about 1.5 to 2.5 cm, and shoot emergence after planting is several days slower than in beans.

During the vegetative phase of the first year, beet plants form a rosette of fleshy, large ribbed leaves. Leaf colour may vary from dark red to light green (Ware and McCollum 1980, Yamaguchi 1983, Nonnecke 1989). In the rosette form, leaf petioles are attached to a compresssed stem, forming the root crown. Mean daily temperatures of 16 to 18^{0}C are optimum during vegetative growth (Yamaguchi 1983, Peirce 1987). Extreme temperatures may trigger bolting in beets (Thompson and Kelly 1957) - if plants are subjected to relatively low temperatures (4.5 to 10^{0}C), for a period of fifteen or more days, bolting will occur before the root reaches marketable size. In home gardens, bolting occurs mainly because of vernalization, caused by sowing beet seeds too early (Nonnecke 1989). Flower formation in beets is accelerated by long days, although under most growing conditions, bolting in the first season is rare (Peirce 1987).

The storage root of beet is as a result of swelling of the hypocotyl plus a small portion of the tap root. Storage roots are usually red in color, although golden cultivars are also grown. The red color is due to betacyanin pigment, a nitrogen containing compound (Yamaguchi 1983, Nonnecke 1989), and yellow pigments, betaxanthins, are also prominent (Peirce 1987, Nonnecke 1989). The remainder of the root system consists of a prominent taproot, that develops rapidly and may reach a depth of 3 m, plus lateral roots that emerge from the base of the swollen edible structure. Some of the lateral roots may extend a substantial distance from their source, both horizontally and vertically. The root system is not especially dense. Close spacing does not seem to increase below-ground competition to a level that detracts from root quality (Peirce 1987).

Beta vulgaris requires a well drained, loamy soil often with soil organic matter built up with legumes in a three to four year rotation, or with additions of well rotted manure. For optimum growth, beets require a slightly acidic soil, with soil pH being between 6.0 and 7.0. In monoculture, beets are planted in rows spaced at 30 to 75 cm, and seedlings are thinned after emergence to achieve within-row spacing of 5 to 10 cm (Peirce 1987, Lorenz and Maynard 1988, Nonnecke 1989). Growth of beets is limited by lack of adequate moisture, and irrigation is recommended to supplement rainfall during droughty periods. Fertilizer requirements vary with the soil type and fertility. Excessive applications of N may favour above-ground biomass formation at the expense of root growth, and roots may have poor color (Yamaguchi 1983). Other than in research situations, beets have not been exploited as intercrops. In an intercrop, the boron requirements and tolerances of beets and their companion crops needs to be considered, since beet has a higher requirement for boron than many other species.

The time of harvesting of beets depends on the intended use. They can be harvested early during the time of growth as leafy greens, or they can be harvested for fresh market (bunching) when the roots attain a diameter of about 3 to 4 cm (Salukhe and Desai 1984). Beets are also harvested for pickling and canning when the roots are about 7 cm in diameter. The mature harvesting stage is when the diameter of the roots is about 7 to 10 cm. The mature roots have their tops removed and can be stored for several months after harvest (Shoemaker

1953). Commercially grown beets, used for processing, are harvested mechanically, while garden beets are manually harvested.

Disease problems are usually a minor factor in beet production (Peirce 1987), but the most important diseases which occur are: (i) bacterial disease, particularly scab (*Streptomyces scabies*), (ii) fungal diseases including aphanomyces (black) root rot (*Aphanomyces cochlioides*), leaf spot (*Cercospora beticola*), downy mildew (*Peronospora farinosa*), fusarium wilt (*Fusarium oxysporum*), phoma leaf spot and root rot (*Phoma betae*), pythium root rot (*Pythium aphanidermatum*), rhizoctonia root rot (*Rhizoctonia solani*), and white rust (*Albugo occidentalis*), and (iii) viral disease, particularly curly top virus. The most common insect pests in beet production include: leaf miners, aphids, leafhoppers, and flea beetles (Howard *et al.* 1994.). Nematode pests are northern root-knot (*Meloidogyne hapla*), root-lesion (*Pratylenchus penetrans*) and sugarbeet cyst (*Heterodera schachtii*). Lack of boron in the soil may cause heart rot in storage roots of beet (Shoemaker 1953, Howard *et al.* 1994).

3. Effects of soil fertility and time of growth on competitive balances in mixtures of bush bean (*Phaseolus vulgaris* L.) and common beet (*Beta vulgaris* L.)

3.0 Summary

Field experiments were conducted during the summers of 1994 and 1995 to study the effects of soil fertility and within- and between-species competition on plant growth in associations of bush bean (*Phaseolus vulgaris* L. cv Contender) and common beet (*Beta vulgaris* L. cv Ruby Queen) plants. At two soil fertility regimes, plants were grown in pure stands at three population densities and in nine mixed stands at different combinations of species population densities, in a split plot randomized complete block design. At the end of each season several measures of plant growth were taken for each species, including leaf area, dry masses of aboveground parts, bean pod dry mass and beet storage root fresh mass. All of these measures decreased with increasing species population densities. Inverse yield-density models indicated that bean was the stronger competitor in 1994, while beet was the stronger competitor in 1995. Competitive impacts, however, differed among different measures of plant growth and also differed between the two fertility regimes. In both species, there were relatively strong competitive responses at the higher soil fertility level, while for many measures of plant performance competition was not detected at the lower soil fertility level.

3.1 Introduction

Plants growing in close proximity, either in mixed species associations or in pure stands, tend to interfere. Interference is assessed according to plant responses to the presence of their neighbours (Harper 1961), and interference typically intensifies as plant population density increases. Inverse yield-density models reflect this pattern, describing the decline in mean size per plant with increasing plant population density. Such models arose following the work of Kira *et al.* (1953) on pure stands, and have been used to evaluate competition in binary mixtures since the early 1980's (Suehiro and Ogawa 1980, Wright 1981, Spitters 1983, Firbank and Watkinson 1985, Connolly 1988, Jolliffe 1997). Parameters of inverse yield-density models can be used to quantify the within- and between-species competitive influences (Wright 1981, Spitters 1983).

Various mechanisms of interference are possible, including competition for mutually required environmental resources, and allelochemical interactions. It is often difficult to disentangle the individual components of interference. For the purpose of this presentation, I will assume that competition is the dominant component, although the occurrence of other contributors to interference cannot be ruled out. This follows the approach of Welden and Slauson (1986) and Aspinall and Milthorpe (1959), who have used plant competition to denote that restriction in the growth of a plant which arises from its association with other plants. It follows that a strong competitor is one that strongly retards the growth of its neighbours, while a weak competitor is one that has less effect on associated plants. For example, in an experiment using mixed populations of barley (*Hordeum vulgaris* L.) and persicaria (*Polygonum lapathifolium* L), Aspinall and Milthorpe (1959) found that barley was the stronger competitor: barley significantly decreased the relative growth rate of persicaria, while persicaria had little effect on barley.

There is accumulating evidence that the competitive balances between mixed species are not fixed, but can be modified by other factors (Jolliffe 1997). Some modifying factors include time of emergence (Mann and Barnes 1947, Milthorpe 1961), salinity (Suehiro and Ogawa 1980), light (Muli 1995), time of growth (Mchaina 1991, Minjas 1981), and source of plant material and time of observation (Turkington and Jolliffe 1996). The ability of the circumstances of growth to change competitive relationships is of interest in several ways, including the connections such changes have with plastic responses of growth (Chapter 5) and patterns of mixture productivity (Chapter 6). In addition, such changes are pertinent to two alternative views of the relationship between competition and productivity. It has been argued (Grime 1973, Grime 1977, Grime 1979) that the intensity of plant competition should increase along an increasing productivity gradient, but others have argued that the intensity of competition should not change with increasing productivity (Newman 1973, Tilman 1982, Grubb 1985, Tilman 1988, Tilman 1990a). Although such concepts were developed for natural plant communities, and are often considered in connection with community dynamics and succession, they can be explored through investigations during one time of growth using simple agricultural crop associations.

Soil fertility is one of the factors which has been reported to influence plant competition. For example in studies on two plant species, *Erica* sp. and *Molinia* sp., Berendse and Elberse (1990) found that *Erica* was the stronger competitor under low nutrient conditions while *Molinia* became the stronger competitor when nutrient supply was increased. Stern and Donald (1962) studied canopy development in a grass/clover mixture at four levels of N application. They found that at low N levels clover was the stronger competitor, while at high N levels the grass dominated. Using a binary mixture of annuals, *Poa annua* and *Stellaria media*, Connolly *et al.* (1990) found that under high nutrient levels *Stellaria* was a stronger competitor than *Poa*, but with time *Poa* became stronger than *Stellaria*. They attributed this reversal to *Stellaria*'s earlier and more substantial diversion of resources to reproductive development. Interactions of fertility with competitive balances may also contribute to some patterns of plant production in agronomic mixtures. These include the occurrence of relative yield improvements under low nitrogen supply (Reddy *et al.* 1980, Hiebsch and McCollum 1987, Ofori and Stern 1987, Russell and Caldwell 1989) and the improvements in nitrogen relations in legume/non-legume intercrops (Agboola and Fayemi 1972, Natarajan and Willey 1980, Bandyopadhyay and De 1986, Elmore and Jackobs 1986, Gliessman 1986, Patra *et al.* 1986, Senaratne and Ratnasinghe 1993, Bulson *et al.* 1997).

The present study utilizes inverse yield-density models to evaluate the stability of competitive balances in bush bean (*Phaseolus vulgaris* L.) and common beet (*Beta vulgaris* L.) associations grown at two levels of soil fertility during two different seasonss. Several measures of plant growth will be assessed in order to determine whether within- and between-species competitive balances are consistent for different measures, different seasonss and different levels of soil fertility. Results from this study will also be used to address the question as to whether the intensity of competition changes at different levels of productivity.

3.2 Materials and methods

3.2.1 Site description, crop production practices and experimental design

Field experiments were conducted during the summers of 1994 and 1995 on two sites at the Totem Park Field Station of the University of British Columbia. For both sites, the soil was a

silt loam, with an average plow pan of about 0.20 metres. Textural analysis indicated that the soil for 1994 site was more silty than the 1995 site, which was more sandy (Appendix 1a). Soil analysis, carried out using the method of van Lierop and Gough (1989) prior to planting in both years, indicated that N, Mg and S were low in the 1994 site, while N, P, K, Mg and S were low in the 1995 site. Soil pH was 5.9 at the 1994 site, and 5.6 at the 1995 site (Appendix 1a). Soil organic matter content was 4.0% at both sites. In each year dolomitic limestone, 600 kg ha^{-1}, was incorporated into the top 15 cm of the soil three weeks before planting. Two fertility levels were established through fertilizer application at the time of planting: 0 kg ha^{-1} or 200 kg ha^{-1} of 20:10:10+10S compound fertilizer. In both years, fertilizer was broadcast and raked into the soil for the plots receiving the fertilizer application. *Rhizobium* inoculation was not done. (The experimental scenario was intended to reflect the difference between farmers who can afford to use fertilizer and those who cannot afford soil amendments.)

Bush bean (*Phaseolus vulgaris* L. cv "Contender") and common beet (*Beta vulgaris* L. cv "Ruby Queen") were used in both years. The experiments involved a split plot randomized complete block design, in which the plant population density treatments (Table 3.1) were randomly assigned to the subplots, and the two fertilizer treatments randomly assigned to the main plots, with two replications per treatment per year.

Table 3.1. Population density combinations.

Bean population density (plants m^{-2})	Beet population density (plants m^{-2})			
	0	16	32	48
	bean:beet			
0	0:0	0:16	0:32	0:48
16	16:0	16:16	16:32	16:48
32	32:0	32:16	32:32	32:48
48	48:0	48:16	48:32	48:48

Four weeks before planting the experimental sites were treated with 400 kg ha^{-1} of dazomet (BASF Basamid Granular 90%) for weed control. Subsequent weed control involved

hand-weeding the plots during the time of growth. The two species were sown in rows in a square planting pattern, at equal within- and between-row distances (Table 3.2), in square subplots measuring 2.3m on a side. The planting pattern in the mixed associations was dictated by the proportion of the species in each subplot, e. g. for 1:1 mixtures, the planting pattern was alternating rows; for 1:2 or 2:1 mixtures, two rows of beets or beans were alternated with one row of each of the species, and so on. Planting was scheduled in June to minimize the risk of chilling in bean. Also, the early growth of beet plants is slower than in beans (Mchaina 1991), so beets were planted earlier than beans. In the 1994 experiment the beets were planted by hand on June 9 with sowing done at one seed per hill. Beans were planted by hand on June 16, also at one seed per hill. The same procedure was carried out for the 1995 experiment, in which beets were planted on June 16 followed by beans, on June 23. Pre-planting tests had indicated that germination rate exceeded 95% in both species. Gaps in experimental plots were filled, within two weeks of planting, by taking seedlings from reserve plots prepared for each species. After planting, irrigation was applied as necessary to supplement natural rainfall, using ground sprinklers.

Table 3.2. Total population density and within- and between-row distances.

Plant population density combination (bean:beet)	Total population density (plants m^{-2})	Within- and between-row distances (m)
0:16 or 16:0	16	0.25
0:32 or 32:0	32	0.18
16:16	32	0.18
16:32 or 32:16	48	0.14
0:48 or 48:0	48	0.14
16:48 or 48:16	64	0.12
32:32	64	0.12
32:48 or 48:32	80	0.11
48:48	96	0.10

3.2.2 Harvesting and data collection

Bean plants can undergo rapid leaf senescence and abscission at the end of pod filling. Harvests were timed to precede significant bean leaf loss due to abscission, and to precede loss due to fungal infestations in bean near the end of the time of growth. In 1994, bean plants were harvested between August 23 and August 26, and beets were harvested between August 27 and September 1. In 1995, beans were harvested between August 23 and August 28 while beets were harvested between August 29 and September 2. In both years ten plants per species were harvested from the central region of each subplot, randomly selecting them from plants growing at least three rows away from the sub-plot border to avoid edge effects. For beans, the shoots were cut at the ground level, whereas for the beets the shoots plus the storage roots were pulled from the ground.

Harvested plants were separated into leaves, stem and pods for beans, and leaves and storage root for beets. Leaf area per plant was measured using a LI-COR LI-3000 leaf area meter. Total number of pods per plant for the beans was counted and recorded. Dry masses of the separated plant parts were measured after harvested samples were dehydrated for five days at 70^0C under forced ventilation. Beet storage roots required additional time to dry and were kept at 70^0C for 30 days to reach constant mass. Nitrogen fixation by the bean plants was not quantitatively assessed. The occurrence of N-fixation, however, was suggested by the presence of root nodules on plants, pink in cross-section, in both the fertilized and unfertilized treatments.

Bean pods and beet storage roots were harvested from an additional ten plants per species per subplot, again taking them from the central region of the sub-plots. These were used to determine both the fresh and dry masses of both marketable bean pods and marketable beet storage roots. The marketability criteria used were as described by the Horticulture Branch of the B. C. Ministry of Agriculture (1977). Bean pods were considered to be marketable if they were greater than 0.05 m in length, green, fresh, free from stringiness, attractive to the eyes and with little outward sign of seed formation. Beet storage roots were considered to be marketable if the roots were intact, red in color, with small to medium crowns, free from splits, scaling and sunburn and with the inside of the roots free from light color and cutting smoothly.

3.2.3 Statistical analysis

Data analysis involved two main steps. Firstly, analysis of variance was used to detect significant sources of experimental variation for each plant measure. Secondly, inverse yield-density models were developed in order to quantify within- and between-species influences.

For every plant measure, homogeneity of variance was tested using Bartlett's test and graphically assessed as outlined by Weisberg (1985). Normality of the data was also assessed graphically. In both years the data lacked homogeneity of variance, which necessitated data transformation. The data were ln-transformed and the assessments of homogeneity of variance and normality were repeated. Ln-transformation improved the homogeneity of variance and normality of the data. Analysis of variance (ANOVA) was carried out on all the ln-transformed plant measures as outlined by Federer (1993). The primary measures (y) included: leaf areas (LA) of beans and beets, pod number (PN) of beans, fresh and dry masses of marketable pods (FWMP and WMP, respectively), leaf dry masses (WL) of beans and beets, stem dry mass (WS) of beans, dry mass of beet storage roots (WSR) and fresh and dry masses of marketable storage roots of beets (FWMSR and (WMSR respectively). A final measure was the combined dry biomass of harvested components (W).

For each of the above measures of plant component size, inverse yield-density relationships were evaluated using multiple non-linear regressions of y^{-1} on component species population densities (X):

$$y_1^{-1} = a_{10} + a_{11}X_1 + a_{12}X_2 \qquad (2.2a)$$

$$y_2^{-1} = a_{20} + a_{22}X_2 + a_{21}X_1 \qquad (2.2b)$$

where subscript 1 designates bean, and subscript 2 designates beet. Because variance typically declined with increasing population density, the regressions were weighted by total population density (Spitters 1983). In performing the regressions separate models were developed for the data from each year, but data from the blocks were pooled because block effects were seldom significant in the ANOVAs. Separate models were developed for the two fertility levels, however, because significant fertility influences were detected by the ANOVAs.

3.3 Results

3.3.1 Visual observations

In both years of this study, bean shoots started to emerge seven days after planting and beet emergence began six days after planting. Eleven days after planting bean emergence exceeded 90%, while beet emergence was about 70% in 1994 above 90% in 1995. Differences in beet emergence between the two years seemed to be related to sowing depth, ground compaction, and soil texture. Sowing was deeper in 1994 (about 2 cm) than in 1995 (1 to 1.5 cm), and in 1994 there was more tramping on the plots during planting. The finer soil texture at the 1994 site was related to the formation of a thin crust at the soil surface, which retarded beet emergence and caused occasional bean hypocotyls to break during shoot emergence. Hence, more gap-filling was required in 1994, especially for beets. Beet plants transplanted into gaps initially appeared to be weak, but were not distinguishable from other plants later in the time of growth. The few bean plants that were transplanted remained weak throughout the season.

In the high-density sub-plots canopy closure, *i. e.* overlap of the foliage between adjacent shoots, occurred about four weeks after bean emergence in 1994 and three weeks after bean emergence in the 1995 experiment. Plants in the fertilized plots appeared to be more vigorous and healthier than plants in the unfertilized plots. Apparent symptoms of P deficiency were observed in the unfertilized plots in 1994, particularly in beet plants. In 1995, symptoms of P and Mg deficiencies were visible in both beans and beets in the unfertilized plots, with symptoms being more severe in beans. Plants from densely populated subplots were noticeably smaller, more slender, taller, and had smaller, more erect leaves, compared to plants grown in less densely populated subplots.

Late in the 1994 experiment there were occasional incidences of white mold (*Sclerotinia sclerotiorum*) on bean plants growing in densely populated subplots. This necessitated early harvesting (about 1 week earlier than intended) as advised by the departmental plant pathologist, Dr. R. J. Copeman (personal communication). Also, there were minor incidences of gray mold (*Botrytis cinerea*) on a few bean plants late in the 1995

experiment, again in the highly densely populated subplots. Diseases were not notable on beet plants in either year.

3.3.2 Analysis of variance (ANOVA)

Statistical significance, here and in the rest of this thesis, was judged at the level of $P \leq 0.05$. The ANOVAs (Tables 3.3 to 3.6) frequently detected significant effects of bean (X_1) and beet population densities (X_2). Significant effects of soil fertility (N) were less frequently found. Significant effects of blocks, or treatment interactions, were infrequent.

For beans in 1994, soil fertility did not have significant independent effects, although the degrees of freedom available to test this source of variation were small. There were significant influences of bean population density on all primary measures of bean growth except WS (Table 3.3). Beet population density significantly influenced PN, FWMP, MWP, WP and WL, but not LA, WS and W. There were significant interactions between fertility and beet population density for LA, WP and WL.

For beans in 1995, soil fertility exerted significant effects ($P < 0.05$) on FWMP, WMP and WP (Table 3.4). There were also significant influences of beet population density (X_2) on all of the bean primary measures except for WS. Bean population density had no significant influence on any of the bean primary measures. There was a significant interaction between fertilizer treatment and beet population density for FWMP. Here, a significant three-way interaction did occur for PN. The fresh and dry masses of marketable bean pods are given in Appendix 1c.

Table 3.3. Analysis of variance for ln-transformed bean data (1994): variance ratios for the effect of fertilizer (N), bean population density (X_1) and beet population density (X_2) on the mean primary variables per subplot.

Source of variation	df	y Variables							
		PN	LA	FWMP	WMP	WP	WL	WS	W
Block	1	0.90ns	0.50ns	0.20ns	0.20ns	0.70ns	0.70ns	0.0040ns	0.50ns
N	1	2.9ns	13ns	1.6ns	1.0ns	2.8ns	4.0ns	5.3ns	3.3ns
Error 1	1	-	-	-	-	-	-	-	-
X_1	2	7.4*	4.7*	11*	8.3*	5.4*	7.4*	4.7ns	5.8*
X_2	3	3.2*	1.6ns	4.6*	3.9*	3.2*	3.2*	1.3ns	2.5ns
NxX_1	2	3.2ns	1.1ns	0.40ns	0.50ns	0.50ns	2.5ns	1.2ns	0.70ns
NxX_2	3	2.1ns	3.5*	2.2ns	2.8ns	3.5*	3.6*	1.8ns	2.9ns
X_1xX_2	6	1.8ns	1.1ns	1.2ns	1.1ns	1.0ns	0.90ns	0.70ns	0.90ns
NxX_1xX_2	6	0.60ns	1.8ns	0.70ns	0.70ns	0.60ns	0.80ns	0.90ns	0.80ns
Error 2	22	-	-	-	-	-	-	-	-
Total	47	-	-	-	-	-	-	-	-

*Significant at $P<0.05$; ns: not significant.

Table 3.4. Analysis of variance for the ln-transformed bean data (1995): variance ratios for the effect of fertilizer (N), bean population density (X_1) and beet population density (X_2) on the mean primary variables per subplot.

Source of variation	df	PN	LA	FWMP	WMP	WP	WL	WS	W
B	1	77ns	92ns	1200.*	33ns	78ns	18ns	8.4ns	24ns
N	1	88ns	113ns	6200.*	160*	180*	32ns	5.8ns	31ns
BxN (Error 1)	1	-	-	-	-	-	-	-	-
X_1	2	2.0ns	0.020ns	0.080ns	0.060ns	1.6ns	0.20ns	0.20ns	0.40ns
X_2	3	16*	6.0*	11*	9.2*	13*	10*	1.1ns	6.9*
NxX_1	2	0.30ns	0.060ns	1.2ns	0.80ns	0.50ns	0.010ns	0.090ns	0.20ns
NxX_2	3	0.80ns	0.50ns	3.0*	1.6ns	0.80ns	0.80ns	0.20ns	0.60ns
X_1xX_2	6	1.2ns	0.90ns	1.2ns	1.0ns	0.50ns	0.60ns	1.1ns	0.90ns
NxX_1xX_2	6	2.8*	0.90ns	0.20ns	0.10ns	0.80ns	0.60ns	0.70ns	0.90ns
BxNxX_1xX_2 (Error 2)	2	-	-	-	-	-	-	-	-
Total	47	-	-	-	-	-	-	-	-

*Significant at $P<0.05$; ns: not significant.

For beets in 1994, there were significant soil fertility effects on four of the six primary measures of beet: FWMSR, WL, WSR and W (Table 3.5). Beet population density (X_2) did not affect the fresh and dry masses of marketable storage roots, but did significantly affect LA, WL, W and WSR. Bean population density (X_1) significantly influenced all measures except LA. Significant interactions between fertility and the population density of either species occurred for WSR. Also there was significant interaction between the two species population densities for FWMSR and WMSR. For W, there was a significant three-way interaction.

For beets in 1995, soil fertility had significant direct effects on WSR and W of beets (Table 3.6). Species population densities significantly influenced all primary measures of beets. There were no significant interactions for any of the primary measures, except for WL, which showed a significant interaction involving the species population densities. The fresh and dry masses of marketable beet storage roots are given in Appendix 1d.

Table 3.5. Analysis of variance for the ln-transformed beet data (1994): variance ratios for the effect of fertilizer (N), beet population density (X_2) and bean population density (X_1) on the mean primary variables per subplot.

Source of variation	df	FWMSR	WMSR	LA	WL	WSR	W
				y Variables			
Block	1	0.01ns	1.01ns	6.83ns	15.34ns	94.47ns	86.04ns
N	1	167.87*	109.76ns	38.64ns	464.96*	686.85*	783.74*
Error 1	1	-	-	-	-	-	-
X_1	3	5.25*	7.15*	2.13ns	2.89*	8.77*	7.50*
X_2	2	1.49ns	1.03ns	14.76*	9.48*	4.79*	6.91*
N$\times X_2$	2	2.00ns	1.82ns	0.72ns	0.20ns	3.63*	2.25ns
N$\times X_1$	3	0.68ns	0.69ns	2.58ns	0.85ns	3.43*	2.41ns
$X_1 \times X_2$	6	3.41*	3.46*	0.92ns	0.71ns	0.85ns	0.62ns
N$\times X_1 \times X_2$	6	1.14ns	1.00ns	1.55ns	1.50ns	3.05ns	2.77*
Error 2	22	-	-	-	-	-	-
Total	47	-	-	-	-	-	-

*Significant at $P<0.05$; ns: not significant.

Table 3.6. Analysis of variance for the ln-transformed beet data (1995): variance ratios for the effect of fertilizer (N), beet population density (X_2) and bean population density (X_1) on the mean primary variables per subplot.

| Source of variation | df | y Variables |
		FWMSR	WMSR	LA	WL	WSR	W
Block	1	6.3ns	9.9ns	0.10ns	0.80ns	140*	25ns
N	1	60ns	86ns	11ns	16ns	1100*	220*
Error 1	1	-	-	-	-	-	-
X_1	3	15*	15*	7.9*	15*	11*	13*
X_2	2	8.6*	7.3*	24*	27*	15*	20*
N×X_2	2	0.20ns	0.10ns	0.40ns	0.40ns	0.10ns	0.10ns
N×X_1	3	0.50ns	0.80ns	0.60ns	1.5ns	1.0ns	0.40ns
X_1×X_2	6	2.5ns	2.4ns	2.5ns	3.0*	1.9ns	2.4ns
N×X_1×X_2	6	0.40ns	0.40ns	0.20ns	0.20ns	0.20ns	0.10ns
Error 2	22	-	-	-	-	-	-
Total	47	-	-	-	-	-	-

*Significant at $P<0.05$; ns: not significant.

3.3.3 Yield-density responses

It should be noted that the yield-density regressions evaluated the effects of population densities in a different scale of y compared to the ANOVAs: y^{-1} vs. ln(y). In the majority of cases significant inverse yield-density relationships were obtained, but significance occurred more commonly at high soil fertility (Tables 3.7 to 3.10). Significant inverse yield-density relationships were obtained in 21 of 24 cases for the high fertility regime, but in only 10 of 24 cases at low fertility. For each of the significant regressions, T-tests were used to evaluate the individual regression parameters, and parameter values were nearly always significantly different from zero. A density interaction term (X_1X_2) was not included in the regressions because interactions were seldom significant, and where they were significant the interactions were correlated with the larger direct effects of the individual species population densities.

In the inverse scale of measurement, each multiple yield-density relationship describes a plane (Fig. 3.1), the slopes of which indicate the responsiveness of y^{-1} to variation

in X_i and X_j. The values of the parameters of the yield-density models are interesting biological measures. Reciprocals of the regression intercepts, $1/a_{10}$ and $1/a_{20}$, measure the growth potential of the target species in the absence of competition. The regression coefficients measure target species response to intensity of competition from within-species (a_{11} or a_{22}) and between-species competition (a_{12} or a_{21}) sources. The ratios a_{12}/a_{11} and a_{21}/a_{22}, known as substitution rates (Spitters 1983), indicate the balance of within- to between-species influences. The multiple coefficient of determination measures the importance of competition (Welden and Slauson 1986) as a source of overall yield variation.

For beans at low soil fertility, significant inverse yield-density regressions were obtained for FWMP in both 1994 and 1995, and also for WP and WL in 1995, but other measures of bean did not exhibit density dependence (Tables 3.7(a) and 3.8(a)). At high soil fertility, however, significant models were obtained for all bean measures, except for LA, WL and WS in 1995 (Tables 3.7(b) and 3.8(b)). For the significant regressions, values of R^2 averaged 0.65 and varied from 0.46 to 0.80. In the significant 1994 regressions, values of a_{11} were always higher than a_{12}. Accordingly, the substitution rates a_{12}/a_{11} were less than 1.0, indicating that, for bean as target species, bean was a stronger competitor than beets. In 1995, however, values of a_{12}/a_{11} exceeded 1.0 at low fertility and in two of four cases at high fertility (Table 3.8). Hence, in 1995 with bean as target species, beet was a stronger competitor than bean, except in fertile soil when performance was measured as PN and WP.

For beet, significant inverse yield-density regressions were obtained for all of the primary measures (Tables 3.9 and 3.10), except for the 1994 low fertility treatments where only the FWMSR model was significant. For the significant regressions, values of R^2 averaged 0.75 and ranged from 0.52 to 0.94. All of the substitution rates were less than 1.0 for the 1994 models, and the same was true for the majority of the 1995 models. Hence, for beet as the target species, within-species influences tended to be stronger than between-species competition.
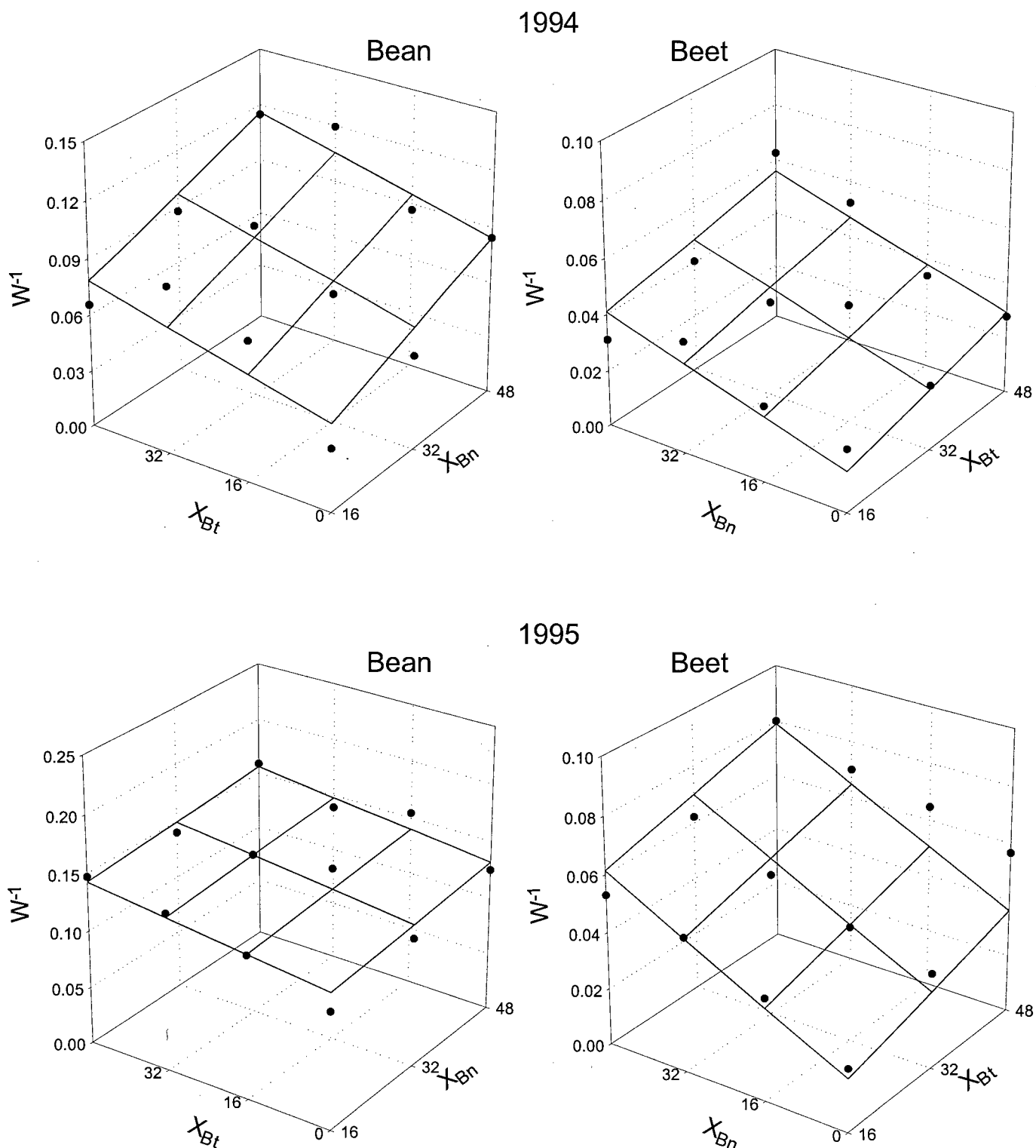
Figure 3.1. Mean values (symbols) and inverse yield-density relationships (plane surfaces) for mean dry mass per plant of bean (left panels) and beet (right panels) in 1994 (top panels) and 1995 (bottom panels).

Table 3.7. Parameters and statistics for inverse yield-density models (eqn. (2.2a)) describing the response of bean primary variables to bean and beet population densities in 1994.

Dependent variable	a_{10}	a_{11}	a_{12}	a_{12}/a_{11}	R^2	P
(a) Under low fertility (N_0)						
PN^{-1}	-	-	-	-	0.01	0.96
LA^{-1}	-	-	-	-	0.12	0.56
$FWMP^{-1}$	0.291* (0.00561)	0.00423* (0.000125)	0.000334* (0.0000939)	0.08	0.70	0.0046
WP^{-1}	-	-	-	-	0.18	0.42
WL^{-1}	-	-	-	-	0.14	0.50
WS^{-1}	-	-	-	-	0.09	0.65
W^{-1}	-		-	-	0.15	0.48
(b) Under high fertility (N_1)						
PN^{-1}	0.0497* (0.00341)	0.00251* (0.0000761)	0.00121* (0.0000570)	0.48	0.77	0.0014
LA^{-1}	0.000547* (0.0000747)	0.0000455* (0.00000167)	0.0000149* (0.00000125)	0.33	0.66	0.0084
$FWMP^{-1}$	0.157* (0.00325)	0.00235* (0.0000726)	0.00101* (0.0000544)	0.43	0.75	0.0020
WP^{-1}	0.0543* (0.00368)	0.00206* (0.0000820)	0.00138* (0.0000614)	0.67	0.71	0.0038
WL^{-1}	0.0973* (0.0100)	0.00798* (0.000224)	0.00391* (0.000168)	0.49	0.80	0.0008
WS^{-1}	0.121* (0.00721)	0.00400* (0.000161)	0.00151* (0.000121)	0.38	0.62	0.012
W^{-1}	0.0279* (0.00191)	0.00118* (0.0000425)	0.000654* (0.0000319)	0.55	0.72	0.0033

*Regression coefficients and intercepts significantly different from zero according to a T-test ($P<0.05$). Values in brackets below the regression parameters are standard errors of estimate.

Table 3.8. Parameters and statistics for inverse yield-density models (eqn. (2.2a)) describing the response of bean primary variables to bean and beet population densities in 1995.

Dependent variable	a_{10}	a_{11}	a_{12}	a_{12}/a_{11}	R^2	P
		(a) Under low fertility (N_0)				
PN^{-1}	-	-	-	-	0.35	0.14
LA^{-1}	-	-	-	-	0.34	0.16
$FWMP^{-1}$	0.101*	0.00108*	0.00138*	1.3	0.63	0.012
	(0.00346)	(0.0000771)	(0.0000578)			
WP^{-1}	0.848*	0.000606	0.0172*	28	0.52	0.037
	(0.0466)	(0.00104)	(0.000779)			
WL^{-1}	1.12*	0.00410*	0.0151*	3.7	0.57	0.023
	(0.0380)	(0.000847)	(0.000635)			
WS^{-1}	-	-	-	-	0.07	0.72
W^{-1}	-		-	-	0.34	0.15
		(b) Under high fertility (N_1)				
PN^{-1}	0.121*	0.000774*	0.000527*	0.68	0.46	0.055
	(0.00240)	(0.0000535)	(0.0000401)			
LA^{-1}	-	-	-	-	0.32	0.18
$FWMP^{-1}$	0.0220*	0.000149*	0.000181*	1.2	0.58	0.019
	(0.000501)	(0.0000112)	(0.00000838)			
WP^{-1}	0.272*	0.00433*	0.00331*	0.76	0.73	0.0029
	(0.00792)	(0.000177)	(0.000132)			
WL^{-1}	-	-	-	-	0.38	0.12
WS^{-1}	-	-	-	-	0.17	0.44
W^{-1}	0.112*	0.000411*	0.000501*	1.2	0.53	0.034
	(0.00156)	(0.0000349)	(0.0000261)			

*Regression coefficients and intercepts significantly different from zero according to a T-test ($P<0.05$). Values in brackets below the regression parameters are standard errors of estimate.

Table 3.9 Parameters and statistics for inverse yield-density models (eqn. (2.2b)) describing the response of beet primary variables to bean and beet population densities in 1994.

Dependent variable	a_{20}	a_{22}	a_{21}	a_{21}/a_{22}	R^2	P
(a) Under low fertility (N_0)						
LA^{-1}	-	-	-	-	0.18	0.41
$FWMSR^{-1}$	0.229*	0.00532*	0.00193*	0.36	0.52	0.037
	(0.0118)	(0.000264)	(0.000198)			
WSR^{-1}	-	-	-	-	0.10	0.63
WL^{-1}	-	-	-	-	0.14	0.52
W^{-1}	-	-	-	-	0.02	0.74
(b) Under high fertility (N_1)						
LA^{-1}	0.000394*	0.0000228*	0.00000990*	0.43	0.81	0.0006
	(0.0000264)	(0.000000588)	(0.000000441)			
$FWMSR^{-1}$	0.0631*	0.00104*	0.000391*	0.38	0.61	0.015
	(0.00195)	(0.0000434)	(0.0000325)			
WSR^{-1}	0.00792*	0.000766*	0.000688*	0.90	0.71	0.0036
	(0.00159)	(0.0000354)	(0.0000265)			
WL^{-1}	0.0416*	0.00198*	0.00129*	0.65	0.77	0.0012
	(0.00297)	(0.0000661)	(0.0000495)			
W^{-1}	0.00725*	0.000550*	0.000458*	0.83	0.74	0.0025
	(0.00103)	(0.0000229)	(0.0000172)			

*Regression coefficients and intercepts significantly different from zero according to a T-test ($P<0.05$). Values in brackets below the regression parameters are standard errors of estimate.

Table 3.10. Parameters and statistics for inverse yield-density models (eqn. (2.2b)) describing the response of beet primary variables to bean and beet population densities in 1995.

Dependent variable	a_{20}	a_{22}	a_{21}	a_{21}/a_{22}	R^2	P
(a) Under low fertility (N_0)						
LA^{-1}	0.00119* (0.0000467)	0.0000297* (0.00000104)	0.00000708* (0.000000781)	0.24	0.66	0.0082
$FWMSR^{-1}$	0.00806* (0.000299)	0.0000930* (0.00000667)	0.000117* (0.00000500)	1.3	0.62	0.013
WSR^{-1}	0.0438* (0.00361)	0.00157* (0.0000804)	0.00176* (0.0000603)	1.1	0.73	0.0028
WL^{-1}	0.109* (0.00428)	0.00269* (0.0000954)	0.00119* (0.0000715)	0.44	0.70	0.0046
W^{-1}	0.0311* (0.00185)	0.000993* (0.0000413)	0.000873* (0.0000310)	0.88	0.75	0.0020
(b) Under high fertility (N_1)						
LA^{-1}	0.000521* (0.0000242)	0.0000225* (0.000000539)	0.0000109* (0.000000404)	0.48	0.84	0.0003
$FWMSR^{-1}$	0.00940* (0.000462)	0.000244* (0.0000103)	0.000407* (0.00000772)	1.7	0.88	<0.0001
WSR^{-1}	0.0124* (0.00111)	0.00142* (0.0000247)	0.000845* (0.0000185)	0.60	0.92	<0.0001
WL^{-1}	0.0391* (0.00261)	0.00237* (0.0000582)	0.00158* (0.0000436)	0.67	0.87	<0.0001
W^{-1}	0.00990* (0.000628)	0.000891* (0.0000140)	0.000549* (0.0000105)	0.62	0.94	<0.0001

*Regression coefficients and intercepts significantly different from zero according to a T-test ($P<0.05$). Values in brackets below the regression parameters are standard errors of estimate.

3.4 Discussion

The finding that various primary measures of plant growth, for both beans and beets, tend to decrease with increasing population densities is in agreement with previous studies on these species (e. g. Mchaina 1991, Muli 1995). This finding also agrees with numerous studies on other plant species grown in both pure stands and in mixtures (e. g. Kira *et al*. 1953, Holliday 1960, Willey and Heath 1969, Wright 1981, Spitters 1983, Firbank and Watkinson 1985, Gaye *et al*. 1992, Jolliffe 1997). Since interference is plant response to their neighbours (Harper 1961), this finding is indicative of the intensification of interference as plants are crowded. Although other forms of interference cannot be ruled out, it seems likely that plant competition for environmental resources was an important contributor to interference. This is implied by the ability of inverse yield-density models to describe plant behavior, since such models can be derived by assuming the occurrence of competition for resources (Jolliffe 1988). It is also implied by the greater growth and productivity of both species at the higher soil fertility level (Chapter 6). The occurrence of competition for environmental resources is also supported by observations of plant nutrient content and light interception, which will be reported in Chapter 4.

In both species, responsiveness to interference varied among different measures of plant performance, and differed between different seasons (1994 and 1995) and levels of soil fertility. The interpretation of these responses is not simple, since complex physiological adjustments may be involved. For example, leaf area development at different population densities may be affected by morphogenetic responses to the canopy light environment (Chapter 4), as well as the formation of assimilates needed for leaf formation and expansion. The observation that different components of total dry mass are unequal in their responses to increasing plant population densities is evidence that changes have occurred in the proportional allocation of dry matter to various plant parts, which has been found previously (e. g. Weiner 1984, Weiner 1985, Jolliffe *et al*. 1988, Theodose *et al*. 1996). As population density increases the growth of reproductive organs often suffers more than vegetative growth (Willey and Heath 1969). In this study, bean pod numbers and dry masses were usually affected by population density, but it is not clear by inspecting the regression results that they were more affected than the vegetative measures. The differences in the responses to

increasing plant population densities of various measures of growth are interesting because they detail how plants adjust to interference, and the differences will be analyzed in detail in Chapter 5.

Another important implication of such differences among plant responses should be noted. The choice of what plant attributes will be measured in an investigation is arbitrary. Because different attributes do not show the same quantitative responses to increasing plant population densities, the conclusions drawn from a study of plant interference may reflect the arbitrary selection by an investigator of which plant responses are to be observed. Where competition for environmental resources is the focus of a study, however, it can be argued that the best indicators of competitive response are those measures that most closely relate to the acquisition of environmental resources by plants. For example, total dry biomass would be a good indicator of overall competition for resources, and observations of the acquisition of individual environmental resources, such as particular nutrients or light (Chapter 4), will also give detailed evidence of competitive behaviour.

The inverse yield-density regressions and regression coefficients were usually significant for the higher soil fertility treatment, but were often not significant at low soil fertility. Hence, interference was more important and more intense (Welden and Slauson 1986) in fertilized treatments than in the unfertilized treatments. The importance of plant competition in the higher soil fertility treatments (indicated by the multiple coefficients of determination, R^2) is less than that found in many binary mixture studies (Jolliffe, 1997), although this was also the case for other studies on associations of beans and beets (Mchaina 1990, Muli 1995).

The reciprocals of the regression intercepts, $1/a_{10}$ and $1/a_{20}$, measure the growth potential of the target species in the absence of competition. These parameters may be poorly assessed by yield-density studies: they are out of the range of the data, and yield per plant is often highly variable at very low population densities. Where significant regressions were obtained for the same plant measure at both low and high soil fertility, values of either a_{10} and a_{20} were less at high soil fertility, indicating the greater growth potential which existed in the more fertile regime. For W at high soil fertility, values of a_{10} were greater than a_{20}, indicating that beets had higher potential than bean to grow in the absence of competitors. However, it

should be noted that the storage root was included as part of W in beet, while for bean the root system was not included. Hence, this apparent difference in growth potentials of the two species may not truly reflect whole-plant differences.

The substitution rates, a_{12}/a_{11} and a_{21}/a_{22} in Tables 3.7 to 3.10, provide a convenient and direct assessment of the balance of within- and between-species interferences. The results show that the balances are not fixed according to species, variable observed, seasons (1994 and 1995) or soil fertility. For example in 1994, beans responded more strongly to themselves than to beets (Table 3.7), while beets responded less strongly to beans than to themselves (Table 3.9); within each year these responses were consistent at both fertility levels and for all measures for which significant regressions were obtained. Mchaina (1991) also found beans to be more competitive than beets. In 1995, however, interference from beets had greater impact on beans than did within-species influences, except in the case of pod production (Table 3.8). In 1995 for beets, within-species interference was stronger than between-species in seven of ten assessments (Table 3.10). Also in 1995 for beets, the within- to between-species balances were reversed for WSR^{-1} at the low fertility level (Table 3.10).

Soil conditions may have contributed to the seasonal differences in competitive balances. In 1994, the emergence of beets was hindered by surface crusting of the soil, and this may have helped to make beans to be more competitive. In 1995, the site had more sand than any other textural fraction (Apendix 1a), and beet emergence was more rapid. Under the more sandy conditions, beans established their root systems close to the surface, while the roots of beets tended to be deeper. The more complete occupation of the soil, and better utilization of soil resources may have improved the competitive ability of beets in 1995.

These findings expand the literature that has reported plasticity in competitive relationships between associated species. In other work with associations of beans and beets, Muli (1995) found that beets dominated beans under full sunlight but not in partial shade. Many other factors appear to be able to shift competitive balances, including salinity (Suehiro and Ogawa 1980), time of observation and previous history of the associated species (Turkington and Jolliffe 1995). In associations of young red alder and Douglas-fir trees, Shainsky *et al.* (1991) observed that within-species competition became less intense as

between-species competition increased, and that between-species competition became less as within-species competition increased.

Several other reports have shown that soil fertility is influential in plant competition. For example in studies on two plant species, *Erica* spp. and *Molinia* spp, Berendse and Elberse (1990) found that *Erica* was the stronger competitor under low nutrient conditions while *Molinia* became the stronger competitor when the nutrient supply was increased. Stern and Donald (1962) studied canopy development in a grass/clover mixture at four levels of N application and reported that at low N levels clover was the stronger competitor, while at high N levels the grass dominated. Using a binary mixture of annuals, *Poa annua* and *Stellaria media*, and on the basis of response functions (Connolly 1987), Connolly *et al.* (1990) found that under high nutrient levels *Stellaria* was a stronger competitor than *Poa*; but with time *Poa* became stronger than *Stellaria*. Connolly *et al.* (1990) attributed this reversal of competition strength to *Stellaria's* earlier and more substantial diversion of resources to reproduction.

Such changes in competitive balances might directly reflect adjustments in the relative abilities of associated species to utilize soil resources at different levels of soil fertility. However, indirect responses, *via* other physiological systems such as photosynthesis, are also possible. For example, it has been argued that fertilizer application enables higher potential growth of plants (Berendse and Elberse 1990, Berendse 1994), consistent with the present findings for a_{io} and a_{jo}, and this leads to higher photosynthetic capacity of the shoots. The ways in which additional photosynthesis is exploited by plants could affect competitive balances. In addition, other feedbacks may ensue, such as greater mutual shading in the fertilized treatments. Such responses may have contributed to the more rapid decline in mean yield per plant with increasing in plant population density in the fertilized treatments as compared with the unfertilized treatments.

The results of this research bear upon alternative perspectives as to whether the intensity of competition varies along a productivity gradient (Grime 1977, 1979, Tilman 1982, 1988). The findings of the research work carried out here agrees with Grime's (1973, 1979) prediction that the intensity of competition will increase along increasing productivity gradients. In this study, competition was more important (higher R^2 values for the

regressions) at high soil fertility. The higher fertility plots were more productive and the intensity of competition was stronger in the fertilized treatments than in the unfertilized treatments. These results are not in agreement with the hypothesis that competition is more intense at low fertility (Newman 1973, Tilman 1982, Tilman 1988). The results are contrary to Goldberg and Barton's (1992) assertion that data from natural associations conform with Grime's (1973) hypothesis and that data from experimental productivity gradients are consistent with the opposing Newman's (1973) and Tilman's (1982, 1988) hypothesis. The results are in agreement with those of Turkington *et al.* (1993) who studied associations of grasses with clover and found that competition intensity increased along a productivity gradient, supporting Grime's (1973) theory and contrasting with Goldberg and Barton's (1992) assertion. These issues will be considered in more detail in Chapter 4.

In summary, analysis of variance has shown that mean yield per plant of each target species significantly decreased with increase in population densities of the two species. Interactions between species, and species and fertilizer, were only occasionally significant. Inverse yield-density regression models indicated that beans were the stronger competitor than beets in 1994; but in 1995, beets were the stronger competitor. In both species, competition for resources was more intense under fertilized than under unfertilized treatments.

The majority of previous research has focussed on the competitive responses of one, or only a few, measure(s) of plant performance. In addition, previous research has often been undertaken in only one growing season, or under one environmental condition. Highlights of this study are that the choice of plant measure has important implications with respect to the competitive response that is obtained, and that competitive balances are not constant but vary with growing season and soil fertility.

In Chapter 4 this analysis will be extended to assess competition for light and for specific nutrients: N, P, K, Ca and Mg. Chapter 5 will interpret the growth responses using growth indices to explore yield component responses and allometric relationships between W and the other primary variables. Inverse yield-density models will again be used in Chapter 6, which will focus on the total productivity of the mixed associations of beans and beets, and will consider whether the mixtures were more productive than pure stands.

4. Effects of soil fertility and seasons (1994 and 1995) on competition for inorganic nutrients and photosynthetically active radiation in mixtures of bush bean (*Phaseolus vulgaris* L.) and common beet (*Beta vulgaris* L.)

4.0 Summary

Neighbouring plants can compete for mutually required environmental resources, and resource availability may in turn influence plant competition for resources. Physiological concepts of limiting factors suggest that competition for soil resources should be relatively important, as a limitation on plant performance, in poorly fertile soils; conversely, competition for light should be relatively important in sites rich in soil nutrients and water. Field experiments were conducted in the summer seasons of 1994 and 1995 to characterize plant competition for soil nutrients and photosynthetically active radiation (PAR). The experiments used common bean (*Phaseolus vulgaris* L.) and table beet (*Beta vulgaris* L.) plants grown in mixtures and pure stands at two soil fertility levels. Analysis of variance indicated that mean mineral nutrient content per plant was influenced by species population density treatments, and relationships among these variables were specified using inverse yield-density regressions. Regressions were often not significant for the low soil fertility treatment, indicating that plant population density could not account for the variation in nutrient content under low soil fertility. Where the regressions were significant at low soil fertility, and for all the high fertility treatment regressions, nutrient accumulation per plant declined with increasing population densities of each species. Beans were the stronger competitor for all the mineral nutrients in 1994, while beets were the stronger competitor in 1995. In the case of photosynthetically active radiation, beets were found to intercept more PAR than beans. Response to increasing population densities was strongest at the higher soil fertility level, but evidence was also obtained for the occurrence of competition at low soil fertility. At low fertility, however, the expression of competitive responses was restricted by nutrient supply.

4.1 Introduction

Competition among neighbouring plants, for mutually required environmental resources, has long been considered to be an important factor in the ecology of natural plant associations. In

addition, the extensive literature in horticulture and agronomy, pertaining to crop responses to population density, weeds and resource inputs, provides further justification for considering competition to be a significant determinant of plant performance. Investigations of competition within plant populations have been facilitated by methods of quantifying competitive influences within- and between-species (Wright 1981, Spitters 1983). There is growing evidence that competitive balances are not constant but change according to the circumstances under which the associated species are grown (Jolliffe 1997). In particular, the availability of resources may influence competition for resources: because plant species respond differently to changing resource levels, competition may vary in response to resource availability (King and Purcell 1997).

Different perspectives have been proposed concerning the relationships to be expected among plant competition, resource availability and productivity in mixed species associations. Grime (1973, 1977, 1979) argues that the intensity of plant competition for resources will increase along an increasing productivity gradient, but others have argued that the intensity of competition will not change with increasing productivity (Newman 1973, Tilman 1982, Grubb 1985, Tilman 1988, Tilman 1990a). Although such concepts were developed using outcomes (responses) in natural plant communities, they can be explored through studies of resource capture in simple agricultural crop associations.

Competitive interactions among associated plants develop through intermediaries such as an environmental resource, its availability, and its utilization by plants (Goldberg 1990). In that context, two distinct competitive processes are recognized: plants can influence the abundance or availability of an intermediary, and they can also respond to changes in the abundance of the intermediary. Tilman (1990a, 1990b) and Tilman and Wedin (1991) emphasized that a basic mechanism of competition for a resource is the ability of a plant to reduce the availability of the resource to other plants. For example, as a plant absorbs a soil nutrient, it reduces the concentration of that nutrient thereby denying its neighbours some of the resource. These researchers further suggested that the species that reduces a resource most, or is most tolerant to resource reduction, becomes the superior competitor. Many competition studies have dwelt on the outcome (response), but not on the effect of the species on the intermediary (*e. g.* Goldberg 1990, Tilman 1990a, 1990b and Tilman and Wedin 1991,

Theodose *et al.* 1996). Relatively few studies have attempted to investigate plant competition *via* the effect of the species on the intermediary (Tilman 1982, 1988, 1990a, 1990b, Tilman and Wedin 1991, Caton *et al.* 1997a, 1997b, Huston and DeAngelis 1994).

Connected to these ideas is the concept of limiting resource: competition ought to be intense for those resources that are most limited in their availability in relation to physiological demands. *i. e.* the negative effects of competition will be expressed primarily in terms of plant responses to the most limiting resource (Huston and DeAngelis 1994). For example, a study by Wilson and Tilman (cited by Tilman 1990b) was carried out using three grass species grown with and without neighbours at different levels of soil fertility. Competition for a soil resource (nitrogen) was observed under low nitrogen level, while under higher nitrogen level competition was attributed to light and not to soil nutrients.

Additional experimental studies are needed to document and test these concepts of plant competition. The present experiment involves simple associations of common bean and table beet plants grown in the field at different levels of soil fertility. Previous studies have usually explored competition in terms of its influences on the formation of biomass or other major plant constituents. Here, within- and between-species components of competition will be assessed in terms of the acquisition of individual nutrient elements (N, P, K, Ca and Mg) and the interception of photosynthetically active radiation (PAR). Results of this study will test whether consistent patterns of competition exist when different resources are considered. In addition, the results will be used to evaluate concepts concerning the relationships among plant competition, resource availability, and plant performance.

4.2 Materials and methods

Experiments were conducted at the Totem Park Field Station of the University of British Columbia, Canada, during the summer seasons of 1994 and 1995. Two plant species, common bean (*Phaseolus vulgaris* L. cv "Contender") and table beet (*Beta vulgaris* L. cv "Ruby Queen") were grown at different population densities in pure stands and mixtures at two levels of soil fertility. The experiments involved randomized complete block split plot designs, with two replications each year. Based on soil analysis carried out prior to planting,

two fertilizer levels (0 kg ha^{-1} or 200 kg ha^{-1} of 20:10:10+10S compound fertilizer) were randomly assigned to the main plots at the time of planting.

Experimental site, plant material, procedures and layout were detailed in Chapter 3. Here, the focus will be on plant acquisition of specific environmental resources, inorganic nutrients and photosynthetically active radiation, as estimated from observations of inorganic nutrient contents at harvest and shoot canopy light interception during growth. At harvest, five plants per species were taken per subplot, washed using distilled water, and dried using forced ventilation at 65^{0}C. These plants were additional to those harvested for the studies reported in Chapter 3, and were collected using the same procedure described earlier. Dried material from each sub-plot was weighed and ground to pass through a five millimeter sieve, using a Wiley Thompson Laboratory Mill Grade 4. The ground samples were analyzed at Norwest Labs (Langley, B. C.) for concentrations of N, P, K, Ca and Mg. Elemental content per plant was then estimated by multiplying its concentration (%) by the total mean dry biomass harvested per plant (Appendix 2).

Interception of PAR in the experimental plots was measured using a LI-COR LAI-2000 Plant Canopy Analyzer (LI-COR Inc., Lincoln, Nebraska). These measurements commenced after the start of shoot canopy closure, due to leaf overlap between adjacent plants. These measurements started at the fourth week following emergence of beans in 1994, and three weeks after emergence in 1995. Thereafter, PAR measurements were carried out weekly for four weeks up to the harvesting time. In each subplot, PAR was measured above and below the plant canopy. The measurements were taken at the middle of each subplot, where the sensor was placed above the leaf canopy twice, and four times randomly below the canopy for each determination. The readings were taken at one week intervals, on clear days between 7:00 am and 10:00 am. The data were recorded as the fraction of incident PAR intercepted (LIN).

Inverse yield-density models were fitted to the data, using the models previously used in Chapter 3:

$$y_1^{-1} = a_{10} + a_{11}X_1 + a_{12}X_2 \qquad (2.2a)$$

$$y_2^{-1} = a_{20} + a_{22}X_2 + a_{21}X_1 \qquad (2.2b)$$

Here, X indicates species population density and y represents mean content per plant of N, P, K, Ca or Mg, or it represents LIN. Once again, the subscripts denote plant species, 1 for bean and 2 for beet. For the nutrient content data, these models were fitted using a weighted non-linear regression procedure, weighted according to total population density (Spitters 1983). For the LIN models the constants of the models (a_{10} and a_{20}) were omitted and best subset regressions used to evaluate regression coefficients. Also, LIN applies to both species, so separate regressions for the two species were not developed for LIN. As described in Chapters 2 and 3, parameters of these models evaluate potential resource acquisition in the absence of competition ($1/a_{10}$ and $1/a_{20}$) within-species competitive responses (a_{11} and a_{22}) and between-species competitive responses (a_{12} and a_{21}).

The parameter values, however, are not only dependent on competition, they also reflect the scale of $1/y$; the average contents of mineral elements in plants vary depending on plant species, stage of growth and also the organ. For example while N varies from 2-5% of dry mass of plants, the average content of P in plants range between 0.3-0.5% (Marschner (1995). To bring competition for the different nutrients to a similar scale, a new index called Relative Competitive Response (RCR) was calculated as given in eqn 4.1. RCR is an attempt to provide a scale-independent measure of competitive response. It is the relative growth response of "Y" (uptake per land area), expressed as a percentage, in a balanced mixture $X_1=X_2$) at the midpoint density used in this study (24 plants m^{-2}). A rationale for RCR is developed in Appendix 3.

$$RCR_1 = 100/"Y" \, d"Y"/dX = 100(a_{11}+a_{12})/a_{10}+(a_{11}+a_{12})x24 \text{ or}$$
$$RCR_2 = 100(a_{22}+a_{21})/a_{20}+(a_{22}+a_{21})x24 \quad (4.1)$$

4.3 Results

4.3.1 Analysis of variance.

ANOVA results for the ln-transformed data for the nutrient uptake results are presented in Tables 4.1 and 4.2, for bean and beet respectively. For bean, population densities of both species significantly influenced the uptake of N, P, K, Ca and Mg in 1994, but in 1995 only beet population density was significant. Significant interactions between fertilizer and beet

population density treatments occurred for all of the nutrient elements, between fertilizer and bean population density treatments for Mg, and between bean and beet population densities for K and Mg in 1994. Where effects of plant population density treatments on plant nutrient uptake were significant, increasing population density resulted in decreased mean nutrient uptake per plant. That decrease was greater in the fertilized treatments than in the unfertilized treatments.

Table 4.2 shows that for the mineral uptake by beets in 1994, bean population density significantly influenced the uptake of N, Ca and Mg, while beet population density significantly influenced uptake of all the nutrients. In 1994, there were no significant interactions for the uptake of any of the mineral nutrients, except for K, which recorded a significant interaction between fertilizer and bean population density. Significant interactions between fertilizer and bean population density treatments occurred for N, K and Mg, and between bean and beet population densities for all the mineral nutrients, except for P, in 1995. Again, where plant population density effects on plant nutrient uptake were significant, increasing population density resulted in a decrease in mean nutrient uptake per beet plant. Decrease in nutrient uptake due to the plant population density treatments was greater in fertilized treatments than in the unfertilized treatments.

Table 4.1. Analysis of variance for ln-transformed data: variance ratios for the effects of block (B), fertilizer (N), and density of beans (X_1) and beets (X_2) on nutrient contents of beans.

Source of variation	df	Nutrient contents				
		N	P	K	Ca	Mg
				1994		
B	1	0.12ns	0.12ns	0.17ns	0.14ns	0.050ns
N	1	2.7ns	3.8ns	4.6ns	3.3ns	5.5ns
BxN (Error 1)	1	-	-	-	-	-
X_1	2	10*	7.7*	13*	11*	9.9*
X_2	3	4.4*	3.8*	7.6*	3.6*	5.1*
NxX_1	2	2.1ns	3.2ns	2.0ns	1.4ns	3.6*
NxX_2	3	6.0*	3.3*	5.5*	5.2*	4.4*
X_1xX_2	6	1.5ns	1.4ns	2.7*	1.4ns	2.5*
NxX_1xX_2	6	1.6ns	0.9ns	0.84ns	1.1ns	2.2ns
BxNxX_1xX_2 (Error 2)	22	-	-	-	-	-
Total	47	-	-	-	-	-
				1995		
B	1	21ns	350*	9.8ns	3.8ns	5.5ns
N	1	3.6ns	1400*	16ns	7.7ns	4.5ns
BxN (Error 1)	1	-	-	-	-	-
X_1	2	2.4ns	0.83ns	0.74ns	1.1ns	1.8ns
X_2	3	9.6*	6.4*	6.9*	5.0*	5.4*
NxX_1	2	0.33ns	0.080ns	0.010ns	0.10ns	0.79ns
NxX_2	3	0.25ns	0.050ns	0.080ns	0.27ns	0.13ns
X_1xX_2	6	1.9ns	0.57ns	0.76ns	0.96ns	0.68ns
NxX_1xX_2	6	0.70ns	0.53ns	0.34ns	0.29ns	0.56ns
BxNxX_1xX_2 (Error 2)	22	-	-	-	-	-
Total	47	-	-	-	-	-

*Significant at $P<0.05$; ns: not significant.

Table 4.2. Analysis of variance for ln-transformed data: variance ratios for the effects of block (B), fertilizer (N), and density of beans (X_1) and beets (X_2) on nutrient contents of beets.

Source of variation	df	Nutrient contents				
		N	P	K	Ca	Mg
		1994				
B	1	40ns	6.29ns	13.41ns	35.17ns	3.3ns
N	1	52*	11.94ns	35.96ns	38.01ns	2600*
BxN (Error 1)	1	-	-	-	-	-
X_1	3	5.5*	2.0ns	2.9ns	4.2*	5.1*
X_2	2	8.7*	5.8*	7.6*	6.0*	8.1*
NxX_1	3	2.8ns	1.3ns	3.1*	0.98ns	2.7ns
NxX_2	2	2.0ns	1.5ns	3.1ns	0.12ns	1.0ns
X_1xX_2	6	0.81ns	0.40ns	0.88ns	0.75ns	0.70ns
NxX_1xX_2	6	1.2ns	2.1ns	2.4ns	0.23ns	0.84ns
BxNxX_1xX_2 (Error 2)	22	-	-	-	-	-
Total	47	-	-	-	-	-
		1995				
B	1	0.22ns	12ns	25ns	0.030ns	0.06ns
N	1	18ns	12ns	700*	19ns	5.0ns
BxN (Error 1)	1		-	-	-	-
X_1	3	27*	5.6*	7.0*	22*	27*
X_2	2	30*	7.7*	21*	31*	27*
NxX_1	3	8.9*	2.7ns	8.3*	1.2ns	5.8*
NxX_2	2	1.8ns	0.98ns	0.64ns	1.7ns	0.59ns
X_1xX_2	6	5.3*	1.6ns	3.1*	4.1*	6.3*
NxX_1xX_2	6	0.37ns	0.15ns	0.45ns	0.91ns	0.62ns
BxNxX_1xX_2 (Error 2)	22	-	-	-	-	-
Total	47	-	-	-	-	-

*Significant at $P<0.05$; ns: not significant.

4.3.2 Competition for nutrients

As for the yield-density relationships developed in Chapter 3, the inverse yield-density regressions were usually significant ($P<0.05$) only at the higher soil fertility level (Tables 4.3 to 4.6). At low soil fertility, the regressions were only significant for the beet results for 1995 (Table 4.6). Where significant regressions were obtained, all of the regression parameter values were also significantly different from zero. Values of a_{11}, a_{12}, a_{22} and a_{21} were always positive, indicating a decline in mineral nutrient content per plant with increasing population densities of both species.

For the significant regressions, the within- and between-species competitive balances are indicated by the substitution rates, a_{12}/a_{11} and a_{21}/a_{22}. In 1994, substitution rates for all nutrients were less than 1.0 for both species (Tables 4.3 and 4.5), indicating mutual antagonism between the species. *i. e.* each species responded to the other more than it did to itself. In 1995 the patterns of competitive balances varied between species, fertility levels and nutrient elements. For beans as the target of competition at high soil fertility, beets were the weaker competitor for N, P and K, but were the stronger competitor for Mg (Table 4.4). For beets as the target of competition at high soil fertility, beans were the stronger competitor for all elements except for Mg (Table 4.6). At low fertility in 1995, with beets as the target of competition, beans were the stronger competitor except for P (Table 4.6).

Values of $1/a_{10}$ and $1/a_{20}$ estimate the potential nutrient accumulation per plant expected in the absence of competitors, for beans and beets respectively. As can be seen by comparing values of $1/a_{10}$ with $1/a_{20}$ for individual elements, the potential contents tended to be higher for beet than for bean (Tables 4.3 to 4.6). It is well known that for the different elements the contents that occur in plant material are in different ranges of value. e. g. N is normally accumulated to much higher levels in tissue than P. This property is reflected by the different values for $1/a_{10}$ and $1/a_{20}$ obtained for the different elements. This also means that the scales of the other parameters, a_{ii} ... a_{ji}, are different for the different elements. This prevents the direct comparison of the values of parameters a_{ii} ... a_{ji} across the various elements. The substitution rates reported above, however, are dimensionless and can be compared across the different elements.

As a result of the foregoing, Relative Competitive Response (RCR) values for the various mineral elements were computed for the two species as given in eqn. 4.1 and the results are presented in Table 4.7. The RCR values indicate that the nutrient elements were competed for with almost the same strength. Table 4.7 also shows that beets had stronger competition for the elements than the beans in 1995.

Table 4.3. Yield-density regression parameters and statistics for the response of nutrient uptake of beans to bean (X_1) and beet (X_2) population densities (1994).

Variable[-1]	a_{10}	$1/a_{10}$	a_{11}	a_{12}	a_{12}/a_{11}	R^2	P (reg.)
(a) At low soil fertility (N_0)							
N	-	-	-	-	-	0.39	0.11
P	-	-	-	-	-	0.17	0.44
K	-	-	-	-	-	0.28	0.23
Ca	-	-	-	-	-	0.27	0.25
Mg	-	-	-	-	-	0.09	0.64
(b) At high soil fertility (N_1)							
N	-	-	-	-	-	0.33	0.16
P	13.2* (0.835)	0.08	0.542* (0.0186)	0.210* (0.0140)	0.39	0.70	0.0047
K	1.35* (0.158)	0.74	0.101* (0.00353)	0.0543* (0.00264)	0.54	0.73	0.0029
Ca	1.10* (0.113)	0.91	0.0939* (0.00251)	0.0483* (0.00188)	0.51	0.82	0.0005
Mg	9.34* (0.748)	0.11	0.464* (0.0167)	0.192* (0.0125)	0.41	0.68	0.0056

*Regression parameters significantly different from zero according to a T-test ($P<0.05$). Values in brackets below the regression parameters are standard errors of the parameters.

Table 4.4. Yield-density regression parameters and statistics for the response of nutrient uptake of beans to bean (X_1) and beet (X_2) population densities (1995).

Variable[-1]	a_{10}	$1/a_{10}$	a_{11}	a_{12}	a_{12}/a_{11}	R^2	P
(a) At low soil fertility (N_0)							
N	-	-	-	-	-	0.49	0.050
P	-	-	-	-	-	0.43	0.081
K	-	-	-	-	-	0.27	0.24
Ca	-	-	-	-	-	0.34	0.16
Mg	-	-	-	-	-	0.45	0.069
(b) At high soil fertility (N_1)							
N	4.16* (0.0822)	0.24	0.0209* (0.00183)	0.0257* (0.00137)	1.2	0.52	0.038
P	58.4* (1.07)	0.02	0.219* (0.0238)	0.509* (0.0179)	2.3	0.67	0.0072
K	6.99* (0.109)	0.14	0.0121* (0.00243)	0.0451* (0.00182)	3.7	0.59	0.018
Ca	-	-	-	-	-	0.43	0.077
Mg	41.2* (0.595)	0.02	0.347* (0.0133)	0.209* (0.00994)	0.60	0.71	0.0039

*Regression parameters significantly different from zero according to a T-test ($P<0.05$). Values in brackets below the regression parameters are standard errors of the parameters.

Table 4.5. Yield-density regression parameters and statistics for the response of nutrient uptake of beets to bean (X_1) and beet (X_2) population densities (1994).

Variable[-1]	a_{20}	$1/a_{20}$	a_{22}	a_{21}	a_{21}/a_{22}	R^2	P
(a) At low soil fertility (N_0)							
N	-	-	-	-	-	0.01	0.96
P	-	-	-	-	-	0.11	0.59
K	-	-	-	-	-	0.068	0.75
Ca	-	-	-	-	-	0.43	0.077
Mg	-	-	-	-	-	0.15	0.48
(b) At high soil fertility (N_1)							
N	0.261* (0.0534)	3.8	0.0386* (0.00119)	0.0225* (0.0140)	0.58	0.78	0.0010
P	3.07* (0.366)	0.33	0.165* (0.00815)	0.106* (0.00611)	0.64	0.61	0.015
K	0.305* (0.0405)	3.3	0.0182* (0.00903)	0.00782* (0.00264)	0.43	0.54	0.032
Ca	1.05* (0.0934)	0.95	0.0427* (0.00208)	0.0188* (0.00156)	0.44	0.55	0.028
Mg	1.49* (0.166)	0.67	0.0925* (0.00370)	0.0477* (0.00277)	0.52	0.67	0.0073

*Regression parameters significantly different from zero according to a T-test ($P<0.05$). Values in brackets below the regression parameters are standard errors of the parameters.

Table 4.6. Yield-density regression parameters and statistics for the response of nutrient uptake of beets to bean (X_1) and beet (X_2) population densities (1995).

Variable[-1]	a_{20}	$1/a_{20}$	a_{22}	a_{21}	a_{21}/a_{22}	R^2	P
(a) At low soil fertility (N_0)							
N	1.79* (0.107)	0.56	0.0562* (0.00239)	0.0131* (0.00179)	0.23	0.56	0.024
P	12.1* (1.22)	0.08	0.362* (0.0271)	0.623* (0.0203)	1.72	0.71	0.0037
K	0.759* (0.0987)	1.32	0.0630* (0.00220)	0.0547* (0.00165)	0.87	0.81	0.0006
Ca	1.81* (0.117)	0.55	0.0629* (0.00262)	0.0406* (0.00196)	0.65	0.69	0.0055
Mg	3.58* (0.259)	0.28	0.165* (0.00577)	0.0551* (0.00432)	0.33	0.68	0.0063
(b) At high soil fertility (N_1)							
N	0.221* (0.0620)	4.5	0.0595* (0.00138)	0.0478* (0.00104)	0.80	0.90	<0.0001
P	5.79* (0.602)	0.17	0.355* (0.0134)	0.0204* (0.0101)	0.06	0.60	0.017
K	0.808* (0.0465)	1.2	0.0336* (0.00104)	0.00192* (0.00777)	0.06	0.69	0.0051
Ca	0.148* (0.0426)	6.8	0.0697* (0.000950)	0.0429* (0.000712)	0.62	0.95	<0.0001
Mg	1.75* (0.167)	0.57	0.105* (0.00372)	0.120* (0.00279)	1.1	0.85	0.0002

*Regression parameters significantly different from zero according to a T-test ($P<0.05$). Values in brackets below the regression parameters are standard errors of the parameters.

Table 4.7 Relative Competitive Response (RCR) for the various nutrient elements.

Year	Element	Fert. Level	Bean				Beet			
			a_{10}	a_{11}	a_{12}	RCR_1	a_{20}	a_{22}	a_{21}	RCR_2
1994	N	High	-	-	-	-	0.261	0.0386	0.0225	3.54
1994	P	High	13.2	0.542	0.210	2.41	3.07	0.165	0.106	2.83
1994	K	High	1.35	0.101	0.0543	3.06	0.305	0.0182	0.00782	2.80
1994	Ca	High	1.10	0.0939	0.0483	3.15	1.05	0.0427	0.0188	2.43
1994	Mg	High	9.34	0.464	0.192	2.62	1.49	0.0925	0.0477	2.89
1995	N	Low	-	-	-	-	1.79	0.0562	0.0131	2.01
1995	P	Low	-	-	-	-	12.1	0.362	0.623	2.76
1995	K	Low	-	-	-	-	0.759	0.0630	0.0547	3.28
1995	Ca	Low	-	-	-	-	1.81	0.0629	0.0406	2.41
1995	Mg	Low	-	-	-	-	3.58	0.165	0.0551	2.48
1995	N	High	4.16	0.0209	0.0257	0.880	0.221	0.0595	0.0478	3.84
1995	P	High	58.4	0.219	0.509	0.960	5.79	0.355	0.0204	2.54
1995	K	High	6.99	0.0121	0.0451	0.68	0.0808	0.0336	0.00192	3.81
1995	Ca	High	-	-	-	-	0.148	0.0697	0.0429	3.95
1995	Mg	High	41.2	0.347	0.209	1.02	1.75	0.105	0.120	3.15

RCR_1: Relative Competitive Response for the beans.

RCR_2: Relative Competitive Response for the beets.

4.3.3 PAR Interception

Results for PAR interception are summarized in Tables 4.8 and 4.9. The proportion of incident PAR intercepted by beets was often higher than the proportion intercepted by beans, as indicated by a_{x2}/a_{x1}. This was particularly evident in 1995, while in 1994 PAR was shared more equally, except during the second week under the high soil fertility regime when beets intercepted twice as much PAR as beans.

It is noteworthy that in both years the regressions for PAR interception were significant in both unfertilized and fertilized regimes, unlike the biomass (Chapter 3) and nutrient uptake regressions that were usually not significant at low soil fertility. Tables 4.8 and 4.9 also show that coefficients of determination, R^2, were higher in unfertilized than in the fertilized soil. R^2 decreased as time progressed, and the decrease was even more conspicuous in the fertilized than in the unfertilized treatments. This indicates that plant

population densities diminished in their contributions to the variation in PAR interception as growth progressed, particularly under the higher fertility regime.

Table 4.8. Parameter values for the effect of bean (a_{X1}) and beet (a_{X2}) population densities on light interception (LIN) in 1994.

Week	a_{X1}	a_{X2}	a_{X2}/a_{X1}	R^2	P(reg.)
		(a) At low soil fertility (N_0)			
1	0.00534*	0.00491*	0.92	0.64	0.0024
	(0.000219)	(0.000219)			
2	0.00539*	0.00621*	1.2	0.77	0.0001
	(0.000178)	(0.000178)			
3	0.00475*	0.00474*	1.0	0.83	<0.0001
	(0.000119)	(0.000119)			
4	0.00588*	0.00492*	0.84	0.74	0.0003
	(0.000181)	(0.000181)			
		(b) At high soil fertility (N_1)			
1	0.00541*	0.00561*	1.0	0.62	0.0031
	(0.000244)	(0.000244)			
2	0.00250*	0.00519*	2.1	0.53	0.011
	(0.000220)	(0.000220)			
3	0.00547*	0.00436*	0.80	0.43	0.036
	(0.000324)	(0.000324)			
4	0.00350*	0.00400*	1.1	0.38	0.057
	(0.00183)	(0.00177)			

*Regression parameters significantly different from zero according to a T-test ($P<0.05$). Values in brackets below the regression parameters are standard errors of the parameters.

Table 4.9. Parameter values for the effect of bean (a_{X1}) and beet (a_{X2}) population densities on light interception (LIN) in 1995.

Week	a_{X1}	a_{X2}	a_{X2}/a_{X1}	R^2	P(reg.)
		(a) At low soil fertility (N_0)			
1	0.00555*	0.00952*	1.7	0.81	<0.0001
	(0.00145)	(0.00145)			
2	0.00430*	0.00724*	1.7	0.74	0.0003
	(0.00138)	(0.00138)			
3	0.00443*	0.00761*	1.7	0.64	0.0021
	(0.00180)	(0.00180)			
4	0.00400*	0.00768*	1.9	0.63	0.0026
	(0.00183)	(0.00183)			
		(b) At high soil fertility (N_1)			
1	0.00552*	0.00718*	1.3	0.70	0.0007
	(0.00160)	(0.00160)			
2	0.00250*	0.00650*	2.6	0.64	0.0022
	(0.00145)	(0.00145)			
3	0.00548*	0.00588*	1.1	0.50	0.015
	(0.00216)	(0.00216)			
4	0.00390*	0.00584*	1.5	0.54	0.0096
	(0.00177)	(0.00177)			

*Regression parameters significantly different from zero according to a T-test ($P<0.05$). Values in brackets below the regression parameters are standard errors of the parameters.

4.4 Discussion

As described in Chapter 3, previous studies (*e. g.* Kira *et al.* 1953, Holliday 1960, Willey and Heath 1969, Wright 1981, Spitters 1983, Firbank and Watkinson 1985, Gaye and Jolliffe 1995, Jolliffe 1997) have used inverse yield-density relationships to characterize competition in terms of the formation of plant biomass and or major components of biomass. The present study extends the application of inverse relationships to individual nutrient elements and PAR. Although other forms of interference cannot be ruled out, the results obtained here are consistent with the occurrence of plant competition for environmental resources, particularly at the higher soil fertility level. As indicated in the significant regressions, mean content per plant of each nutrient element decreased with increases in species population densities. This result is to be expected if an approximately constant supply of soil nutrients, at one of the fertility levels, was being partitioned by competition among individual plants as population densities increased.

Parameters of the inverse yield-density models help in the interpretation of resource utilization by the associated species. Values of $1/a_{10}$ and $1/a_{20}$ measure the potential mineral nutrient content per plant that would occur in the absence of competitors, for bean and beet respectively. Values of $1/a_{20}$ were higher than $1/a_{10}$, for each nutrient element and in both years, indicating that beet had greater potential to accumulate nutrient elements than bean at negligible population densities. For all of the nutrient elements, values of a_{11}, a_{12}, a_{22} and a_{21} indicated that the decline in mean mineral uptake per plant with increasing species population densities was steeper and more conspicuous at higher soil fertility than in the unfertilized treatment. Indeed, in most cases, regressions were not significant in the unfertilized treatment; the low coefficients of determination (R^2) indicate that for those treatments competitive changes associated with changing plant population density were not important (*sensu* Weldon and Slauson 1986) as sources of variation.

The present study is in agreement with the finding in Chapter 3 that choice of response variable influences the result obtained when competition is evaluated: within- and between-species competitive balances varied among the different elements tested. This study is also in accord with the results in Chapter 3 and elsewhere (Jolliffe 1997) that competitive balances can be altered by growing conditions, such as soil fertility. Previous research on

associations of bean and beet has indicated that relative time of establishment (Mchaina 1991) and light availability (Muli 1995) can also change competitive balances in these associations. The present results indicate that when fertility was high both species responded to the presence of the other.

Although bean is a legume, it did not seem to have advantage over the beets in terms competition for N. It may be that the beans did not fix sufficient N to suppress the beets, possibly due to poor nodulation or poor nodule functioning. Nodules were observed on bean plants grown in these studies, but it must be noted that the plots were not treated with *Rhizobium* inoculation, (since from previous work carried out in Totem Park Field Station (Jolliffe (personal communication) nodulation of beans had been observed to take place) and also, the unfertilized soil was low in P which is known to be necessary for biological N-fixation.

The observations reported here are for individual nutrient elements, but it is difficult to separate the effects of the nutrients on each other, especially under field conditions, since interacting effects of nutrients are known to occur. There are also possible interactions between light and mineral nutrients, and it is difficult to separate competition for these resources since mutual shading may reduce mineral uptake in the roots. That interaction may be through reduced root proliferation (hence reduced foraging for soil resources), reduced physiological capacity for nutrient uptake by roots, or through reduced photosynthate supply to the roots (Cui and Caldwell 1997).

Berendse (1994) and Berendse and Elberse (1990) considered some feedbacks that may occur between fertilizer application, growth and photosynthesis. Fertilizer application can enhance plant growth, which in turn may expand plant capacity for photosynthesis. The higher productivity in a fertilized treatment may result in more mutual shading. Due to both the shading and greater plant size, competition for light and nutrients may be more intense at higher fertility than in an unfertilized treatment. However, the RCR values, which assess competition at a common scale of measurement, indicated that each plant species competed for the different nutrient elements with about the same strengths. Also the competition for the elements was stronger in 1995 in beets than in beans. This agrees with the findings in Chapter three that beets were stronger competitor than the beans in 1995.

Taking into account the finding that significant inverse yield-density regressions were developed for both nutrient elements and PAR, the possibility exists that simultaneous competition for soil resources and for PAR took place. In the present study, however, competition for PAR does not seem to have been the primary determinant of growth in either species. An indication of this is that competition for PAR was regularly detectable in the low fertility treatment, while competitive influences on biomass formation (Chapter 3) and nutrient accumulation were seldom significant at low fertility. It should be noted, however, that there is a connection between the nutrient content results presented in this Chapter and the biomass results reported in Chapter 3. Nutrient contents were determined from nutrient concentrations multiplied by total harvested biomass. This may account for some similarities in the pattern of competition results observed here to those observed in Chapter 3. The details for particular nutrient elements, however, vary. Hence, the nutrient content results cannot entirely be explained by their connection with the biomass measurements.

When PAR interception was partitioned into contributions from the constituent species, beet made a greater contribution than bean. This difference may be related to the difference in shoot architecture between the two species: beet has a more erectophilic leaf arrangement, while in bean the arrangement is more planophilic. It has been suggested that competition for light is more complicated, and more difficult to interpret, than competition for soil resources (Berendse 1994, Tilman 1990a). Competition for light involves individual leaves casting shade on each other, thereby pre-empting the resource (Harper 1977), and photomorphogenetic adjustments may take place as shading changes during shoot growth.

However, the results from this experiment indicate that the competition effects observed for the soil resources may have been influenced by light. This is because competition was found to be stronger in fertilized than in the unfertilized treatments. This does not imply that competition for soil resources might not have been taking place in the unfertilized regime; it could have been taking place (McGraw and Chapin 1989, Muller and Garnier 1990, Latham 1992, (cited by Lusk *et al.* 1997)), but since the plant canopy did not close enough for the plants to interact (see Harper 1977), the statistical approach may not have been sensitive enough to sense the competition.

The results of the current research bear upon alternative perspectives as to whether the intensity of competition varies along a productivity gradient (Grime 1977, 1979, Tilman 1982, 1988). At first inspection, the present findings clearly agree with Grime's (1973, 1979) suggestion that the intensity of competition increases along increasing productivity gradients. The intensity of competitive response is expressed by parameters a_{ii} ... a_{ji}, and at low soil fertility those parameters were often not significant. At the higher fertility level plant growth was greater (Chapter 6), parameters a_{ii} ... a_{ji} were usually significant, and competition for nutrients was more important (as indicated by the higher R^2 values for the regressions (Welden and Slauson 1986)). When significant yield-density regressions did occur at both fertility levels, competition was stronger in the fertilized treatment.

Simply accepting the yield-density relationships as complete assessments of competitive behaviour, however, may be inappropriate. For the present study, such an acceptance would lead to the paradoxical result that competition for resources was often absent in the low fertility regime, where resources were most scarce. A resolution of this problem may arise from the recognition of the different component processes contributing to competition, referred to in the introduction to this Chapter. It seems possible that competition did occur among plants growing in the low fertility regime, but was not detectable because of their inability to exhibit a significant competitive response. Evidence for competition in the low fertility regime is that fertilizer application resulted in increase in growth, presumably due to partial alleviation of competition for nutrients. *i. e.* in the low fertility regime, variations in the quantity of nutrients which could be acquired by plants, among the different population density treatments, were too limited to support detectable variations in growth or nutrient accumulation. At higher fertility, competitive response was expressed and detectable by the regressions. This argument suggests that the different perspectives on plant competition presented by Grime (1977, 1979), and by Newman (1973) and Tilman (1982) are not necessarily in conflict, but may deal with different stages in the sequence of events by which competition acts on plant performance.

An original feature of the work described in this chapter is its exploration of plant competition for individual nutrient elements for the first time. Yield-density relationships have not previously been used for this purpose. Also, a new index called Relative

Competitive Response (RCR) was introduced in an attempt to provide a scale-independent measure of the response of different nutrient elements to increasing species population densities. RCR values showed that the different nutrient elements were competed for with approximately the same strengths. Also, light interception by the binary mixture was successfully partitioned into portions intercepted by the component species, and beets were observed to intercept more light than the beans in both the 1994 and 1995 growing seasons.

5. Variations in growth, allometry and yield of common beans (*Phaseolus vulgaris* L.) and table beets (*Beta vulgaris* L.) grown in pure and mixed populations at two levels of soil fertility

5.0 Summary

Common beans (*Phaseolus vulgaris* L.) and table beets (*Beta vulgaris* L.) were grown in field plots at various population densities in mixtures and pure stands, at two levels of soil fertility during the summer seasons of 1994 and 1995. Fertilizer treatments were assigned to the main plots, and density treatments were assigned to the subplots, in a split plot randomized complete block design involving two replications per season. At harvest, leaf area and dry masses of different plant parts were expressed as ratios in order to obtain growth indices for each species: leaf area index, leaf area ratio, specific leaf area, leaf weight ratio, stem weight ratio, and harvest index. The growth indices indicated that plant proportions, including dry matter allocation among various parts, were influenced by experimental treatments. For bean, patterns of dry matter allocation differed between the two years of the study: allocation to pods predominated in the first year, but allocation to stems was larger in the second year. For beet, dry matter allocation was dominated by storage root formation. Further analysis measured allometric and non-allometric influences of experimental treatments on combined dry mass per plant. Much of the variation in combined dry mass per plant was related to adjustments in allometry, although direct, *i. e.* non-allometric, experimental influences on dry mass per plant also occurred. In addition, variations in yields per unit land area, *i. e.* dry mass of bean pods or beet storage roots, were analyzed as the products of morphological yield components using a two-dimensional partitioning procedure involving stepwise multiple regression and analysis of variance. For both species, leaf area index was the most important direct contributor to yield variation, while for beans pod filling was also important.

5.1 Introduction

Plant interference, due to competition for resources and other interactions among associated plants, has been defined as plant responses to the presence of their neighbours (Harper 1961). Accordingly, measurements of plant responses to their neighbours provide a means to quantify and analyze interference. This is an important element of studies of the population density-dependence of plant growth, since interference increases as populations are more crowded. Results presented in Chapters 3 and 4 indicate that different measures of plant performance do not necessarily respond similarly to within- and between-species competitive influences, and that soil fertility can influence the pattern of responses. A deeper examination of the diversity of plant responses to interference may provide further insight into the interactions, and their consequences, that take place among closely associated plants.

Plant responses to their neighbours can be assessed using a variety of indices of growth and productivity. For example, conventional plant growth analysis emphasizes physiological and morphological sources of variation in growth rates (Warren Wilson 1981, Hunt 1982, Hunt 1990). Another technique, yield component analysis, analyzes variation in crop yield as the mathematical product of a set of yield components (Fraser and Eaton 1983, Eaton *et al.* 1986). Conventional plant growth analysis and yield component analysis are often used to evaluate trends in growth and yield variation over time, but both approaches include some indices that can be evaluated using data from a single time of observation.

Conventional plant growth analysis and yield component analysis both deal with plant proportions, as expressed through ratios of morphological measures. Accordingly, these two approaches are interrelated *via* allometry (Jolliffe and Courtney 1984). Allometry has been defined in various ways (Gould 1966, Smith 1980, Causton and Venus 1981, Morris and Myerscough 1986, Weiner and Thomas 1992, Weiner and Fishman 1993, Bonser and Aarssen 1994, Niklas 1994, McLachlan, *et al.* 1995). Here, the term will be used to denote the quantitative relationships between different measures of plant growth (Jolliffe *et al.* 1988). Allometric techniques typically assess the proportionality between pairs of growth measures, and this can deepen the interpretation of the ratios used in the other methods of analysis.

Methods of growth and allometric analysis have both been used to investigate plant responses to environmental influences, including soil fertility and competition. For example, in studies involving *Helianthus annuus* L., fertilizer application increased leaf area ratio (LAR) and net assimilation rate (NAR, also referred to as unit leaf rate (ULR)), but increase in light intensity decreased LAR (Blackman 1960). Roush and Radosevich (1985) used plant growth analysis to characterize aggressiveness as a measure of competitive ability of four weed species. They found that LAR and ULR were among the major contributors to the aggressivity of the weed species. Bazzaz *et al.* (1989) used growth analysis to study competition between C_3 and C_4 annuals at different CO_2 levels. They found that competitive adjustments were related to an increase in ULR with increasing CO_2 concentrations. Buttery (1969) found that LAR of soybeans decreased with increase in population density, but fertilizer application had no effect on LAR at 60 days after emergence. Using yield component analysis Jolliffe and Gaye (1995) observed that node number per plant was strongly affected by population density in bell peppers (*Capsicum annuum* L.). Jolliffe *et al.* (1990) used both conventional plant growth analysis and yield component analysis to interpret the effects of population density on forage maize. They found that complicated physiological and morphological adjustments underlie perturbations of yield by interference. In a previous study on competition in common beans and table beets, Mchaina (1991) used growth and allometric analysis to investigate the effects of population densities on the two species at one level of soil fertility.

A considerable portion of the literature on plant allometry has involved studies on forest trees (Gower *et al.* 1987, Weller 1987, Clough and Scott 1989, Cromer and Jarvis 1990, Johnson 1990, Kolb and Steiner 1990a and b, Le Maitre and Midgley 1991, Makela and Albrektson 1992, Shainsky *et al.* 1992, Elliott and Clinton 1993, Gower *et al.* 1993, Harrington and Fownes 1993, Scatena *et al.* 1993, Bonser and Aarssen 1994, Weiner and Fishman 1994, Niklas 1994,1995). In recent years, fewer studies have evaluated allometric relations in herbaceous species (Jolliffe *et. al.* 1988, Weiner *et al.* 1990, Stutzel and Aufhammer 1991, Mchaina 1991, Weiner and Thomas 1992, McLachlan *et al.* 1995, Nagashima and Terashima 1995, Gedroc *et al.* 1996).

Plant allometry has been investigated for a variety of purposes, including the assessment of structure-function relationships, the comparison of different taxonomic groups (Gould 1968, Niklas 1994) and tests of the adaptive value of traits (Le Maitre and Midgley 1991). For example, Geiger et al. (1996) stated that the regulation of dry matter partitioning acts to maintain allometric growth among plant parts, and to maintain the functional balance between the supply and use of carbon, under diverse environmental conditions. They suggested that a key mechanism contributing to the regulation of carbon partitioning is the expression of genes that control enzymes of sucrose metabolism in particular plant parts and at different stages of ontogeny. Using allometric studies, Pilbeam (1996) suggested that the largest seed yield is often associated with the largest harvest index (H), which then becomes an important selection criterion in plant breeding. McLachlan et al. (1995) applied allometric relationships and determined that competition altered reproductive effort in *Amaranthus retroflexus* L. Weiner et al. (1990) and Weiner and Fishman (1994) recorded significant influences of plant competition on allometry of some annuals and *Kochia scoparia*, respectively.

In the present study, plant interference was varied by growing common beans and table beets at different population densities as mixtures and monocultures, at two soil fertility levels. As reported in Chapters 3 and 4, the observations collected in this study allow within- and between-species components of interference to be quantified. Here, those observations will be used again as inputs for several types of plant growth analysis. Some indices of conventional plant growth analysis, as well as allometric analysis, will be used to explore the influence of experimental treatments on several aspects of growth per plant, including dry matter partitioning. Yield component analysis will be used to evaluate variation in crop yield per unit land area. The main objective of this work was to extend the understanding of plant behaviour beyond that achieved in Chapters 3 and 4. Specifically, this work was intended to identify the aspects of growth which were most strongly affected by the experimental treatments, and to explore the relationships between those responses and crop yields.

5.2 Materials and methods

As detailed in Chapter 3, two plant species, bean (*Phaseolus vulgaris* L. cv Contender) and beet (*Beta vulgaris* L. cv Ruby Queen) were grown at different population densities in pure stands and mixtures at two levels of soil fertility. Analyses reported here were based on observations from both the 1994 and 1995 experiments on the following primary variables (mean values per plant obtained from each subplot): leaf area (LA), leaf dry mass (WL), bean stem dry mass (WS), bean pod number (PN), bean pod dry mass (WP, marketable plus unmarketable pods), beet storage root dry mass (WSR), and the combined dry mass of all harvested plant material (W).

Several growth indices, characteristic of conventional plant growth analysis, were calculated for each species as ratios of primary variables. These included: leaf area index (LAI = LA/A, obtained by multiplying LA by species population density), leaf area ratio (LAR = LA/W), specific leaf area (SLA = LA/WL), leaf weight ratio (LWR = WL/W), shoot weight ratio (SWR = WS/W), and harvest index (H = WP/W for beans and H = WSR/W for beets). Tests of homogeneity of variance and normality were carried out on these indices. The data showed lack of homogeneity of variance, which necessitated data transformation. After ln-transformation the homogeneity of variance and normality of the data were improved. ANOVA was carried out on the ln-transformed data for the indices as outlined by Federer (1993). Several other indices characteristic of conventional plant growth analysis, including relative growth rate, unit leaf rate and crop growth rate, were not assessed in this study because data were available from only one time of harvest.

Simple bivariate allometric relationships, between combined dry mass per plant ($y = $ W) and other primary measures ($z = $ LA, WL, WS, WP or WSR), were formed by linear regressions using the ln-transformed allometric power function (Huxley 1932):

$$\ln(y) = \ln(\alpha) + \beta \ln(z) + \ln(\varepsilon) \tag{2.4}$$

Allometric relationships between pod dry mass ($y = $ WP) and leaf area and pod number ($z = $ LA or PN) in beans, and between storage root dry mass ($y = $ WSR) and leaf area in beets, were also carried out. In eqn. (2.4) allometry is characterized through $\ln(\alpha)$, which indicates $\ln(W)$ at unit values of z, and β which reflects the ratio of relative growth rates of W and z (Whitehead and Myerscough 1962). The $\ln(\varepsilon)$ term measures residual, non-allometric,

variation in ln(W). Allometry tends to vary during plant growth, and can alter under the influence of environmental changes. Examination of eqn. (2.4) indicates that experimental treatments can influence ln(W) *via* its allometric relationships with ln(z), assessed by ln(α) and β, by change in ln(z) at constant allometry, and by non-allometric influences, involving ln(ε). Eqn. (2.4) can be expanded to assess such influences (Jolliffe *et al.* 1988):

$$ln(y) = ln(\alpha')+\beta_0 ln(z)+\beta_1 N ln(z)+\beta_2 X_1 ln(z)+\beta_3 X_2 ln(z)+\beta_4 N X_1 ln(z)+\beta_5 N X_2 ln(z)$$

$$+\beta_6 X_1 X_2 ln(z)+\beta_7 N X_1 X_2 ln(z)+\gamma_1 ln(N)+\gamma_2 ln(X_1)+\gamma_3 ln(X_2)+\gamma_4 ln(N X_1)$$

$$+\gamma_5 ln(N X_2)+\gamma_6 ln(X_1 X_2)+\gamma_7 ln(N X_1 X_2)+ln(\varepsilon') \tag{2.5}$$

Variables on the right hand side of eqn. (2.5) were generated from a ln-transformed primary value (*e. g.* ln(LA) = ln(z)) and the experimental treatments of soil fertility (N, set at 1 for unfertilized and 2 for fertilized plots), bean population density (X_1, plants m^{-2}) and beet population density (X_2, plants m^{-2}). In this model, terms involving β express proportionality between ln(W) and ln(z) and explain allometric adjustments to treatments. Terms involving γ account for non-allometric effects of treatments on ln(y). In eqn. (2.5), ln(α') is the result of grouping of terms and includes both allometric and non-allometric components. Eqn. (2.5) is linear additive model that can be specified from experimental data using regression analysis. For each measure of ln(z), a best subset multiple regression procedure (Jandel Scientific Software 1995) was used to select the subset of terms on the right hand side which best expressed variation in ln(y). Best subset multiple regression models were developed using the R^2 criterion in a Sigmastat program (Neter *et al.* 1990). Candidate best subset models were excluded if variance inflation factors (a measure of multicollinearity) were higher than 10 for any model terms (Neter *et al.* 1990). Mallow's C_p, and the change in R^2 when a variable was dropped from the model, were also considered when selecting the best subset model.

For yield component analysis the primary plant measures were re-expressed as ratios, *i. e.* yield components. Yields, the mathematical products of the yield components, were the dry mass of bean pods and beet storage roots per unit land area, WP/A and WSR/A, respectively. Yield components were ordered in multiplicative series according to assumed sequences of development, based on the chronological order of development of the components during growth (eqn. 5.1 and 5.2). *i. e.* leaves are initiated and expand, and then through net photosynthesis they act to generate dry matter, some of which is translocated to

the stem and pods in beans or to the storage root in beets. Note that several yield components (LA/A, WL/LA, WSR/W) are equivalent to, or the inverse of, indices used for conventional plant growth analysis. The multiplicative models (eqn. 5.1 and 5.2) were then ln-transformed to obtain additive models (eqn. 5.3 and 5.4), which provided the framework for the two-dimensional partitioning (TDP) technique of yield component analysis (Eaton *et al.* 1986):

Beans: WP/A = LA/A x WL/LA x WS/WL x PN/WS x WP/PN $\qquad$ (5.1)

Beets: WSR/A = LA/A x WL/LA x W/WL x WSR/W $\qquad$ (5.2)

Beans: ln(WP/A) = ln(LA/A) + ln(WL/LA) + ln(WS/WL) + ln(PN/WS) + ln(WP/PN) $\quad$ (5.3)

Beets: ln(WSR/A) = ln(LA/A) + ln(WL/LA) + ln(W/WL) + ln(WSR/W) $\qquad$ (5.4)

The TDP procedure (Eaton *et al.* 1986, Jolliffe *et al.* 1990) combines stepwise multiple regression analysis with ANOVA. In the procedure, ln-transformed yield component values (Eqn. 5.3 and 5.4) were entered into a stepwise multiple regression procedure in chronological order of their presumed developmental sequence (forward analysis). *e. g.* the sequence followed in the forward analysis for beans was: ln(LA/A) + ln(WL/LA) + ... + ln(WP/PN). This order was reversed in backward yield component analysis. An intermediate step in the regression procedure involved the construction of a set of orthogonal yield components, each of which was independent of components which preceded it in entry into the stepwise regression (Eaton *et al.* 1986, Jolliffe *et al.* 1990). The final stage in the procedure used ANOVA to evaluate experimental sources of variation for yield and the orthogonal yield components. Overall, the main computational steps for the TDP were: (a) selecting and measuring primary variables on a common basis (per unit land area); (b) constructing ratios of these variables and ordering the ratios according to a chronological sequence of development; (c) ln-transforming the ratios; (d) constructing orthogonal variables; (e) measuring incremental contributions of successive orthogonal variables and (f) partitioning sum of squares and cross products for each variable according to the experimental design. The order of yield components used in the TDP procedure provided either a progressive in time (forward) or retrospective (backward) analysis. Forward analysis evaluated successive yield components after yield relationships with chronologically earlier components had been considered; backward analysis assessed the components after yield relationships with chronologically later components had been taken into account.

5.3 Results

5.3.1 Beans

5.3.1.1 Growth indices

ANOVA results for growth indices of beans are presented in Table 5.1. The only significant independent effect of soil fertility (N) was on leaf weight ratio in 1994. Bean population density (X_1) significantly influenced bean LAI in both years, but did not significantly affect the other bean growth indices. Beet population density (X_2) had no significant influence on the bean growth indices in 1994, but significantly affected all but LAR in 1995. Several significant two-way interactions were detected, but no three-way interactions were significant. In 1994 there was an interaction between soil fertility and bean population density affecting LWR, and between soil fertility and beet population density affecting bean LAI, LAR, and H. In 1995 the soil fertility interaction with beet population density had a significant influence on bean SLA.

The effects of species population densities on various growth indices of beans are illustrated in Figs.5.1 to 5.5. It can be seen that specific leaf area (SLA) of beans increased with species population density (Fig. 5.1), while leaf area ratio (LAR) decreased (Fig. 5.2). Dry matter partitioning among leaves, stems and pods is expressed by LWR, SWR and H. Significant influences of experimental treatments and their interactions on these growth indices are illustrated in Figs. 5.3 to 5.5. Bean leaf weight ratio (LWR) decreased with bean population density (Fig. 5.3) while bean harvest index (H) decreased with beet population density (Fig. 5.4). Although there were adjustments in dry matter partitioning due to experimental treatments and their interactions, as noted above, these adjustments were not very large for either season (1994 or 1995). Between the two seasons (1994 and 1995), however, there was a marked difference in partitioning of dry matter among the aboveground plant parts. In 1994 bean pods were the main constituent of harvested dry matter, while stems and leaves were smaller fractions (Fig.5.5a). In 1995 the stems were the largest constituent while pods and leaves were smaller fractions (Fig.5.5b). The effects of species population densities on the growth indices were more conspicuous under high soil fertility than under low soil fertility. The density-dependence of leaf area index of beans will be detailed later in this chapter.

Table 5.1. Analysis of variance for ln-transformed data: variance ratios for the effects of block (B), fertilizer (N), and density of beans (X_1) and beets (X_2) on growth indices of beans

Source of variation	df	Growth indices					
		LAI	LAR	SLA	LWR	SWR	H
				1994			
B	1	0.30ns	0.50ns	1.8ns	6700*	26ns	18ns
N	1	7.7ns	4.00ns	2.3ns	1500*	1.7ns	3.4ns
BxN (Error 1)	1	-	-	-	-	-	-
X_1	2	5.4*	0.70ns	0.60ns	0.40ns	2.1ns	1.6ns
X_2	3	0.80ns	0.90ns	1.2ns	0.50ns	2.2ns	2.6ns
NxX_1	2	0.90ns	0.40ns	0.50ns	4.2*	0.01ns	1.1ns
NxX_2	3	3.0*	3.2*	2.5ns	1.0ns	1.9ns	2.9*
X_1xX_2	6	0.80ns	0.50ns	0.50ns	1.3ns	0.20ns	0.60ns
NxX_1xX_2	6	1.4ns	0.90ns	0.80ns	0.40ns	0.40ns	0.10ns
BxNxX_1xX_2 (Error 2)	22	-	-	-	-	-	-
Total	47	-	-	-	-	-	-
				1995			
B	1	13ns	14ns	62ns	2.2ns	0.40ns	0.30ns
N	1	15ns	3.6ns	38ns	13ns	3.9ns	3.4ns
BxN (Error 1)	1	-	-	-	-	-	-
X_1	2	54*	1.6ns	0.80ns	0.60ns	0.30ns	1.6ns
X_2	3	4.8*	0.10ns	11*	6.8*	12*	10*
NxX_1	2	2.3ns	0.70ns	0.30ns	0.50ns	0.20ns	0.70ns
NxX_2	3	0.10ns	0.08ns	7.1*	2.1ns	1.5ns	1.0ns
X_1xX_2	6	0.38ns	0.37ns	1.44ns	1.03ns	0.69ns	0.60ns
NxX_1xX_2	6	0.50ns	2.1ns	0.50ns	1.2ns	0.70ns	0.50ns
BxNxX_1xX_2 (Error 2)	22	-	-	-	-	-	-
Total	47	-	-	-	-	-	-

*Significant at $P<0.05$; ns: not significant.

A
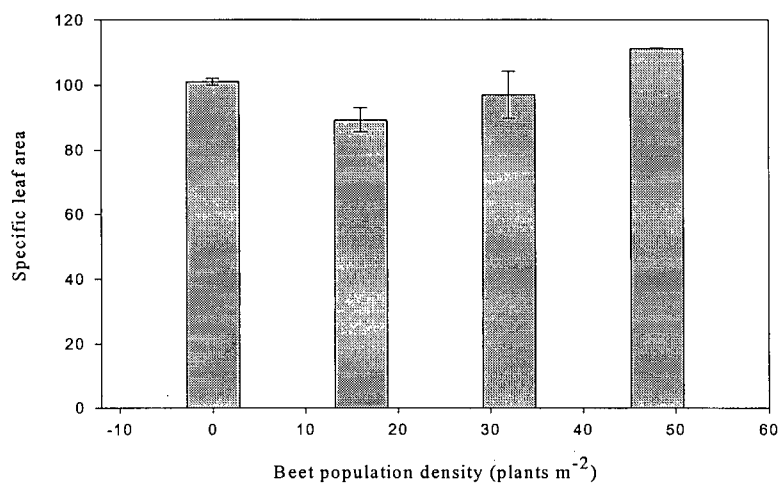
B
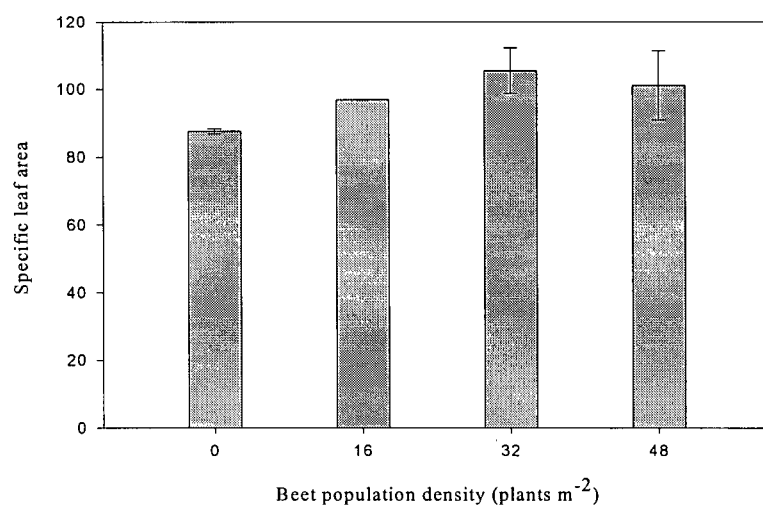
Figure 5.1. Effect of beet population density on specific leaf area (mean values ± standard errors) of beans under low soil fertility (A) and high soil fertility (B) in 1995.

A
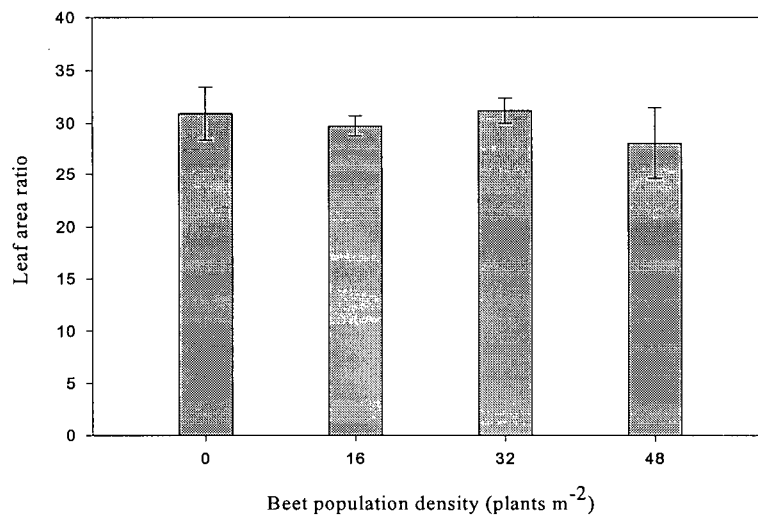
B
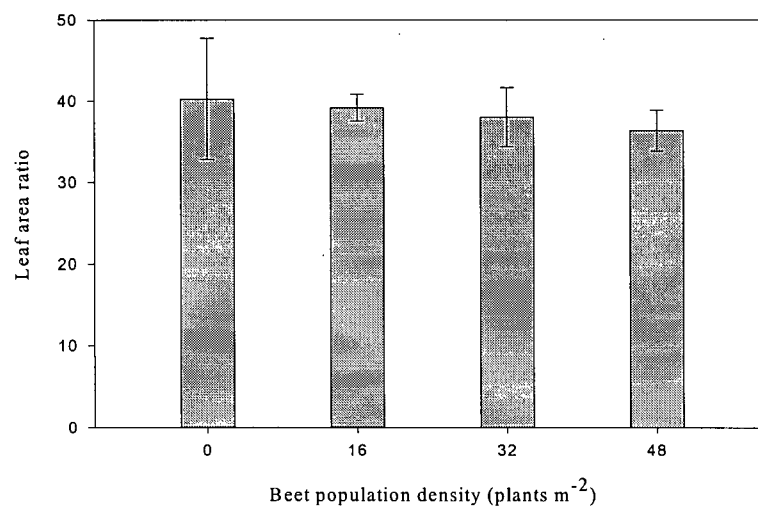
Figure 5.2. Effect of beet population density on leaf area ratio (mean values ± standard errors) of beans under low soil fertility (A) and high soil fertility (B) in 1994.

A
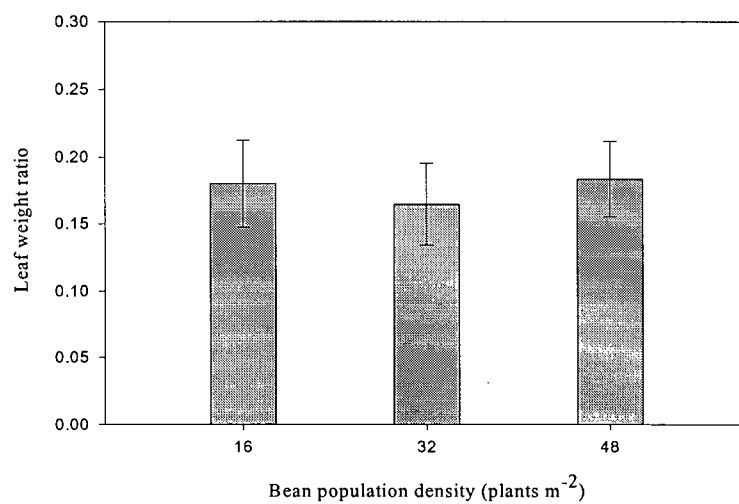
B
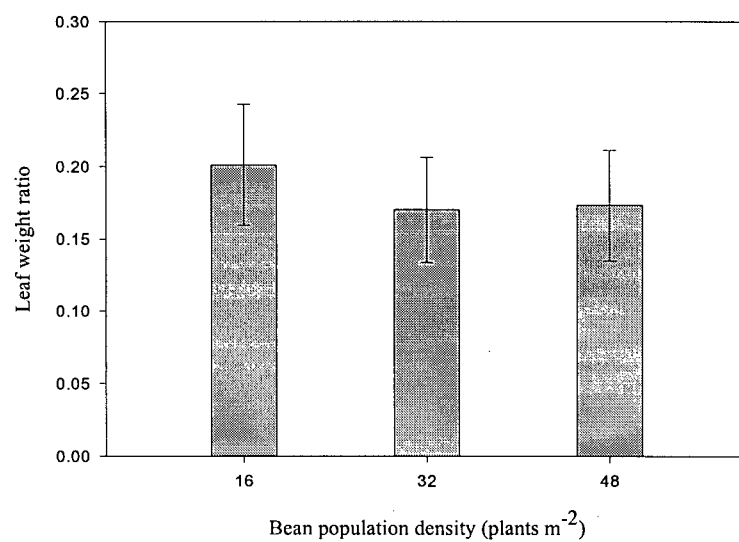
Figure 5.3. Effect of bean population density on leaf weight ratio (mean values ± standard errors) of beans under low soil fertility (A) and high soil fertility (B) in 1994.

A
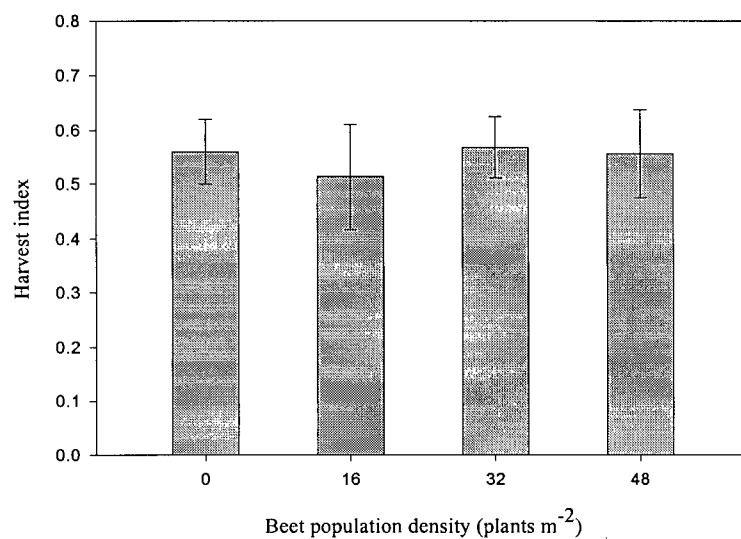
B
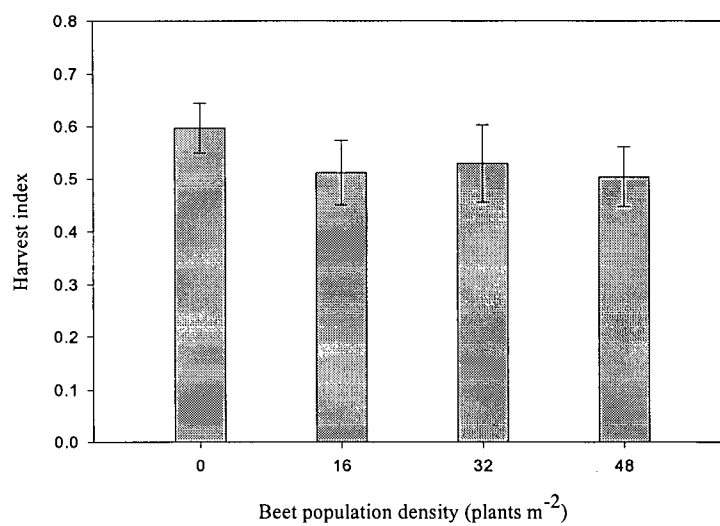
Figure 5.4. Effect of beet population density on harvest index (H) (mean values ± standard errors) of beans under low soil fertility (A) and high soil fertility (B) in 1994.

A
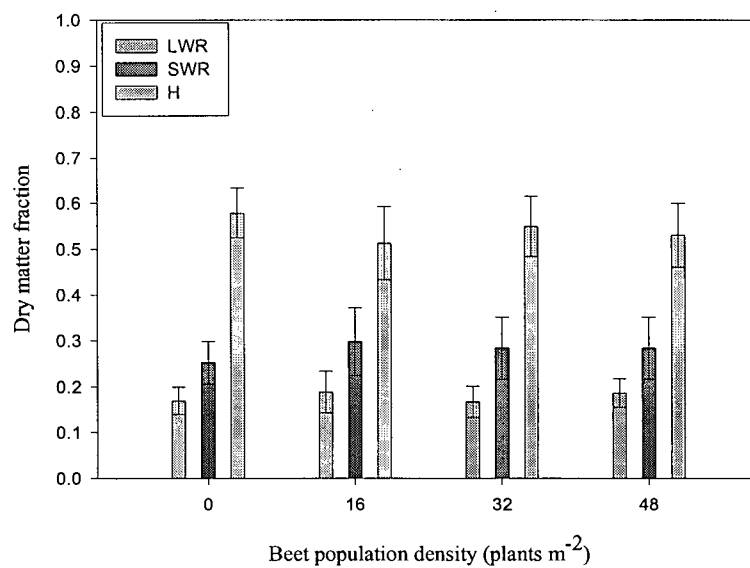
B
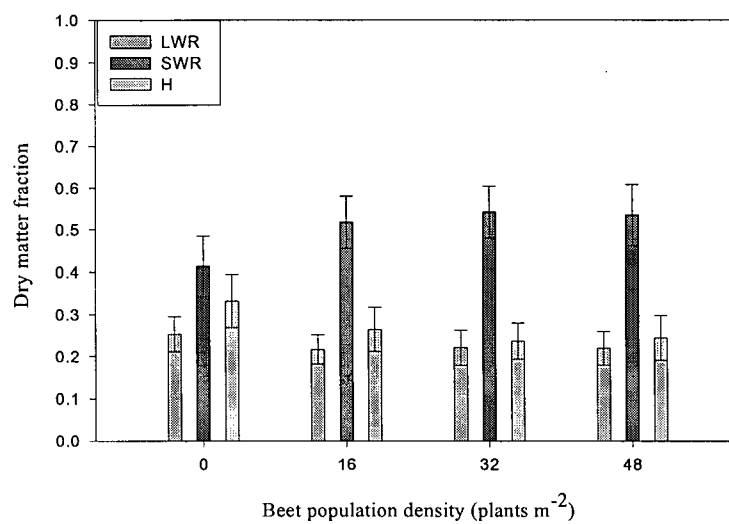
Figure 5.5. Effect of beet population density on dry matter partitioning (mean values ± standard errors) of beans in 1994 (A) and 1995 (B).

5.3.1.2 Allometric analysis

Simple allometric models for bean, relating ln(W) and ln(WP), to other ln-transformed measures per plant, are given in Table 5.2. All these were significant, involved positive values of β, and explained between 35% and 95% of the variation in ln(W). Hence, growth in ln(W) of bean tended to be proportional to growth in other plant measures (Table 5.2a). Also growth in ln(WP) of beans was proportional to leaf expansion and pod filling (Table 5.2b).

Parameter values from the best subset regressions specify the expanded allometric models for beans grown in mixtures with beets (Tables 5.3 to 5.7). Appendix 4 specifies corresponding regressions for pure stands of beans. Parameters β_k and γ_k in each model differ in units of measurement, depending on the identity of the independent variable with which they are associated. To facilitate comparisons, standard partial regression coefficients were calculated for β_k and γ_k values, allowing the contributions of different independent variables to be evaluated in the same scale of measurement. The size and sign of the standard partial regression coefficients were used to indicate the relative magnitude and direction of the relationships between ln(W) and the various z_i's. The expanded allometric models usually accounted for a considerable fraction of the variation in ln(y), as indicated by their high R^2 values. Allometric exponents (terms containing β) were significant ($P<0.05$) in all of the best subset regressions (Tables 5.3 to 5.7 and Appendix 4). Parameter β_0 was usually significant, indicating direct allometric relationships between y and z_i, independent of experimental treatments. Significant terms containing β_k (k>0) indicate that allometry was also affected by the experimental treatments. Increasing species population densities significantly lowered the ratios of y/z_i, as indicated by the negative signs on terms containing β_k (k>0) (Table 5.7 and Appendix 4). The particular terms involving β_k (k>0) which were significant, varied between species and seasons (1994 and 1995), without obvious pattern (Tables 5.3 to 5.7 and Appendix 4).

Significant terms ($P<0.05$) containing γ_k express relationships which were not due to allometry between W and the other primary measures. In bean, ln(N) significantly influenced ($P<0.05$) through the dry weights of stems and pods in both 1994 and 1995 (Tables 5.5 and 5.7 and Appendix 4). Interactions between species population density treatments significantly reduced ln(W) as indicated by significant values of γ_k (k>1) (Tables 5.5 and 5.7).

Table 5.2a. Parameters and statistics for simple bivariate allometric models (eqn. 2.4) between ln(W) and other ln-transformed measures (z) of bean in unfertilized (N_0) and fertilized (N_1) treatments[1].

z	$\ln(\alpha)$	β	Residual mean square	R^2
1994 N_0				
LA	-0.181ns	0.394*	0.201	0.35
WL	1.76*	0.839*	0.038	0.88
WS	1.34*	1.10*	0.077	0.75
PN	0.559*	0.916*	0.097	0.68
WP	0.814*	0.819*	0.016	0.95
1994 N_1				
LA	-1.24*	0.622*	0.073	0.67
WL	1.82*	0.862*	0.035	0.85
WS	1.46*	0.870*	0.052	0.77
PN	1.08*	0.774*	0.074	0.67
WP	0.865*	0.876*	0.015	0.93
1995 N_0				
LA	-2.76*	0.811*	0.045	0.80
WL	1.47*	0.734*	0.047	0.79
WS	0.633*	1.00*	0.031	0.86
PN	0.139*	0.822*	0.068	0.70
WP	1.38*	0.697*	0.039	0.82
1995 N_1				
LA	-2.83*	0.839*	0.024	0.89
WL	1.48*	0.906*	0.024	0.89
WS	0.992*	0.810*	0.028	0.87
PN	0.173*	0.961*	0.074	0.67
WP	1.34*	0.864*	0.046	0.79

*Significant at $P<0.05$; ns: not significant according to a T-test. All regressions were significant at $P<0.001$. LA was in units of m^2 plant^{-1}, and other measures were in g plant^{-1}.

Table 5.2b. Parameters and statistics for simple bivariate allometric models (eqn. 2.4) between ln(WP) and ln-transformed measures, LA and PN as (z) of beans.

z	$\ln(\alpha)$	β	Residual mean square	R^2
		1994		
LA	-1.62*	0.394*	0.142	0.59
PN	0.210ns	0.114*	0.055	0.90
		1995		
LA	-5.30*	1.05*	0.048	0.88
PN	-2.13*	1.50*	0.031	0.92

*Significant at $P<0.05$; ns: not significant according to a T-test. All regressions were significant at $P<0.001$. LA was in units of m^2 plant^{-1}, and other measures were in g plant^{-1}.

Table 5.3. Parameters and statistics for the best subset multiple regression models of the allometric relationship between W and LA in beans (mixtures).

Potential independent variable	Parameter	Parameter estimates		Standard partial regression coefficients	
		1994	1995	1994	1995
Intercept	$\ln(\alpha\grave{})$	1.33*	-3.23*		
		(0.159)	(0.176)		
ln (LA)	β_0	-	0.907*		0.977
			(0.0336)		
Nln(LA)	β_1	0.0945*	-	0.686	
		(0.0172)	-	-	
X_1ln(LA)	β_2	-	-	-	-
X_2ln(LA)	β_3	-	-	-	-
		-	-	-	-
NX_1ln(LA)	β_4	-	-	-	-
		-	-	-	-
NX_2ln (LA)	β_5	-	-	-	-
X_1X_2ln(LA)	β_6	-	-	-	-
		-	-	-	-
NX_1X_2ln(LA)	β_7	-	-	-	-
ln(N)	γ_1	-	-	-	-
ln(X_1)	γ_2	-	-	-	-
ln(X_2)	γ_3	-	-	-	-
		-	-	-	-
ln(NX_1)	γ_4	-	-	-	-
ln(NX_2)	γ_5	-	-	-	-
ln(X_1X_2)	γ_6	-	-	-	-
		-	-	-	-
ln(NX_1X_2)	γ_7	-	-	-	-
R^2		0.47	0.96	0.47	0.96
P(reg.)		<0.001	<0.001	<0.001	<0.001

*Regression parameters significantly different from zero according to a T-test ($P>0.05$). Values in brackets are the standard errors of the parameter estimates given above.

Table 5.4. Parameters and statistics for the best subset multiple regression models of the allometric relationship between W and WL in beans (mixtures).

Potential independent variable	Parameter	Parameter estimates		Standard partial regression coefficients	
		1994	1995	1994	1995
Intercept	$\ln(\alpha`)$	1.77* (0.0198)	1.51* (0.0165)		
$\ln(WL)$	β_0	0.878* (0.0286)	0.877* (0.0300)	0.982	0.981
$N\ln(WL)$	β_1	- -	- -	- -	- -
$X_1\ln(WL)$	β_2	- -	- -	- -	- -
$X_2\ln(WL)$	β_3	- -	- -	- -	- -
$NX_1\ln(WL)$	β_4	-	-	-	-
$NX_2\ln(WL)$	β_5	-	-	-	-
$X_1X_2\ln(WLA)$	β_6	- -	- -	- -	- -
$NX_1X_2\ln(WL)$	β_7	-	-	-	-
$\ln(N)$	γ_1	-	-	-	-
$\ln(X_1)$	γ_2	-	-	-	-
$\ln(X_2)$	γ_3	- -	- -	- -	- -
$\ln(NX_1)$	γ_4	-	-	-	-
$\ln(NX_2)$	γ_5	-	-	-	-
$\ln(X_1X_2)$	γ_6	-	-	-	-
$\ln(NX_1X_2)$	γ_7	- -	- -	- -	- -
R^2		0.97	0.96	0.97	0.96
P(reg.)		<0.001	<0.001	<0.001	<0.001

*Regression parameters significantly different from zero according to a T-test ($P>0.05$). Values in brackets are the standard errors of the parameter estimates given above.

Table 5.5. Parameters and statistics for the best subset multiple regression models of the allometric relationship between W and WS in beans (mixtures).

Potential independent variable	Parameter	Parameter estimates		Standard partial regression coefficients	
		1994	1995	1994	1995
Intercept	$\ln(\alpha`)$	2.28* (0.0628)	0.924* (0.123)		
$\ln(WS)$	β_0	1.18* (0.0979)	0.859* (0.0312)	1.12	0.812
$N\ln(WS)$	β_1	- -	- -	- -	- -
$X_1\ln(WS)$	β_2	-	-	-	-
$X_2\ln(WS)$	β_3	- -	- -	- -	- -
$NX_1\ln(WS)$	β_4	-	-	-	-
$NX_2\ln(WS)$	β_5	-	-	-	-
$X_1X_2\ln(WS)$	β_6	- -	- -	- -	- -
$NX_1X_2\ln(WS)$	β_7	-	-	-	-
$\ln(N)$	γ_1	-0.372* (0.133)	0.376* (0.0419)	-0.261	0.265
$\ln(X_1)$	γ_2	-	-	-	-
$\ln(X_2)$	γ_3	- -	- -	- -	- -
$\ln(NX_1)$	γ_4	-	-	-	-
$\ln(NX_2)$	γ_5	-	-	-	-
$\ln(X_1X_2)$	γ_6	-	-0.0423* (0.0182)	-	-0.0553
$\ln(NX_1X_2)$	γ_7	-	-	-	-
R^2		0.88	0.98	0.88	0.98
P(reg.)		<0.001	<0.001	<0.001	<0.001

*Regression parameters significantly different from zero according to a T-test ($P>0.05$). Values in brackets are the standard errors of the parameter estimates given above.

Table 5.6. Parameters and statistics for the best subset multiple regression models of the allometric relationship between W and PN in beans (mixtures).

Potential independent variable	Parameter	Parameter estimates		Standard partial regression coefficients	
		1994	1995	1994	1995
Intercept	$\ln(\alpha\grave{})$	0.343* (0.123)	-0.384* (0.0837)		
$\ln(PN)$	β_0	0.999* (0.0815)	1.18* (0.0653)	0.814	0.873
$N\ln(PN)$	β_1	-	-	-	-
$X_1\ln(PN)$	β_2	-	-	-	-
		-	-	-	-
$X_2\ln(PN)$	β_3	-	-	-	-
$NX_1\ln(PN)$	β_4	-	0.00155* (0.000478)	-	0.156
$NX_2\ln(PN)$	β_5	0.00243* (0.000680)	- -	0.237	- -
$X_1X_2\ln(PN)$	β_6	-	-	-	-
$NX_1X_2\ln(PN)$	β_7	-	-	-	-
$\ln(N)$	γ_1	-	-	-	-
$\ln(X_1)$	γ_2	-	-	-	-
$\ln(X_2)$	γ_3	-	-	-	-
		-	-	-	-
$\ln(NX_1)$	γ_4	-	-	-	-
$\ln(NX_2)$	γ_5	-	-	-	-
$\ln(X_1X_2)$	γ_6	-	-	-	-
		-	-	-	-
$\ln(NX_1X_2)$	γ_7	-	-	-	-
R^2		0.88	0.95	0.88	0.95
P(reg.)		<0.001	<0.001	<0.001	<0.001

*Regression parameters significantly different from zero according to a T-test ($P>0.05$). Values in brackets are the standard errors of the parameter estimates given above.

Table 5.7. Parameters and statistics for the best subset multiple regression models of the allometric relationship between W and WP in beans (mixtures).

Potential independent variable	Parameter	Parameter estimates		Standard partial regression coefficients	
		1994	1995	1994	1995
Intercept	$\ln(\alpha`)$	0.741*	1.43*		
		(0.0324)	(0.0402)		
$\ln(WP)$	β_0	0.872*	0.901*	0.916	1.05
		(0.0229)	(0.0718)		
$N\ln(WP)$	β_1	-	-	-	-
$X_1\ln(WP)$	β_2	-	--	-	-
		-	-	-	-
$X_2\ln(WP)$	β_3	-	-	-	-
		-	-	-	-
$NX_1\ln(WP)$	β_4	-	0.00737*	-	0.432
			(0.00165)		
$NX_2\ln(WP)$	β_5	-	0.000400*	-	0.124
			(0.000147)		
$X_1X_2\ln(WP)$	β_6	-	-0.000168*	-	-0.225
			(0.0000601)		
$NX_1X_2\ln(WP)$	β_7	-	-	-	-
$\ln(N)$	γ_1	0.200*	-0.592*	0.141	-0.416
		(0.0342)	(0.102)		
$\ln(X_1)$	γ_2	-	-	-	-
$\ln(X_2)$	γ_3	-	-	-	-
		-	-	-	-
$\ln(NX_1)$	γ_4	-	-	-	-
$\ln(NX_2)$	γ_5	-	-	-	-
$\ln(X_1X_2)$	γ_6	-	-	-	-
$\ln(NX_1X_2)$	γ_7	-	-	-	-
R^2		0.98	0.97	0.98	0.97
P(reg.)		<0.001	<0.001	<0.001	<0.001

*Regression parameters significantly different from zero according to a T-test (P>0.05). Values in brackets are the standard errors of the parameter estimates given above.

5.3.1.3 Yield component analysis

The preceding analyses considered growth per plant, while the yield component analysis explores yield variation per unit land area. With total variation in crop yield per unit land area (*i. e.* the sum of squares of WP/A for beans or WSR/A for beets) set at 100%, the two dimensional partitioning results express the percentage contributions to yield variation from the (ln-transformed) orthogonal yield components and experimental sources of variation (Table 5.8). The interpretation of the TDP tables follows the order of the analysis: The stepwise multiple regressions, displayed in the rows labeled "Total", preceded the analysis of variance, results of which are displayed in the yield component columns. It is possible for the ANOVA to detect significant experimental sources of variation for yield components that are not significant in the regression stage. Such instances are ignored (*i. e.* not given an asterisk in the table) because the multiple regression had already established that such components were not significant contributors to yield variation. The interpretation of the TDP tables must also recognize the stepwise nature of the regression stage. In the forward stage, the contributions of successive yield components are assessed after chronologically earlier components have been taken into account. In the backward analysis, the contributions of successively earlier yield components are assessed after chronologically later components have been taken into account. If the final yield component entering the regression is significant, then it can be said to have a direct effect on yield variation because the influences of all other yield components have been taken into account and there is no residual. For significant components preceding the final component entering the regression, however, their contributions may be direct, or they may be expressing relationships that actually exist between yield and later terms remaining to be entered into the regression analysis.

In the forward TDP analysis, leaf area index (LA/A) was the major contributor to variation in bean pod yield per land area, accounting for 51% of total yield variation in 1994 and 82% in 1995 (Table 5.8). The inverse of specific leaf area, WL/LA, contributed significantly in 1994 (30.9%) but had no significant contribution in 1995. Dry mass per pod, WP/PN, significantly contributed to total yield variation in both years (17.4% in 1994 and 12.4% in 1995); this was a direct influence on yield variation because it was the last yield

component entered into the forward analysis. The other bean yield components, WS/WL and PN/WL, made no significant contributions in the forward yield component analysis for bean.

In the backward analysis (Table 5.8), contributions to total yield variation were significant for WP/PN and LA/A. The importance of leaf area index (LA/A) is shown by its large contributions to total yield variation, 70.8% in 1994 and 60.9% in 1995 respectively. These were direct contributions since the influences of all other yield components had already been taken into account. In 1994, WL/LA was not significant in the backward analysis, so its contribution in the forward analysis may have been due to a correlation with WP/PN (which existed before the orthogonal transformation procedure). The other bean yield components, WS/WL, and PN/WS were not significant in the backward analysis.

In both years, bean pod yield per unit land area was significantly affected by species population densities, shown in the right hand column of Table 5.8. Note that this analysis differs from the ANOVA for WP in Chapter 3 in that it is done on a per unit land area basis. In 1994 the interaction of soil fertility with beet population density was also significant. In 1995, the effects of blocks, soil fertility treatments, the interaction of soil fertility with bean population density, and the three-way NxX_1xX_2 interaction were also significant. Other columns within the TDP table (Table 5.8) indicate the contributions of experimental sources of variation to yield component variation, expressed as percentages of total yield variation. Prominent in Table 5.8 are the responses LA/A and WP/PN to the soil fertility and population density treatments, and/or treatment interactions in both years and in both forward and backward directions of the regression analysis. In addition, WL/LA had a significant response to bean population density in the forward analysis for 1994. The largest direct contributions to total yield variation, *via* treatment effects on yield components, were the effects on LA/A of bean population density (20.1%) and soil fertility (11.8%) in 1994, and the effects on LA/A of soil fertility (15.7%) and beet population density (7.7%) in 1995.

Figures 5.6 and 5.7 show the treatment effects on LA/A and WP/PN in 1995. Mean values of these components were higher at high soil fertility. At low fertility, high beet population densities diminished bean leaf area index (Fig. 5.6) and pod filling (Fig. 5.7). Leaf area index of beans increased with increase in bean population density at both fertility levels (Fig. 5.6). Density effects on WP/PN at high soil fertility are not conspicuous (Fig. 5.7B).

Table 5.8. Two dimensional partitioning of yield component contributions to variation in bean pod dry weight per unit land area.

Year	Source[1]	df	Forward						Backward						$Y = WP$
			LA/A	WL/LA	WS/WL	PN/WS	WP/PN	ΣP	WP/PN	PN/WS	WS/WL	WL/LA	LA/A	ΣP	
1994	B	1	0.4[2]	2.5	0.1	0	0.4	3.3	0.4	0.1	0.1	0	1.5	4.6	6.7
	N	1	15.3	0.5	0	0	0	4.8	1.3	0.1	0	0	11.8	7.4	20.6
	BxN (Error 1)	1	0.8	2.3	0	0	0.2	4.3	0.6	0	0	0	3.3	3.7	7.6
	X_1	2	3.4*	3.9*	0.1	0	0	9.2	0.1	0	0	0	20.1*	-3.6	16.5*
	X_2	3	2.0*	1.8	0	0	0.5	0.2	1.3*	0	0	0	2.3*	0.8	4.5*
	NxX_1	2	0.7	0.4	0	0	0.5*	-1.3	1.0*	0	0	0	0.9	-1.6	0.3
	NxX_2	3	4.0*	2.6	0	0	0.8*	-2.7	0.7	0	0	0	1.5	2.5	4.7*
	X_1xX_2	6	2.3	0.9	0	0	0.4	-1.1	0.3	0	0.1	0	2.9	-0.8	2.5
	NxX_1xX_2	6	4.2	0.9	0	0	0	-3.0	1.0	0	0	0	1.1	0	2.1
	$BxNxX_1xX_2$ (Error 2)	22	8.5	9.4	0	0	1.9	-8.9	2.7	0.1	0.2	0	6.0	1.9	10.9
	Residual	47	9.4	5.6	0.2	0.2	12.6	-4.6	17.2	0.4	1.3	0	19.3	-14.7	23.4
	Total		51.0*	30.9*	0.4	0.3	17.4*	0	26.6*	0.7	1.9	0	70.8*	0	100
1995	B	1	17.7*	0.2	0	0	1.0	10.8	9.7*	0	0	0	4.7*	15.3	29.7*
	N	1	16.2*	0.1	0	0	0.7	-6.8	0.5*	0	0	0	15.7*	-6.0	10.2*
	BxN (Error 1)	1	0	0	0	0	0.1	-0.1	0	0	0	0	0	0	0
	X_1	2	6.8*	0	0	0	0	0.5	0.1	0	0	0	6.4*	0.9	7.4*
	X_2	3	16.5*	0.4	0	0	0.4*	-0.6	2.5*	0.1	0	0	7.7*	6.3	16.7*
	NxX_1	2	6.1*	0.2	0	0.1	0	4.0	0.4	0.1	0	0	4.9*	5.0	10.4*
	NxX_2	3	0.8	0	0	0	0.1	0.2	0.2	0	0	0	0.6	0.3	1.1
	X_1xX_2	6	1.0	0.1	0	0	0.2	-0.5	0.4	0	0	0	1.0	-0.6	0.8
	NxX_1xX_2	6	2.0	0.1	0	0.1	0.3	1.0	1.1	0.1	0	0	0.8	1.6	3.6*
	$BxNxX_1xX_2$ (Error 2)	22	3.2	0.4	0	0.2	0.7	0.2	2.0	0.2	0	0	3.5	-1.0	4.7
	Residual	47	11.6	2.0	0.1	1.4	8.9	-8.6	20.4	0.5	0.5	0.1	15.6	-21.8	15.4
	Total		82.0*	3.5	0.2	2.0	12.4*	0	37.2*	1.1	0.7	0.1	60.9*	0	100

[1] Sources of variation are block (B), soil fertility (N), bean population density (X_1) and beet population density (X_2).

[2] Percentages of total sums of squares of Y for each growing season; total sums of squares were 247.8 (1994) and 312.5 (1995). ΣP columns contain sums of products. *significant at $P<0.05$. Discrepancies in column or row totals are due to rounding-off.
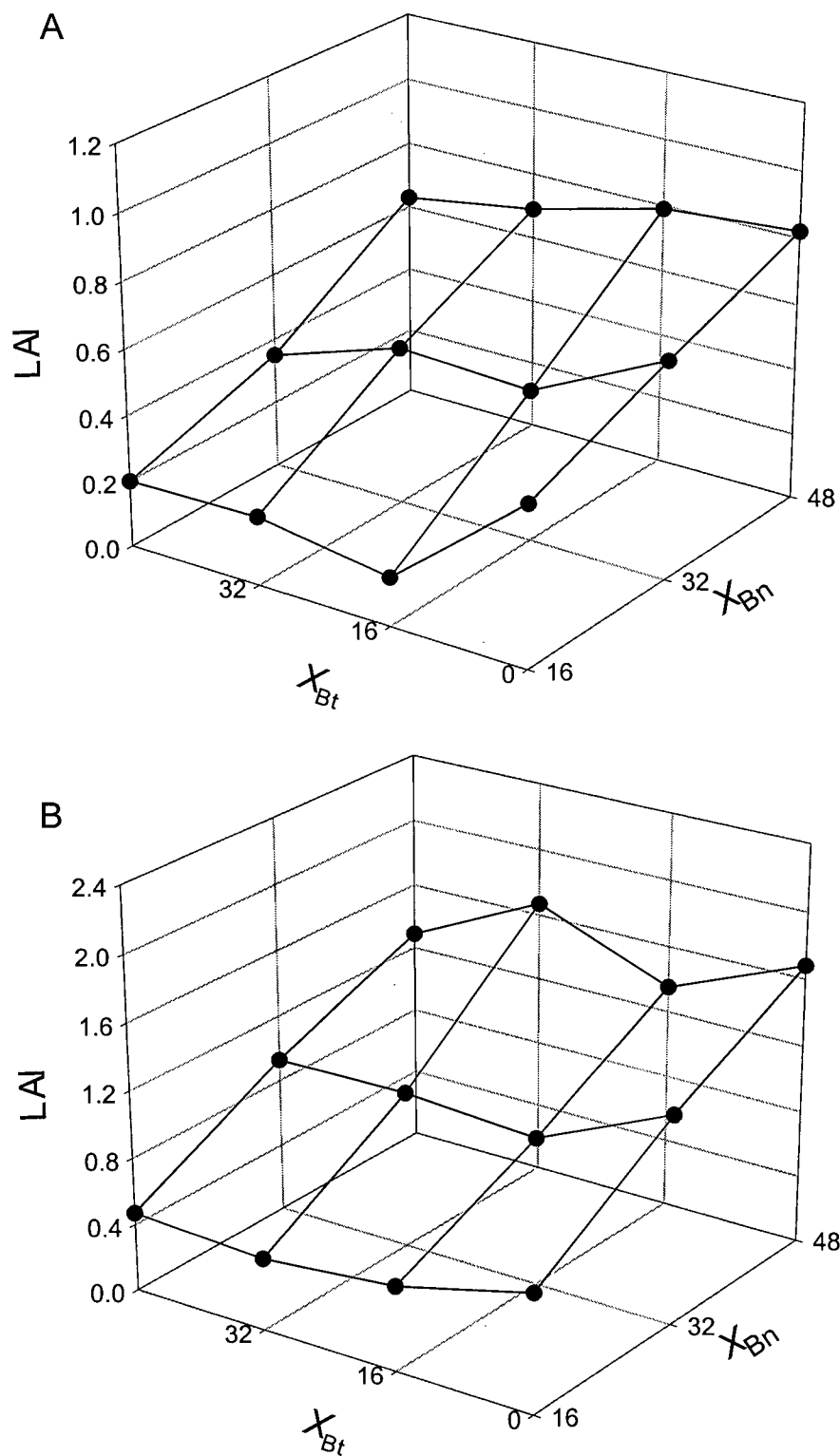
Figure 5.6. Effect of bean and beet population density treatments on leaf area index
of beans in low fertility (A) and high fertility (B) regimes in 1995.
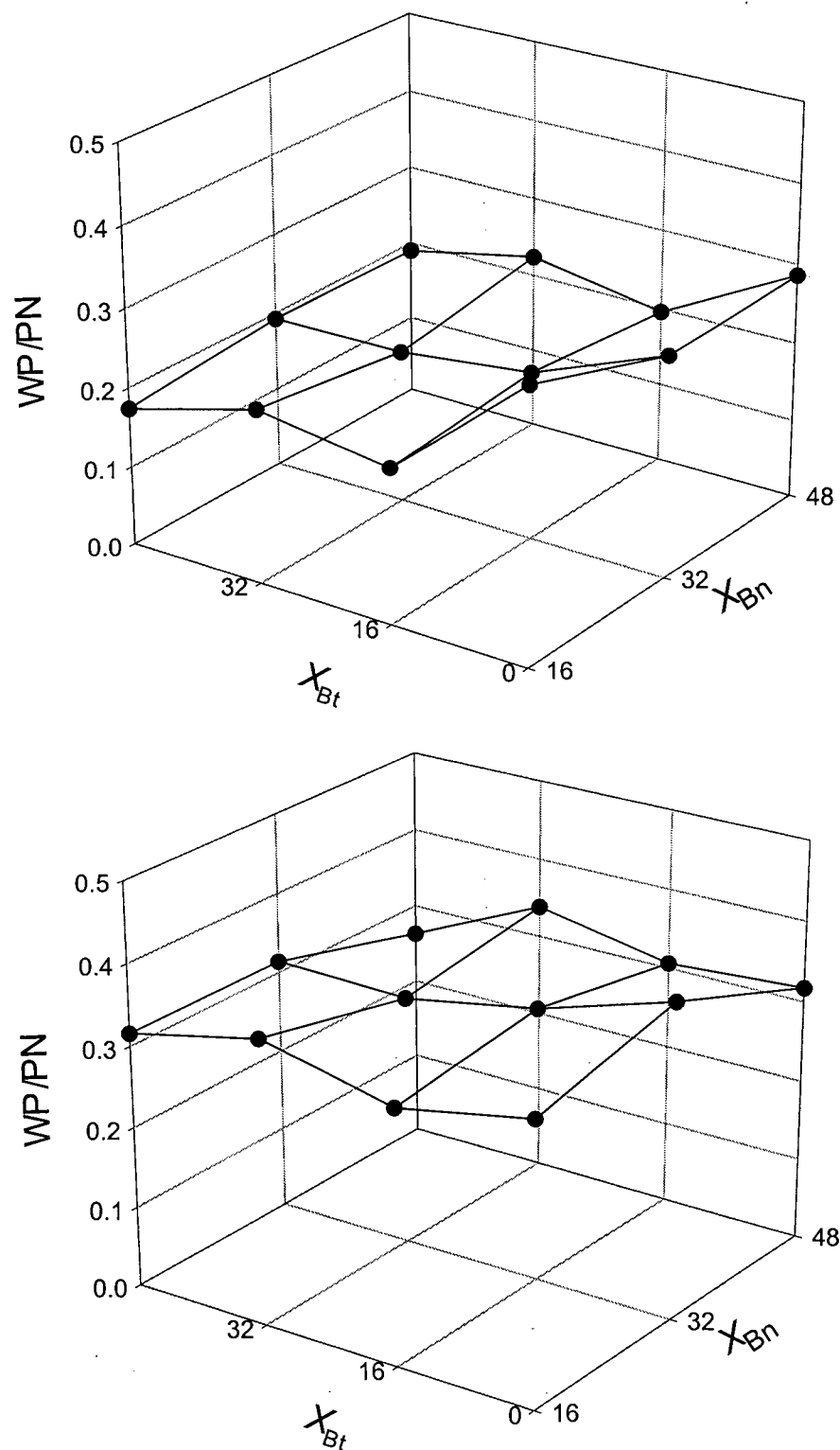
Figure 5.7. Effect of bean and beet population density treatments on WP/PN
of beans in low fertility (A) and high fertility (B) regimes in1995.

5.3.2 Beets

5.3.2.1 Growth indices

ANOVA results for growth indices of beet are presented in Table 5.9. The only significant independent effects of soil fertility (N) were on LWR and H in 1994. Beet population density (X_2) significantly affected the beet growth indices, except SLA, in 1994, but only LAI was affected in 1995. In 1994, bean population density (X_1) significantly affected LAR and LWR of beets, and in 1995 it affected all of the indices except for LWR. In both years LWR and H were subject to significant interactions between soil fertility and bean population density treatments. In 1994 LWR was affected by this interaction, and in 1995 SLA was affected by this interaction. There was one three-way interaction, involving leaf area ratio in 1994.

The effects of species population densities on various growth indices of beets are illustrated in Figs. 5.8 to 5.13. Specific leaf area (SLA) of beets increased with increase in bean population density (Fig. 5.8). Leaf area ratio (LAR) of beets did not vary greatly, but tended to decrease with increasing beet density and decreasing bean density (Fig. 5.9). In both years dry matter allocation to beet storage roots exceeded allocation to leaves (Figs. 5.10 to 5.12). Although significant changes were detected in LWR (Table 5.9), the effects of experimental treatments on dry matter partitioning were not dramatically large (Figs. 5.10 to 5.12). Leaf area index (LAI) of beets increased with beet population density and decreased with bean population density (Fig. 5.13). As with beans, the effect of species population density on LAI was more conspicuous in unfertilized treatments than in the fertilized treatments.

Table 5.9. Analysis of variance for ln-transformed data: variance ratios for the effects of block (B), fertilizer (N), and density of beans (X_1) and beets (X_2) on growth indices of beet.

Source of variation	df	Growth indices				
		LAI	LAR	SLA	LWR	H
1994						
B	1	8.8ns	0.0010ns	4.4ns	3700*	190*
N	1	50ns	7.6ns	0.20ns	8700*	450*
BxN (Error 1)	1	-	-	-	-	-
X_2	2	37*	9.3*	1.0ns	3.6*	3.6*
X_1	3	2.3ns	11*	1.2ns	2.9*	2.7ns
NxX_2	2	0.69ns	2.36ns	0.72ns	2.91ns	3.0ns
NxX_1	3	3.7*	1.5ns	2.6ns	3.1*	3.1*
X_2xX_1	6	0.80ns	2.8*	0.70ns	1.9ns	2.0ns
NxX_2xX_1	6	1.5ns	4.9*	0.80ns	1.4ns	1.4ns
BxNxX_2xX_1 (Error 2)	22	-	-	-	-	-
Total	47	-	-	-	-	-
1995						
B	1	0.10ns	1.4ns	3.1ns	0.80ns	0.60ns
N	1	11ns	0.20ns	2.7ns	1.5ns	1.4ns
BxN (Error 1)	1	-	-	-	-	-
X_2	2	25*	0.70ns	0.30ns	0.90ns	1.0ns
X_1	3	7.1*	5.2*	6.5*	0.90ns	0.90ns
NxX_2	2	0.70ns	1.1ns	1.8ns	0.30ns	0.30ns
NxX_1	3	0.70ns	2.0ns	3.0*	3.7*	3.6*
X_2xX_1	6	1.8ns	0.40ns	1.3ns	0.50ns	0.50ns
NxX_2xX_1	6	0.10ns	0.20ns	0.70ns	0.30ns	0.30ns
BxNxX_2xX_1 (Error 2)	22	-	-	-	-	-
Total	47	-	-	-	-	-

*Significant at $P<0.05$; ns: not significant

A
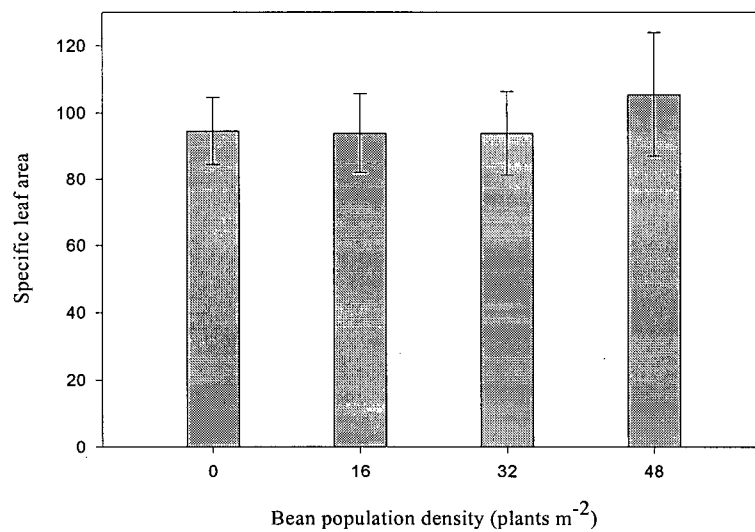
B
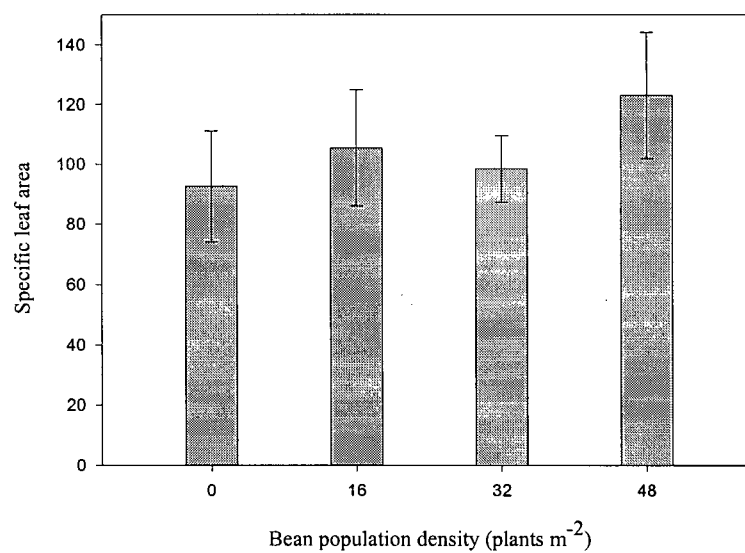
Figure 5.8. Effect of bean population density on specific leaf area (mean values ± standard errors) of beets under low soil fertility (A) and high soil fertility (B) in 1995.

Figure 5.9. Effect of bean and beet population density treatments on leaf area ratio of beets under low fertility (A) and high fertility (B) in 1994.
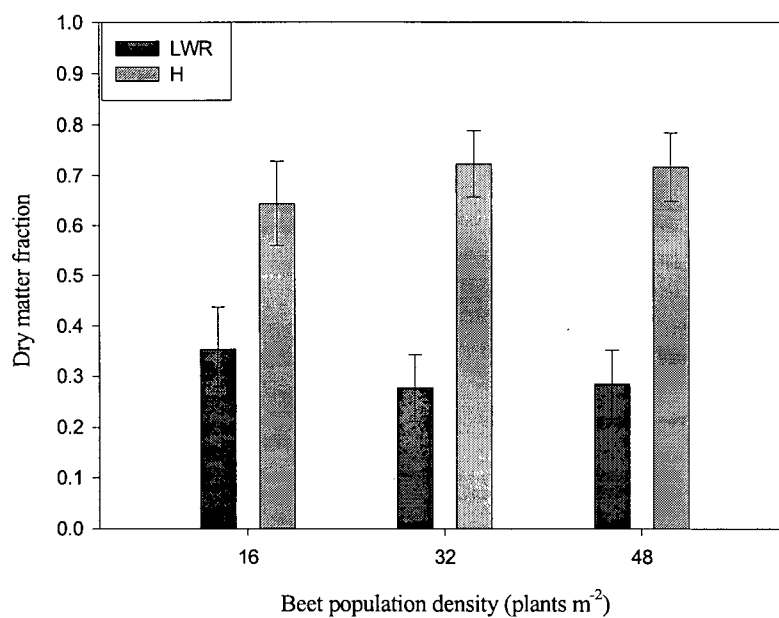
Figure 5.10. Effect of beet population density on dry matter partitioning (mean values ± standard errors) of beets in 1994.

A
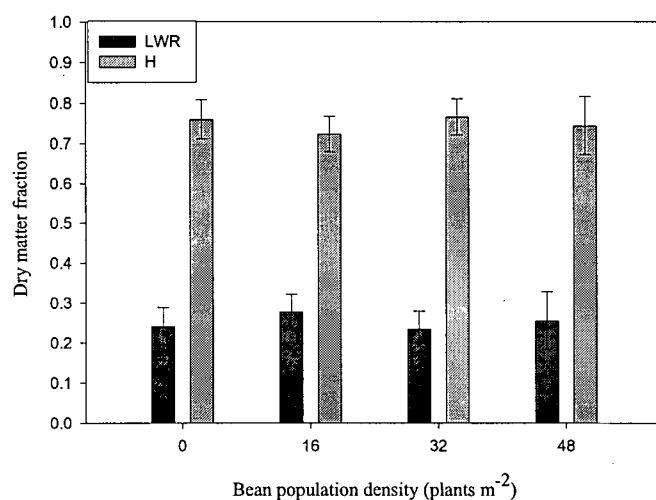
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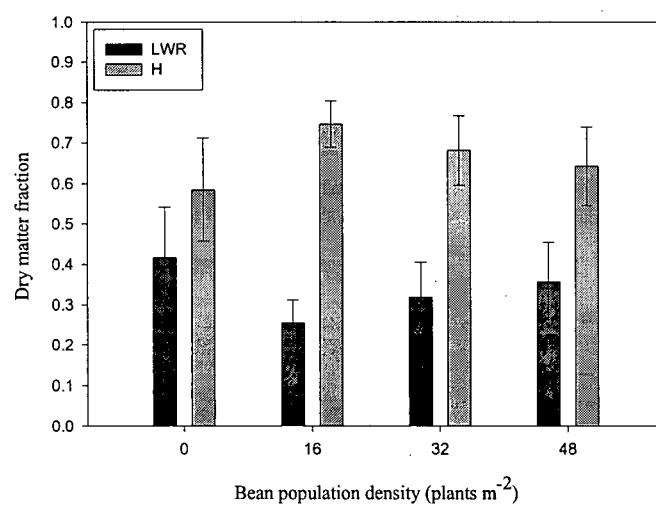
Figure 5.11 Effect of bean population density on dry matter partitioning (mean values ±
standard errors) of beets under low soil fertility (A) and high soil fertility (B) in
1994.

A
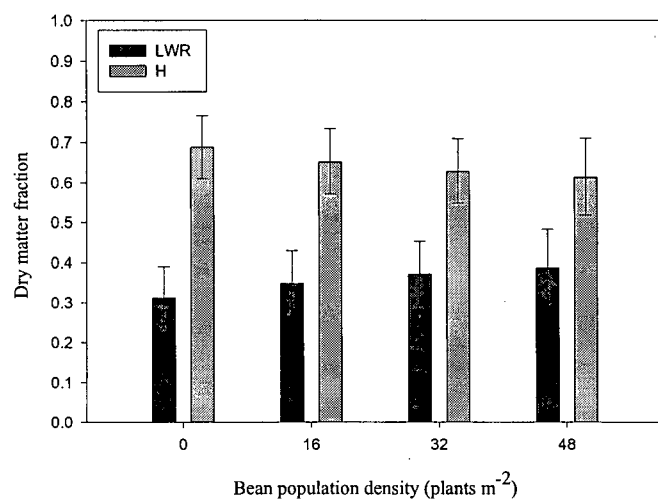
B
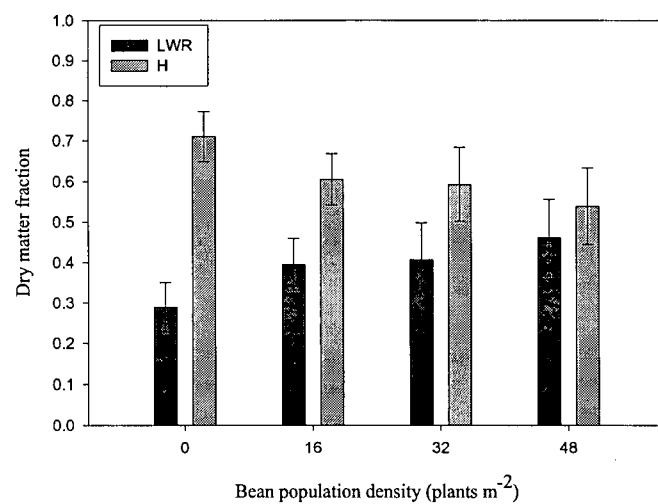
Figure 5.12. Effect of bean population density on dry matter partitioning (mean values ± standard errors) of beets under low soil fertility (A) and high soil fertility (B) in1995.

5.3.2.2 Allometric analysis

Simple allometric relationships between ln(W) and ln(WSR) of beet and other ln-transformed measures per plant, are given in Tables 5.10a and b respectively. All the relationships were significant, had positive values of β, and they explained from 55 to 97% of the variation in ln(W). Hence as with bean, growth in ln(W) of beet tended to be proportional to growth in the other plant measures. Also growth in ln(WSR) of beets was proportional to leaf area expansion process (Table 5.10b).

Parameter values in (Tables 5.11 to 5.13, Appendix 5) specify the best subset regressions for the expanded allometric models for beet. As before, R^2 values were high and parameters β_k and γ_k in each model differ in units of measurement depending on the identity of the independent variable with which they are associated, and standard partial regression coefficients were used to compare contributions made by different terms in the models.

Allometric exponents (terms containing β) were significant ($P<0.05$) in all the best subset regressions. Terms containing β_0 were usually significant ($P<0.05$). Together with the significant allometric coefficients (α') this indicates the common occurrence of direct allometric relationships, independent of the experimental treatments. Significant terms involving β_k ($k>0$) indicate significant interactions between treatments and allometry. As with bean, increasing species population densities significantly lowered the ratio of y to z_i, as indicated by negative signs on the standard partial regression coefficients for terms involving β_k ($k>0$) (Tables 5.11 and 5.12). Again, that there was no obvious pattern as to which terms involving β_k ($k>0$) were significant in the two seasons (1994 and 1995).

Significant terms ($P<0.05$) containing γ_k express relationships between experimental treatments and the variation in ln(W) which are not due to the allometric relationships between W and other primary measures. In all the best subset regressions, ln(N) had no significant influence ($P>0.05$) on ln(W) (Tables 5.11 to 5.13, Appendix 5). Species population density treatments and their interactions significantly reduced ln(W) as indicated by significant values of γ_k ($k>1$) and negative values of standard partial regression coefficients associated with these terms (Tables 5.11 and 5.13).

Table 5.10a. Parameter estimates and statistics for simple bivariate allometric models (eqn. 2.4) between ln(W) and other ln-transformed measures (z) of beet in unfertilized (N_0) and fertilized (N_1) treatments[1].

z	$\ln(\alpha)$	β	Residual mean square	R^2
		1994 N_0		
LA	-2.06*	0.767*	0.085	0.55
WL	1.50*	0.771	0.082	0.57
WP	0.844*	0.798*	0.016	0.92
		1994 N_1		
LA	-2.85*	0.935*	0.047	0.72
WL	1.58*	0.878*	0.050	0.70
WP	0.608*	0.903*	0.005	0.97
		1995 N_0		
LA	-3.44*	0.979*	0.076	0.69
WL	0.984*	1.01*	0.067	0.72
WP	0.870*	0.811*	0.014	0.94
		1995 N_1		
LA	-3.13*	0.937*	0.052	0.75
WL	1.38*	0.840*	0.044	0.79
WP	0.699*	0.897*	0.014	0.93

*Significant at $P<0.05$ according to a T-test. All regressions were significant at $P<0.001$. LA was in units of m^2 plant^{-1}, and other measures were in g plant^{-1}.

Table 5.10b. Parameter estimates and statistics for simple bivariate allometric models (eqn. 2.4) between ln(WSR) and ln(LA) (z) of beet in unfertilized (N_0) and fertilized (N_1) treatments[1].

z	$\ln(\alpha)$	β	Residual mean square	R^2
		1994		
LA	-0.719*	1.11*	0.071	0.76
		1995		
LA	-4.90*	1.14*	0.065	0.78

*Significant at $P<0.05$ according to a T-test. All regressions were significant at $P<0.001$. LA was in units of m^2 plant^{-1}, and other measures were in g plant^{-1}.

Table 5.11. Parameters and statistics for the best subset multiple regression models of the allometric relationship between W and LA in beets.

Potential independent variable	Parameter	Parameter estimates		Standard partial regression coefficients	
		1994	1995	1994	1995
Intercept	$\ln(\alpha`)$	-3.04* (0.542)	-2.17* (0.488)		
$\ln(LA)$	β_0	0.966* (0.0658)	0.651* (0.0901)	0.881	0.568
$N\ln(LA)$	β_1	-		-	
$X_1\ln(LA)$	β_2	-	-0.00116*	-	-0.264
		-	(0.000234)	-	
$X_2\ln(LA)$	β_3	-	-0.00345*	-	-0.754
		-	(0.000650)	-	
$NX_1\ln(LA)$	β_4	-	-	-	-
$NX_2\ln(LA)$	β_5	-	-	-	-
$X_1X_2\ln(LA)$	β_6	-	-	-	-
		-	-	-	-
$NX_1X_2\ln(LA)$	β_7	-	-	-	-
$\ln(N)$	γ_1	-	-	-	-
$\ln(X_1)$	γ_2	-	-	-	-
$\ln(X_2)$	γ_3	-	-	-	-
		-	-	-	-
$\ln(NX_1)$	γ_4	-	-	-	-
$\ln(NX_2)$	γ_5	0.273* (0.0472)	0.448* (0.0801)	0.364	0.727
$\ln(X_1X_2)$	γ_6	-0.172* (0.0445)	-	-0.257	
$\ln(NX_1X_2)$	γ_7	-	-	-	
R^2		0.92	0.92	0.92	0.92
P(reg.)		<0.001	<0.001	<0.001	<0.001

*Regression parameters significantly different from zero according to a T-test ($P<0.05$). Values in brackets are the standard errors of the parameter estimates given above.

Table 5.12. Parameters and statistics for the best subset multiple regression models of the allometric relationship between W and WL in beets.

Potential independent variable	Parameter	Parameter estimates 1994	Parameter estimates 1995	Standard partial regression coefficients 1994	Standard partial regression coefficients 1995
Intercept	$\ln(\alpha`)$	2.39* (0.345)	-0.447* (0.217)		
$\ln(WL)$	β_0	0.853* (0.0949)	1.17* (0.0645)	0.750	0.974
$N\ln(WL)$	β_1	-	-	-	-
$X_1\ln(WL)$	β_2	-	-	-	-
$X_2\ln(WL)$	β_3	-	-0.0142* (0.00229)	-	-0.735
$NX_1\ln(WL)$	β_4	0.00190* (0.000811)	-0.00175* (0.000500)	0.241	-0.233
$NX_2\ln(WL)$	β_5	-	-	-	-
$X_1X_2\ln(WL)$	β_6	0.0000644* (0.0000294)	-	0.145	-
$NX_1X_2\ln(WL)$	β_7	-	-	-	-
$\ln(N)$	γ_1	-	-	-	-
$\ln(X_1)$	γ_2	-0.346* (0.0851)	-	-0.367	-
$\ln(X_2)$	γ_3	-	-	-	-
$\ln(NX_1)$	γ_4	-	-	-	-
$\ln(NX_2)$	γ_5	-	0.550* (0.0781)	-	0.891
$\ln(X_1X_2)$	γ_6	-	-	-	-
$\ln(NX_1X_2)$	γ_7	-	-	-	-
R^2		0.93	0.93	0.93	0.93
P(reg.)		<0.001	<0.001	<0.001	<0.001

*Regression parameters significantly different from zero according to a T-test ($P<0.05$). Values in brackets are the standard errors of the parameter estimates given above.

Table 5.13. Parameters and statistics for the best subset multiple regression models of the allometric relationship between W and WSR in beets.

Potential independent variable	Parameter	Parameter estimates		Standard partial regression coefficients	
		1994	1995	1994	1995
Intercept	$\ln(\alpha')$	0.769* (0.0790)	1.29* (0.180)		
$\ln(WSR)$	β_0	0.911* (0.0171)	0.772* (0.0360)	0.983	0.896
$N\ln(WSR)$	β_1	-	-	-	-
$X_1\ln(WSR)$	β_2	-	-	-	-
		-	-	-	-
$X_2\ln(WSR)$	β_3	-	-	-	-
		-	-	-	-
$NX_1\ln(WSR)$	β_4	-	-	-	-
$NX_2\ln(WS)$	β_5	-	-	-	-
$X_1X_2\ln(WSR)$	β_6	-	-	-	-
$NX_1X_2\ln(WSR)$	β_7	-	-	-	-
$\ln(N)$	γ_1	-	-	-	-
$\ln(X_1)$	γ_2	-	-	-	-
$\ln(X_2)$	γ_3	-0.0571* (0.0174)	-	-0.0606	-
$\ln(NX_1)$	γ_4	-	0.0560* (0.0274)	-	0.0907
$\ln(NX_2)$	γ_5	-	-	-	-
$\ln(X_1X_2)$	γ_6	-	-0.0801* (0.0272)	-	-0.146
$\ln(NX_1X_2)$	γ_7	-	-	-	-
R^2		0.99	0.97	0.99	0.97
P(reg.)		<0.001	<0.001	<0.001	<0.001

*Regression parameters significantly different from zero according to a T-test ($P<0.05$). Values in brackets are the standard errors of the parameter estimates given above.

5.3.2.3 Yield component analysis

In the regression stage of the forward TDP analysis of beet yield variation per unit land area (Table 5.14), leaf area index (LA/A) and the reciprocal of leaf weight ratio (W/WL) were the major contributors to total yield variation in both seasons (1994 and 1995). In 1994 LA/A contributed 71.8% to total variation and in 1995 it contributed 69.5%. In 1994 W/WL contributed 26.9% and in 1995 it contributed 29.5%. In the backward regression analysis, LA/A and WSR/W (*i. e.* harvest index) were the main contributors to total variation in beet storage root yield: LA/A contributed 50.1% and 72.5% to total beet yield variation in 1994 in 1995, respectively, while WSR/W contributed 42.8% and 24.3%. As with bean, the direct effects of LA/A on yield variation stand out, since it contributed more than half of total yield variation after all other components had been taken into account, as shown in the backward analysis. Comparing the forward and backward regressions it can be seen that the effects of WSR/W may have been *via* other yield components, since these effects were significant in the backward regression but not the forward regression.

In both years, soil fertility, species population densities, and most of their interactions had significant effects on total variation in storage root yield, shown in the right hand column of Table 5.14. Individual effects of treatments were larger contributors than their interactions, and block effects were significant in 1995. Soil fertility and beet population density made the largest contributions, although their ranking changed between the two years. This analysis differs from the ANOVA for WSR in Chapter 3 in that it is done on a per unit land area basis.

The yield .component columns in Table 5.14 indicate experimental sources of variation for the ln-transformed yield components. In the forward analysis, direct effects of treatments on yield, *via* WSR/R, were not detected. In the backward analysis, however, there were direct effects of treatments *via* LA/A. The largest of these were effects of beet population density (12.4%) in 1994, and effects of beet population density (27.4%) and soil fertility (12.5%) in 1995. Figure 5.13 illustrates the effects of fertility and species population density treatments on LA/A in beet. The difference between the two soil fertility levels was less than found previously for bean. At both fertility levels, leaf area index of beet increased with increase in beet population density and decreased with increase in bean population density.

Table 5.14. Two dimensional partitioning of yield component contributions to variation in beet root dry weight per unit land area.

Year	Source[1]	df	Forward					Backward					Y = WSR
			LA/A	WL/LA	W/WL	WSR/W	ΣP	WSR/W	W/WL	WL/LA	LA/A	ΣP	
1994	B	1	3.0²	0.1	0.2	0	0.3	1.6	0	0.4	1.3	0.2	3.5
	N	1	19.0	0	1.3	0	11.1	4.1*	0	0.1	10.3	16.9	31.5*
	BxN (Error 1)	1	0.5	0	0.2	0	-0.7	0	0	0.2	0.4	-0.6	0
	X_2	2	19.9*	0	0.3	0	5.2	1.3*	0	0.1	12.4*	11.7	25.5*
	X_1	3	1.7	0	1.7*	0	2.7	1.5*	0	0.4	0.8	3.4	6.1*
	NxX_2	2	0.4	0	0.5	0	1.2	1.3*	0	0	0.1	0.7	2.1*
	NxX_1	3	1.9	0	0.6	0	-0.8	1.6*	0	0.2	1.0	-1.1	1.7*
	X_2xX_1	6	1.4	0	1.7*	0	-1.8	2.7	0	0.2	1.6	-3.0	1.4
	NxX_2xX_1	6	2.6	0	1.7	0	-0.2	1.7	0	0.4	2.0	0	4.2*
	$BxNxX_1xX_2$ (Error 2)	22	6.4	0.1	2.8	0	-4.8	4.2	0.1	0.7	5.9	-6.3	4.6
	Residual	47	14.9	0.6	16.0	0.3	-12.3	22.7	0.5	3.7	14.2	-21.7	19.4
	Total		71.7*	0.9	26.9*	0.4	0	42.8*	0.7	6.5	50.1*	0	100
1995	B	1	10.0*	0	0.5	0	4.5	0.7	0	0	10.3*	4.0	15.0*
	N	1	11.2*	0	0.3	0	4.7	0.1	0	0	12.5*	3.5	16.1*
	BxN (Error 1)	1	0	0	0	0	0	0	0	0	0	-0.1	0
	X_2	2	26.9*	0	0.4	0	0.1	0.4	0	0	27.4*	-0.5	27.4*
	X_1	3	2.2*	0	2.4	0	3.2	0.8	0	0.2	2.8*	4.0	7.8*
	NxX_2	2	0.3	0	1.5	0	1.5	0.5	0	0.2	0.5	2.0	3.3*
	NxX_1	3	0.5	0	0.2	0	0.4	0.1	0	0	0.5	0.4	1.1
	X_2xX_1	6	2.0*	0	0.4	0	0	0.2	0	0	2.3*	0	2.5*
	NxX_2xX_1	6	2.3*	0	1.3	0	1.9	1.5	0	0.1	2.1*	1.8	5.5*
	$BxNxX_1xX_2$ (Error 2)	22	3.0	0.1	6.9	0	-5.9	4.8	0.1	0.3	2.9	-4.0	4.2
	Residual	47	11.0	0.5	15.6	0.3	-10.3	15.1	0.4	1.7	11.1	-11.2	17.0
	Total		69.5*	0.7	29.5*	0.3	0	24.3*	0.5	2.7	72.5*	0	100

[1]Sources of variation are block (B), soil fertility (N), bean population density (X_1) and beet population density (X_2).

[2]Percentages of total sums of squares of Y for each growing season; total sums of squares were 253.7 (1994) and 220.4 (1995). ΣP columns contain sums of products. *significant at $P<0.05$. Discrepancies in column or row totals are due to rounding-off.
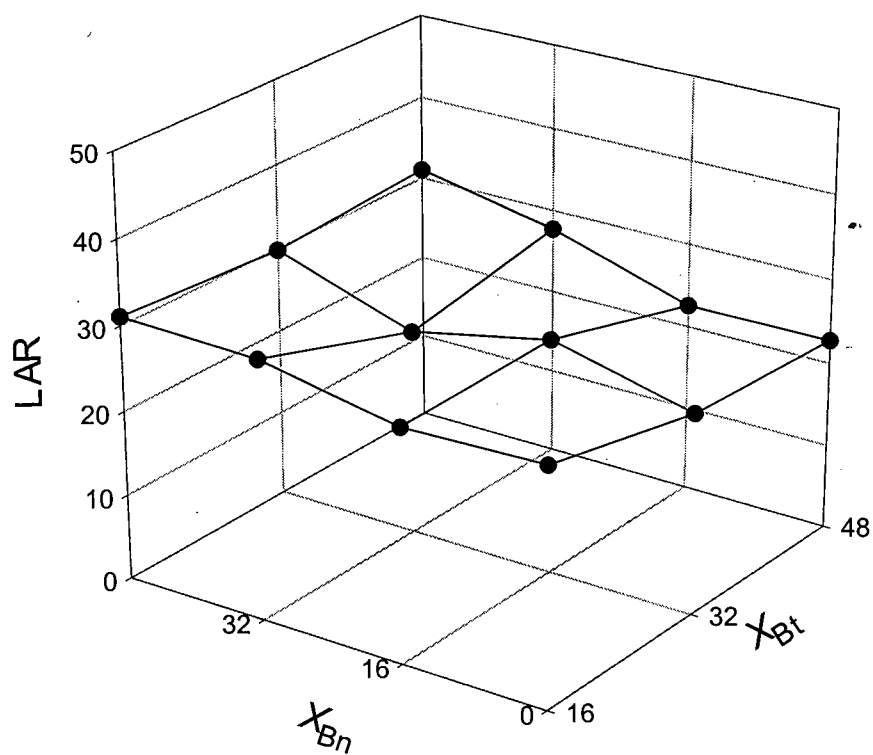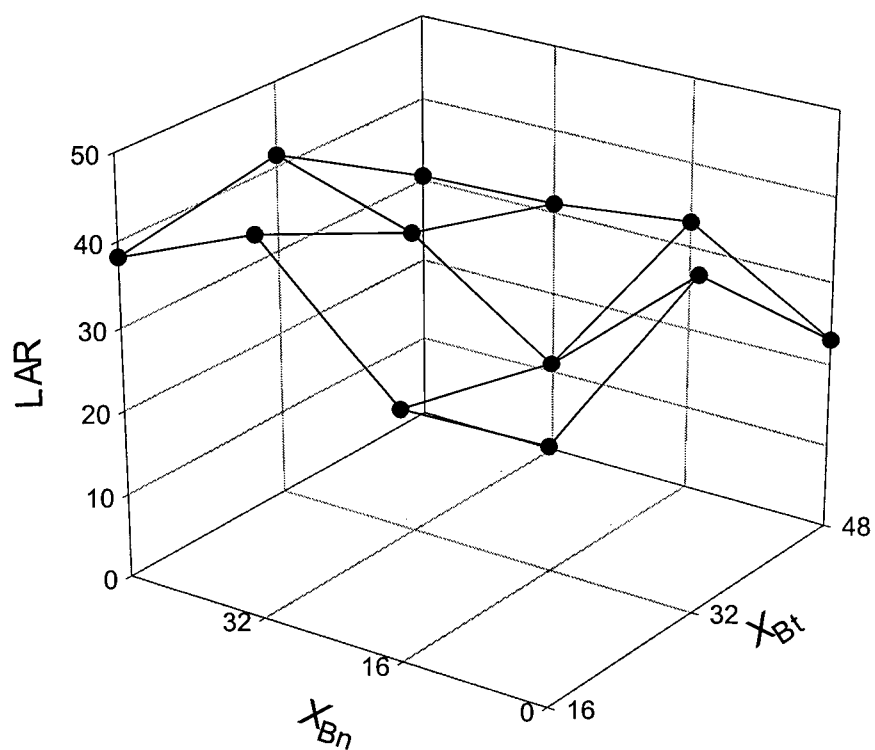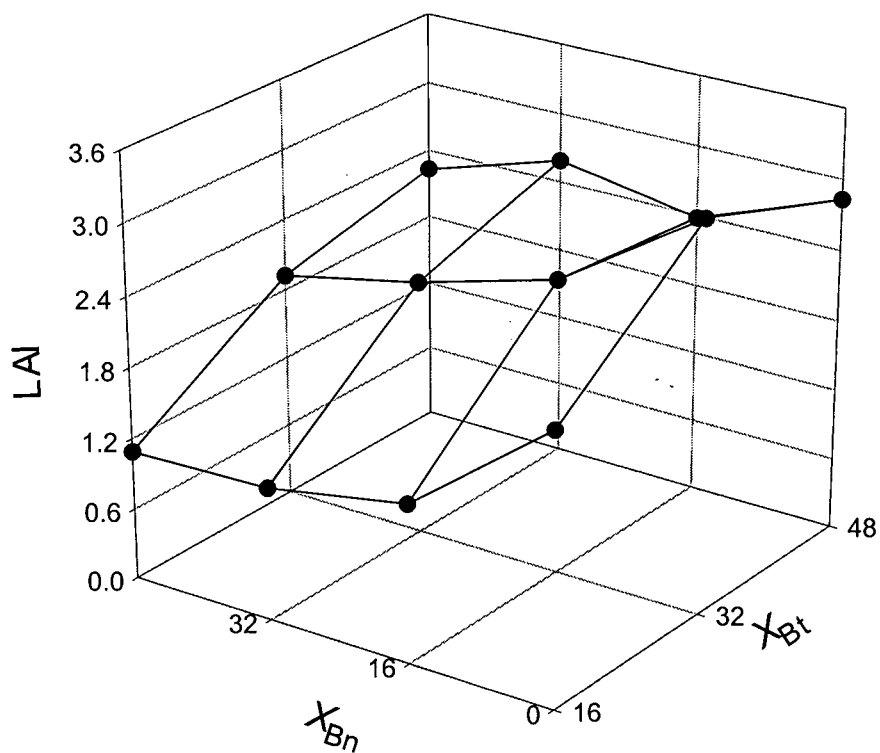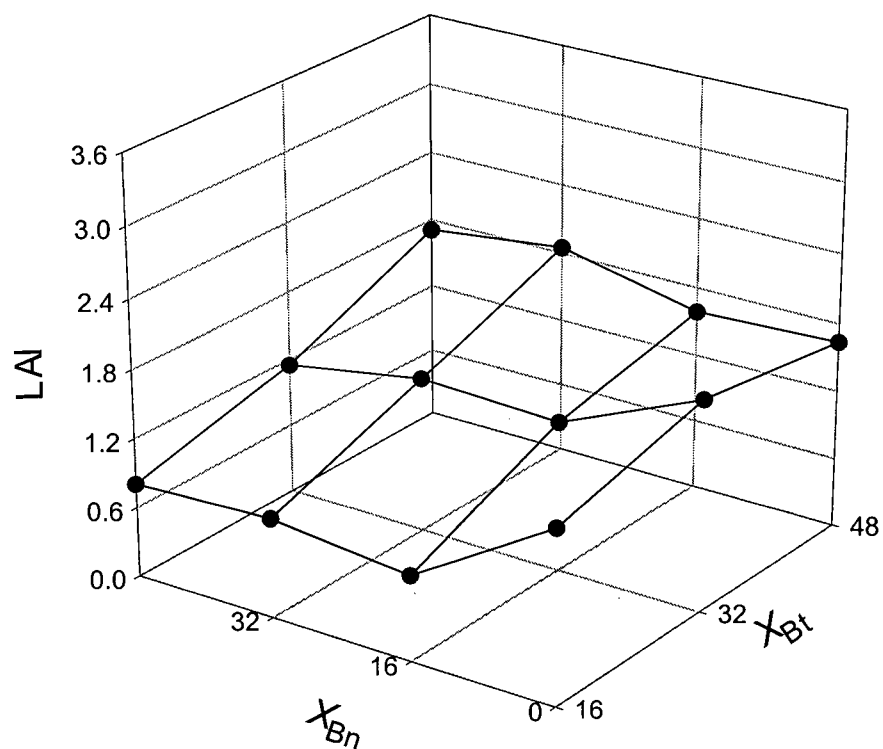
Figure 5.13. Effect of bean and beet population density treatments on leaf area index of beets in the low fertility (A) and high fertility (B) regimes in 1995.

5.4 Discussion

5.4.1 Growth indices

The combined productivity of the crops grown in this study will be considered in Chapter 6. Here, attention will be focused on growth indices, allometry, and yield component relationships to yield variations in each species.

The use of growth indices and yield components, compared to the primary measures, reduces the information available in the primary data set (Hunt 1982). Nevertheless, both growth indices and yield components can summarize and express key aspects of plant behavior more clearly than the primary measures do. *e. g.* leaf area index for a species represents the extent of its leaf array available for photosynthetic carbon assimilation, while WP/PN is an expression of pod filling. Also, the conceptual frameworks provided by conventional plant growth analysis and yield component analysis provide a context for relating primary measures of plant growth to crop performance (Jolliffe and Courtney 1984).

The growth indices used here are ratios of the primary measures whose treatment responses were described in Chapter 3. One of the growth indices, leaf area index, will be discussed in connection with the yield component analysis (section 5.4.3). As with the primary measures, the growth indices and yield components were not uniformly affected by experimental treatments: there were differences between the two species and between the two years of this study. Where the effects of experimental treatments on the growth indices were not significant, which was true in many cases, it is evident that treatments had proportional effects, or no effects, on the primary variables from which the indices were composed. Conversely, where the effects of species population densities on the indices were significant, it can be argued that species population densities had differential effects on the primary variables used to derive the indices. The same primary measures are used in different ways in constructing the growth indices, but the indices can display differences in their behavior. For example, specific leaf area (SLA) is a component of leaf area ratio (LAR = SLA x LWR). LAR of beans decreased with bean population density (Fig. 5.3) while LAR of beets increased with increase in both species' population densities (Fig. 5.9). The SLA of both species, however, increased with increase in species' population densities (Figs. 5.1 and 5.8).

Where significant, the responses of growth indices to experimental treatments were not large. This is consistent with the finding that both species tend to maintain proportionality in their growth under the different experimental treatments, as discussed in the following section (5.4.2). Mchaina (1991) also observed limited plasticity in these species when they were subjected to crowding at high soil fertility. The pattern of significant responses of the growth indices varied greatly between the two years of the study. Hence, it is difficult to interpret these responses as characteristic adjustments to allow each species to exploit environmental resources and tolerate crowding.

Some of the results obtained here, particularly concerning the behavior of leaf area ratio and harvest index, correspond to the findings of previous studies on associations of beet and bean by Mchaina (1991) and Muli (1995) which were done at high soil fertility. With forage maize, Jolliffe *et al.* (1990) observed that leaf area ratio was not significantly influenced by plant population density treatments. Here, small but significant response to increasing plant population densities, of LAR was observed in both species and years, except for bean in 1995.

The patterns of dry matter allocation provide good examples of lack of uniformity of the treatment effects between the two years. For example for beans in 1994, allocation of dry matter to pods was highest, followed by allocation to stems, while allocation to leaves was lowest (Fig. 5.5a). In the 1995 experiment, stems received the highest allocation, followed by pods, while leaves received the lowest (Fig. 5.5b). This difference between the two years, in the patterns of dry matter allocation in beans, may be due to differences in inherent soil fertility of the two experimental sites (see Appendix 1a), differences in the maturity of the bean plants at harvest and the relatively strong competition from beets in the 1995 experiment. These influences may have caused more allocation of dry matter to bean stems, which would tend to reduce lodging (Etherington 1982, Fukai and Trenbath 1993). In 1995, competition may have started earlier, resulting in less dry matter partitioning to the pods than in 1994 (Fukai and Trenbath 1993).

Among all of the growth indices, leaf weight ratio stood out in terms of its dependence on soil fertility, as well as having some responsiveness to population density, for both species in both years of the study. LWR of beans decreased with bean population

density, with the decrease being more conspicuous under higher soil fertility (Fig. 5.3a and b). In beets, LWR increased, at the expense of the storage roots (Fig. 5.12a and b), with increase in bean population density.

The results also revealed some differences between the two species in terms of their responsiveness to each other. For example, beet population density influenced dry matter partitioning of beans more than did bean density, both in the fertilized and the unfertilized treatments. For beets, the response to increasing bean population densities was to allocate a greater proportion of dry matter to storage roots than to leaves, in both years and at both fertility levels. This observation agrees with Mchaina's (1991) findings. Beet population density did not significantly influence dry matter partitioning in beets. Muli (1994) observed a similar behavior.

5.4.2 Allometric analysis

Simple allometric relationships existed between W and other measures, LA, PN, WL, WS WP in beans and LA, WL and WSR in beets. Simple allometric relationships between WP and both LA and PN indicated that leaf area expansion and pod filling were important for the pod dry mass formation in beans, while leaf area development was an important process for the storage root dry mass formation in beets.

Partitioning of the variation in y into various categories, direct treatment effects, direct allometry of W with z_i, treatment effects on the allometry, plus residual variation allowed me to detail the allometric and non allometric responses of the two species. While simple allometric relationships sometimes explained much of the variation in W, the expanded allometric relationships helped in my interpretation by providing better detail of the allometric and non-allometric effects of the experimental treatments. Choice of model and regression procedure are concerns when one attempts to specify allometric relationships. As explained by Riska (1991), a recurring problem in allometric studies has been that of selecting among various regression procedures, such as least squares (LS), major axis, and so forth, when fitting the allometric regression to the data. The LS procedure used here has been used previously (Causton and Venus 1980, Smith 1980). Niklas (1994) has shown that there

is not much difference when one uses LS method compared with major or reduced axis techniques.

The allometric analysis showed that both species tended to exhibit proportional growth in their different measures, across both levels of fertility and both seasons (1994 and 1995), as indicated by the regular significance of the β_0 term in the best subset regressions. Other allometric exponents (terms containing β_k, k>0) were significant in many of the best subset regressions, indicating that treatment factors often changed the allometry between W and the other measures of growth per plant. Here, species population densities were more influential than soil fertility, indicating that in each species similar proportions were maintained at the two fertility levels, as explained by Smith (1980). In bean, non-allometric influences on y (terms containing γ) were often absent; where they did occur they usually involved direct or interacting relationships with soil fertility. $i.$ $e.$ one influence of increasing soil fertility was simply to increase W, without changing the proportionality of W to other plant measures.

Weiner et $al.$ (1990), and Weiner and Fishman's (1994), also reported significant influences of plant competition on plant allometry. In the present study, where plant population densities or their interaction were significant, values of β_k (k>0) were negative. The negative sign of β_k indicates decreasing proportionality of the different measures with W. This indicated that, where these values were negative, the measures decreased proportionately with increase in W, implying that plant competition (within- and between-species) lowered these measures, thereby influencing allometric relationships in the same ways as in other higher plants, as reported by Weiner and Thomas 1992, Weiner and Fishman 1994, and McLachlan et $al.$ 1995. This can be expected to be the case in the present study, since in a preliminary analysis, the plant population densities of both the species had been shown to decrease yields, both in total biomass and in each of the other primary measures. The high R^2 values for the expanded allometric relationships indicated that strong allometric connections existed between W and other measures in both species. Between the two seasons (1994 and 1995), however, there was no obvious pattern as to which terms involving β_k (k>0) were significant. This reflects the complex behavior of allometric responses to experimental treatments, as noted by Jolliffe et $al.$ (1988) and Mchaina (1991).

The allometric relationships between W and the dry biomass of plant components (*e. g.* WL, WP, WSR) provide another means to characterize dry matter partitioning. Strong allometric relationships between W and the dry biomass of plant components, WL, WP and WS for beans, and WL and WSR for beets were observed in this project, indicating proportionate relationships between these measures and W in each species. However, since allometric coefficient β_0, measures proportional increases between various plant parts as time progresses (Smith 1980, Jolliffe *et al.* 1990), it was not possible to characterize dry matter partitioning allometrically, since measures were taken only once, at the time of harvesting.

5.4.3 Yield component analysis

Since its first use as a formal analytical procedure by Engeldow and Wadham (1923), yield component analysis has been used extensively. It has often been used to identify traits that might be selected for crop improvement, and it played a key role in improving grain yield in rice (Matsushima 1970, Yoshida 1972). The two dimensional partitioning (TDP) introduced by Eaton *et al.* (1986) allows the joint analysis of yield component and treatment influences on yield variation. Eaton *et al.* (1986), Jolliffe *et al.* (1990), Mchaina (1991), Jolliffe and Gaye (1995) and Spaner *et al.* (1997) have previously used TDP to analyze treatment effects on yield components. Since the yield component analysis performed here was done on a per unit land area basis, it provides a bridge to issues of crop productivity which will be considered in Chapter 6.

Interpreting the results of a TDP analysis must be done with care. The interpretation needs to take into account the order of entry of the yield components into the stepwise regression. For example, it was consistently found that the yield component that entered the regression first made large contributions to total yield variation. This might be because the first component had strong and direct influences on yield variation. However, subsequent components might really be the important determinants of yield variation; the first component may simply be significant due to correlations with them. The later entries into the regression can only account for residual variation remaining after the earlier components are taken into account. Hence, special attention can be given to significant yield components that enter the regression last. These can be considered to be direct contributors to the total variation, since

they show significance after contributions from all other components have been taken into account.

The TDP results show that it is possible for a yield component to contribute significantly to the total variation in one year, but have no significant contribution in another. For example, WL/LA of beans significantly contributed to the total yield variation in 1994, but did not significantly contribute in 1995. Presumably such differences are due to the uncontrollable (under field conditions) changes in the environmental factors that influence plant growth which may vary from one season to the other, or differ between the experimental sites (1994 and 1995 summer climatic data for the Totem Park Field Station can be accessed at the Department of Soil Science, Faculty of Agriculture, of the University of British Columbia, Vancouver, Canada.).

For both years of the study and for both species, the TDP results highlight leaf area index as a significant contributor to total yield variation. Leaf area index directly contributed to yield variation, accounting for more than 50% of the total variation after the other yield components had been taken into account. Also, leaf area index was the yield component for which most treatment effects were significant. Because light interception by a closed canopy is directly related to leaf area index, and the TDP results for leaf area index reflect the significant yield-density relationships for PAR interception reported in Chapter 4. As with the direct observations of light interception, density treatments affected leaf area index, and this in turn made significant contributions to yield variation.

Leaf area index of each species increased with increases in its population density, but decreased with increases in density of the companion species. The density-dependence of leaf area index is well known. For example, Jolliffe and Gaye (1995) also observed an increase in leaf area index with the increase in plant population of bell peppers (*Capsicum annuum* L.). It should be noted, however, that leaf area index is not independent of population density, since LAI = LA x X. Hence, LAI for a species would be expected to increase as its population density increases. For this reason, treatment effects on leaf area formation in the two species are better interpreted at the level of LA, as was reported in Chapter 3. The decrease in leaf area index of a species, with increasing population density of its companion corresponds to the responses of LA reported in Chapter 3.

For beans, the forward TDP analysis identified pod filling (WP/PN) as a direct contributor to yield variation. In Chapter 3 it was reported that WP and PN were both density-dependent, particularly at the higher fertility level.

To sum up, the analysis of growth indices has shown that experimental treatments influenced dry matter partitioning, with pods receiving most dry matter in 1994 and stem in 1995 in beans; while in beets, more dry matter went to the roots than to the leaves in both years. LWR stood as the most influenced by experimental treatments in both species. Allometric analysis showed that both leaf area development and pod number were important for pod filling in beans, while leaf area expansion was important for the storage root development in beets. Allometric exponents (terms containing β_k, k>0) were significant in many of the best subset regressions, indicating that treatment factors often changed the allometry between W and the other measures of growth per plant. Species population densities were more influential than soil fertility, indicating that in each species similar proportions were maintained at the two fertility levels, as explained by Smith (1980). TDP analysis showed that leaf area index and pod filling ware the major contributors to the total yield variation in beans, while in beets leaf area index was the main contributor to the total variation in storage root yield. Experimental treatments, fertilizer and species population densities were also shown to contribute significantly to the total yield variations in both species.

6. Effects of soil fertility and seasons (1994 and 1995) on productivity and nutrient capture in mixtures of bush beans (*Phaseolus vulgaris* L.) and table beets (*Beta vulgaris* L.)

6.0 Summary

Dry matter productivity, agronomic productivity and nutrient capture were evaluated in mixtures and pure stands of bush beans (*Phaseolus vulgaris* L.) and table beets (*Beta vulgaris* L.) grown at two soil fertility levels in two seasons (1994 and 1995). Inverse yield-density models were found to describe crop yields per unit land area. Productivity was evaluated on the basis of relative yield total (RYT), relative land output (RLO) and total land output (TLO), using the fitted estimates of growth and nutrient content. At high soil fertility, mixtures were more productive than their corresponding pure stands, as found in 11 of 12 cases for both RYT and RLO. The only exception was for Mg capture in 1995, where no yield advantage was found for the mixtures. For some measures the relative yield advantages of mixtures were small, but in 1995 mixtures were up to 24% more productive than pure stands for agronomic yield, and up to 56% more productive for phosphorous capture. When relative yield advantages were found for the mixtures, they often tended to increase with increasing species population densities. Estimates of RYT and RLO were similar in magnitude and were highly positively correlated. On an absolute basis, beets were the more productive species, and TLO values for all measures of productivity were greatest at high beet population densities. The relative indices of intercrop performance (RYT and RLO) were uncorrelated with TLO. Where comparisons could be made for the high fertility level results, similar patterns of productivity were found between the two years, except for relative Mg productivity. Patterns of dry agronomic productivity were compared between the two fertility levels in 1995. Differences in fertility altered the relative and total patterns of mixture productivity, presumably due to altered competitive balances within and between the associated species.

6.1 Introduction

One justification for growing agricultural intercrops is the expectation that mixed crop species may be more productive than their corresponding pure stands (Vandermeer 1989, Fukai 1993). Greater productivity of intercrops may occur because of complementary relationships between the mixture components, leading to more efficient exploitation of environmental resources and/or reduced exposure to environmental hazards (Natarajan and Willey 1980, Snaydon and Satorre 1989, Fukai 1993, Pilbeam *et al.* 1994, Bulson *et al.* 1997) including reduced exposure to disease and pest attacks (Huxley and Maingu 1978, Wahua and Miller 1978, Willey 1979). In addition, there may be socio-economic and/or nutritional benefits associated with mixed crop farming systems. These include improvements in: diversity of diet and income source, stability of production, efficiency of utilization labour and land area (Francis *et al.* 1976, Wahua and Miller 1978, Willey 1979, FAO 1991).

The expectation for higher productivity when intercrops are grown is supported by research on some mixed associations (e. g. Willey and Osiru 1972, Trenbath 1974, Willey 1979, Natarajan and Willey 1980, Ofori and Stern 1987, Snaydon and Satorre 1989, Vandermeer 1989, Yunusa 1989, Pilbeam, *et al.* 1994, Tilman, *et al.* 1996, Jolliffe 1997, Bulson, *et al.* 1997). Crop mixtures, however, are not necessarily superior to pure stands. Yield disadvantages in some intercrops have been reported (Willey and Osiru 1972, Trenbath 1974, Fisher 1979, Pilbeam *et al.* 1994, Jolliffe 1997). Such disadvantages could occur because of competitive antagonisms, allelopathy or the attraction of insect pests and diseases by mixture components (Ministry of Agriculture, Kenya 1983, Willey 1979). Crop mixtures can also be disadvantageous because they can be more complex to manage than monocultures, especially under mechanized agriculture (Willey 1979).

In terms of resource exploitation, several mechanisms might contribute to such yield advantages. For example, greater light interception may occur in an intercrop than in pure stands if the mixed species combine to produce a more complex and extensive leaf display than when they are grown separately. Also, ground cover and soil occupation may be more complete in intercrops than in monocultures, allowing greater acquisition of soil resources (Natarajan and Willey 1981, Reddy and Willey 1981). Nitrogen transfer between associated

species may occur in legume/non-legume intercrops (Agboola and Fayemi 1972, Dalal 1974, Hall 1974, Natarajan and Willey 1980, Reddy and Willey 1981, Bandyopadhyay and De 1986, Elmore and Jackobs 1986, Gliessman 1986, Patra *et al.* 1986, Senaratne and Ratnasinghe 1993, Bulson *et al.* 1997), and available environmental resources may be exploited by different components of crop mixture at different times during growth (Fukai and Trenbath 1993).

Some evidence exists that, in addition to affecting competitive relationships (Chapters 3 and 4), environmental factors may affect the occurrence of yield advantages in intercrops. For example, Suehiro and Ogawa (1980) studied competition in mixtures of *Chenopodium album* L. and *Atriplex gmelini* grown at different salt concentrations. Later re-analysis of their results indicated that salt concentrations affected the relative performance of the species mixtures compared to pure stands (Jolliffe 1997). Also, Reddy *et al.* (1980), Chang and Shibles (1985) and Russell and Caldwell (1989) found yield advantages were particularly prominent under low soil fertility in maize/groundnut, maize/cowpea and maize/soyabean intercrops respectively. Natarajan and Willey (1986) studied mixture performance under moisture stress, and found that yield advantages increased with increasing moisture stress. However, Willey and Osiru (1972), Fisher (1977, 1979) and Pilbeam *et al.* (1994) found yield disadvantages under low moisture conditions in maize/bean intercrops. Hopefully, further research will help to elucidate why yield advantages vary, both within mixtures grown under different circumstances and among different species associations.

Several indices have been utilized to assess the productivity of species mixtures associations, and this has complicated the evaluation of mixture performance. Some indices attempt to compare the relative productivity of mixtures with pure stands. Such indices include land equivalent ratio (LER, Huxley and Maingu 1978, Willey 1979, Mead and Willey 1980), relative yield total (RYT, de Wit and Van den Bergh 1965), relative resource total (Connolly 1987), area-x-time equivalency ratio (Hiebsch and McCollum 1987), area harvest equivalency ratio (Balasubramanian and Sekayange 1990), effective and staple land equivalent ratios (Riley 1985) and relative land output (RLO, Jolliffe 1997). Further complicating the picture are similarities among some of these indices, such as LER and RYT, and the fact that LER has several alternative definitions (Huxley and Maingu 1978, Willey

1979, Mead and Willey 1980). In addition to relative indices, the total combined productivity of mixtures can be assessed, using indices such as total land output (TLO, Jolliffe 1997).

This study will evaluate relative and total production and nutrient capture by intercrops of bush bean (*Phaseolus vulgaris* L.) and table beet (*Beta vulgaris* L.) grown at two levels of soil fertility. Relative productivity and nutrient capture by mixed *vs.* corresponding pure stands will be assessed by both RYT and RLO. The combined production and nutrient capture of the mixed associations will be assessed using TLO. Objectives of this study are: (i) to determine whether mixed bean/beet associations are more productive than their pure stand counterparts, (ii) to determine if patterns of productivity of mixed bean/beet associations are consistent at different levels of soil fertility, different population density combinations and in two different seasons (1994 and 1995), (iii) to determine whether mixed bean/beet associations capture mineral nutrients better than their pure stand counterparts, and (iv) to determine if patterns of mineral nutrient capture in mixed bean/beet associations are consistent at different levels of soil fertility and different seasons (1994 and 1995).

6.2 Materials and Methods

Experimental protocol, including experimental design and data collection, was described in Chapters 3 and 4. Measures of production that will be used here are based on several measures reported in those chapters. They include: the mean dry mass per plant of aboveground plant parts (W) or pods (WP) of beans, the mean dry mass per plant of storage roots (WSR) or storage roots plus aboveground plant parts (W) of beets. As reported in Chapter 3, in both 1994 and 1995 significant inverse yield-density models were obtained for these measures at the higher fertility level (N_1), and in several cases significant models were also obtained at low fertility (N_0). The models are given again in Table 6.1. The models express the decline in mean yield per plant (i. e. the increase in $1/y$) as bean (X_1) and beet (X_2) population densities increase.

Table 6.1. Inverse yield-density models used for dry mass predictions.

Species	Measure (y)	Fertility Level	Year	Model for $1/y$	Observed/Predicted[1] ± s.e.
Bean	W	N_1	1994	$0.0279 + 0.00118X_1 + 0.000654X_2$	1.042 ± 0.056
Beet	W	N_1	1994	$0.00725 + 0.000550X_2 + 0.000458X_1$	0.998 ± 0.0598
Bean	WP	N_1	1994	$0.0543 + 0.00206X_1 + 0.00138X_2$	1.060 ± 0.066
Beet	WSR	N_1	1994	$0.00792 + 0.000766X_2 + 0.000688X_1$	0.998 ± 0.065
Bean	W	N_1	1995	$0.112 + 0.000411X_1 + 0.000501X_2$	1.012 ± 0.023
Beet	W	N_1	1995	$0.00990 + 0.000891X_2 + 0.000549X_1$	1.014 ± 0.034
Bean	WP	N_0	1995	$0.848 + 0.000606X_1 + 0.0172X_2$	1.082 ± 0.064
Beet	WSR	N_0	1995	$0.0438 + 0.00157X_2 + 0.00176X_1$	1.103 ± 0.079
Bean	WP	N_1	1995	$0.272 + 0.00433X_1 + 0.00331X_2$	1.017 ± 0.034
Beet	WSR	N_1	1995	$0.0124 + 0.00142X_2 + 0.000845X_1$	1.004 ± 0.033

[1]Ratio of observed y to predicted y, equivalent to the ratio of observed Y to predicted Y.

In order to predict yield per land area (Y), the per plant estimates were multiplied by species population density (e. g. $Y_1 = y_1X_1$). The fitted estimates of Y were incorporated into three indices of the productive performance of the intercrops. Where possible, the observed mean values were also used to calculate the same indices. The indices were relative yield total (RYT, de Wit and Van den Bergh 1965):

$$RYT = (Y_{12}/Y_{11}) + (Y_{21}/Y_{22})$$ (2.6)

relative land output (RLO, Jolliffe 1997):

$$RLO = (Y_{12} + Y_{21})/(Y_{11} + Y_{22})$$ (2.8)

and total land output (TLO, Jolliffe 1997):

$$TLO = (Y_1 + Y_2)$$ (2.9)

where, subscripts 1 and 2 designate the two crop species, grown as mixtures (12 or 21) and as pure stands (11 or 22). i. e., where subscripts are used in pairs, the first subscript identifies the target species, whose yield is being assessed, and the second subscript identifies the species

whose influence on the target is being assessed. The first two of these indices compare the relative performance of mixtures and pure stands; both indices equal 1.0 when mixtures and pure stands are equivalent, exceed 1.0 when the mixture is advantageous, and are less than 1.0 when the mixture is disadvantageous (Willey 1979, Willey and Osiru 1972, Jolliffe 1997). Total Land Output is simply the combined productivity of the species per unit land area, and TLO equals monoculture productivity per unit land area for the pure stands.

It should be noted that, in calculating a value of RYT, total population density (X_1 + X_2) was the same for each Y-estimate, as exists in a single-density replacement series. In calculating a value of RLO, the number of individuals (n) in a component species population and land area of the mixture or total pure stands (A) was the same for each Y-estimate (Jolliffe 1997). *i. e.*, RLO measures the relative yields of mixture to pure stand, based on the same number of individuals populating the same total land area. RYT is predicted from the yield-density models by:

$$RYT = \frac{[n_1/(a_{10}+a_{11}n_1/A+a_{12}n_2/A)]}{[n_1/(a_{10}+a_{11}(n_1+n_2)/A)]} + \frac{[n_2/(a_{20}+a_{22}n_2/A+a_{21}n_1/A)]}{[n_2/(a_{20}+a_{22}(n_1+n_2)/A)]} \quad (2.14)$$

RLO is predicted by:

$$RLO = \frac{[n_1/(a_{10}+a_{11}n_1/A+a_{12}n_2/A)] + [n_2/(a_{20}+a_{22}n_2/A+a_{21}n_1/A)]}{[n_1/(a_{10}+a_{11}(n_1+n_2)/A)] + [n_2/(a_{20}+a_{22}(n_1+n_2)/A)]} \quad (2.15)$$

and TLO was calculated from the yield-density models using:

$$TLO = [(n_1/A)/(a_{10}+a_{11}n_1/A+a_{12}n_2/A)] + [(n_2/A)/(a_{20}+a_{22}n_2/A+a_{21}n_1/A)] \quad (2.16)$$

The above computations were repeated for each of the mineral nutrients N, P, K, Ca and Mg, whose contents had been assessed (Chapter 4). In these cases, Y in the above equations would then represent mineral nutrient content per unit land area, derived from either the direct experimental observations or from the regressions reported in Tables 4.3 to 4.6.

Correlations between the observed and predicted estimates of RYT, RLO and TLO were tested for all measures of Y, and correlations between the different indices of production (RYT and RLO, RYT and TLO, RLO and TLO) were also assessed.

6.3 Results

6.3.1 Predicted and observed indices of productivity

Before dealing with specific aspects of productivity in the binary species mixtures, some consideration needs to be made concerning how the indices of productivity, RYT, RLO and TLO were derived from the experimental data. The interpretations made here were done using the indices that had been computed using the inverse yield-density relationships, not the primary experimental observations. This was possible because the inverse yield-density relationships were effective in predicting yields per unit land area. There were strong significant ($P<0.05$) positive correlations between the predicted and observed yields per land area, as illustrated by scattergrams of observed and predicted yields per area (Figs. 6.1 and 6.2). Figs. 6.1 and 6.2 also show that there were significant yield differences between the two seasons, with 1994 yields being higher than the 1995 ones. This difference in yields could be due change in soil factors for the two sites (Appendix 1a) or seasonal climatic changes (1994 and 1995 summer climatic data for the Totem Park Field Station can be accessed at the Department of Soil Science, Faculty of Agriculture, of the University of British Columbia, Vancouver, Canada.). On average, the ratios of observed to predicted values of y were within a few percent of, and not significantly different from, 1.00 (Table 6.1). The same is also true on a per unit land area basis, since Y is obtained by multiplying both the observed and predicted values by the same value (X), thereby conserving the same ratio of observed to predicted value of yield per unit land area.
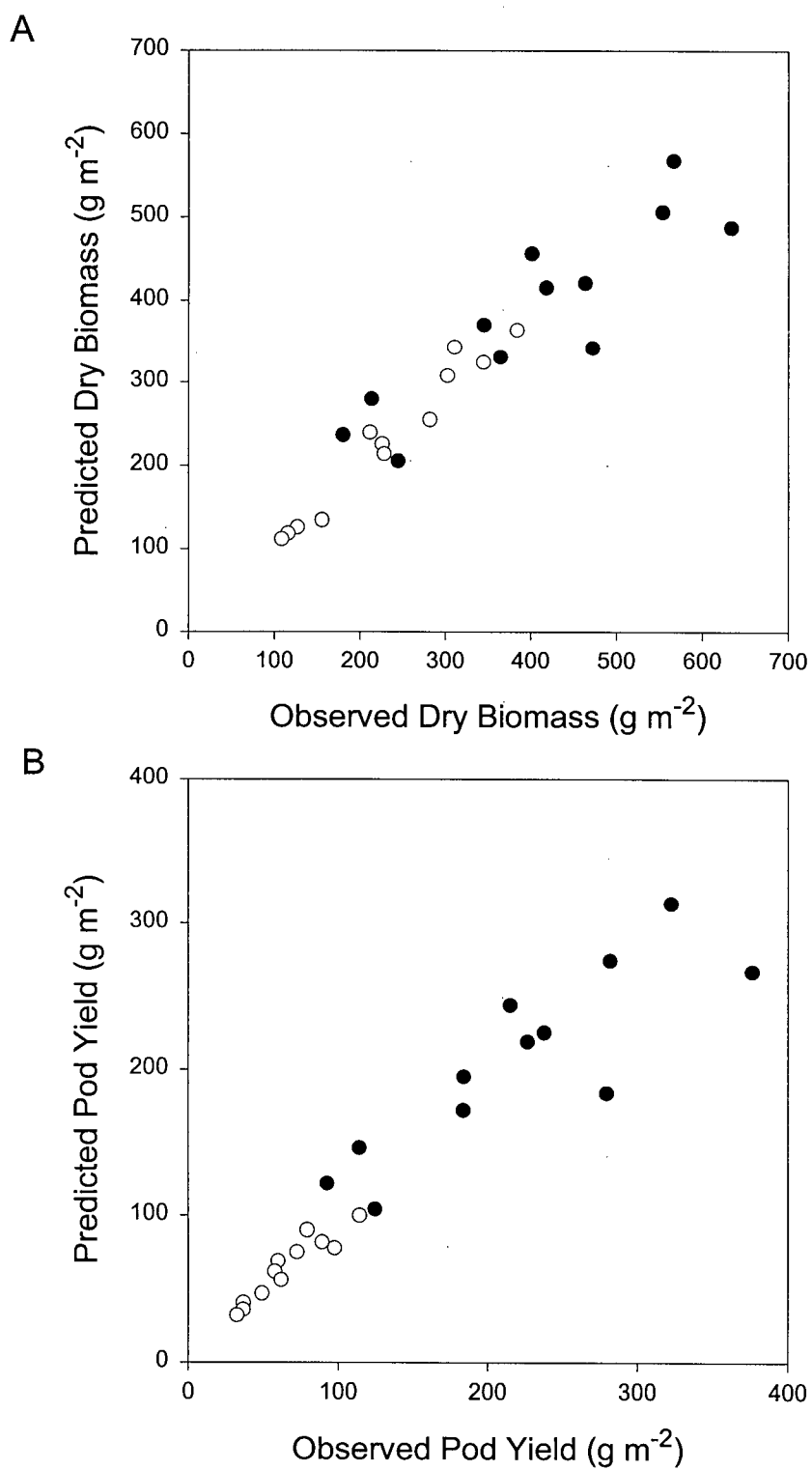
Figure 6.1. Predicted and observed dry matter (A), or pod (B), yields per unit land area of beans in 1994 (closed symbols) and 1995 (open symbols).
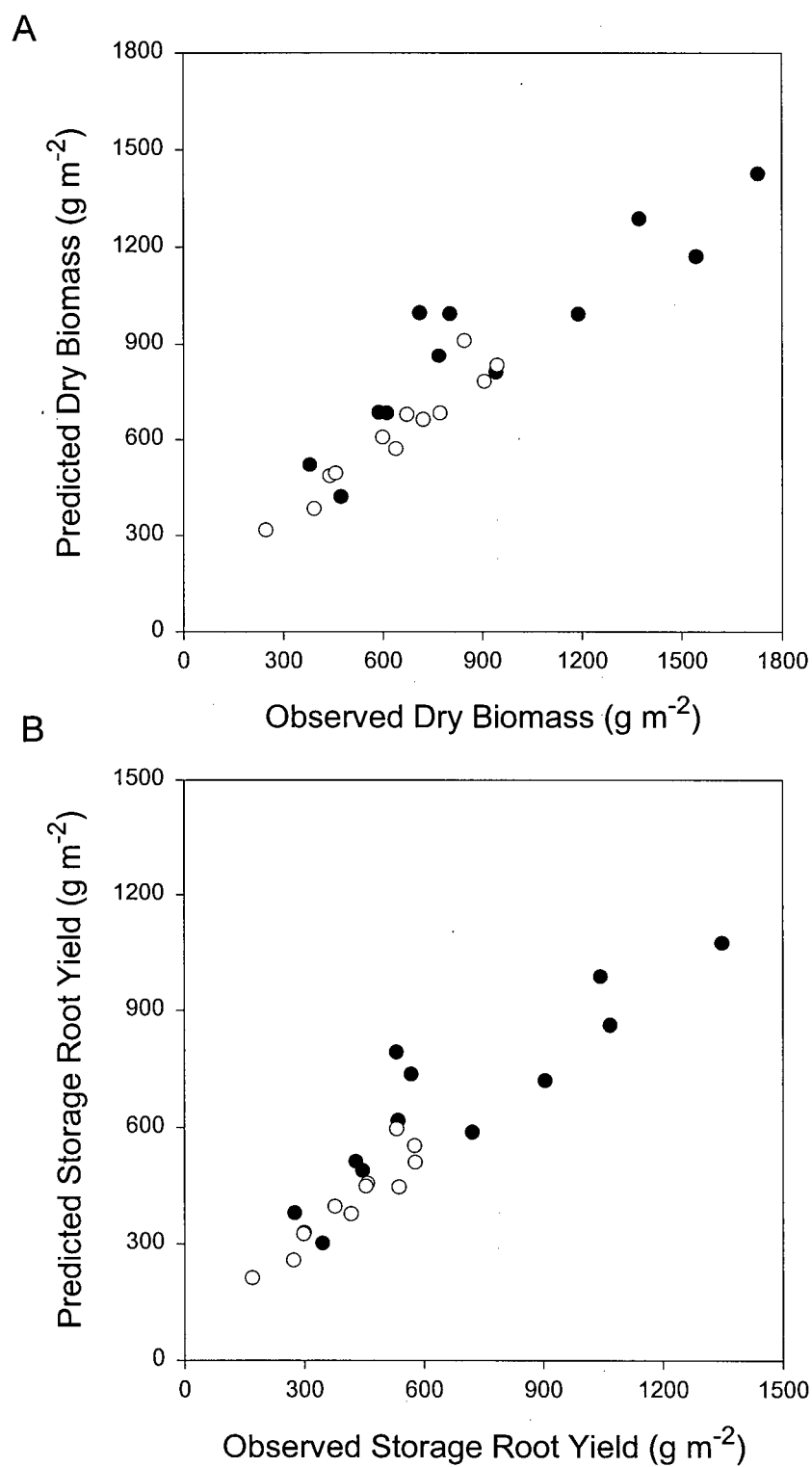
Figure 6.2. Predicted and observed dry matter (A), or pod (B), yields per unit land area of beets in 1994 (closed symbols) and 1995 (open symbols).

Similarly, observed and fitted estimates of TLO agreed well (Table 6.2), and TLO could be calculated directly from the fitted relationships, or the experimental observations, at every density combination used in this study. At any particular density combination, however, an estimate of TLO made using the fitted relationships will involve a broader data base (i. e. higher degrees of freedom) than an estimate made directly from pairs of the observed experimental means.

In the case of RLO or RYT, it was only possible to use the observed values at a few density combinations (the 16:16, 16:32 and 32:16 mixtures), while the fitted relationships could again be used at all density combinations. RLO and RYT involve ratios of summed yield estimates, or sums of yield ratios, respectively. Because of their mathematical construction, these measures are sensitive to errors in estimation of their underlying Y-terms. The greater degrees of freedom involved in taking those ratios, using the fitted estimates compared to the direct observations, resulted in a clearer picture of the effects of experimental treatments on aspects of productivity. The importance of using as large a data base as possible is illustrated in Table 6.2. Pooling both years, RLO or RYT for dry matter or agronomic yields, estimated directly from the experimental means, were not correlated with the fitted estimates (n=6 or 9). When these comparisons are made for RLO or RYT for nutrient capture, where more cases were available (n=24), significant correlations were obtained (Table 6.2). Appendix 6 includes the RLO and RYT estimates made directly from the experimental means.

The two indices of relative performance of mixtures compared to monocultures, RLO and RYT, consistently gave similar results, and were highly correlated (Table 6.2). For that reason, the RYT results will be not considered here, but are presented in Appendix 7.

Table 6.2. Correlations among indices of mixture productivity.

Characteristic	Measure 1	Measure 2	Pearson correlation coefficient	Number of data pairs[1]	P
Dry biomass productivity	Observed TLO	Predicted TLO	0.933	30	<0.001*
	Observed RLO	Predicted RLO	0.292	6	0.588ns
	Observed RYT	Predicted RYT	-0.665	6	0.150ns
Dry agronomic productivity	Observed TLO	Predicted TLO	0.949	45	<0.001*
	Observed RLO	Predicted RLO	0.422	9	0.259ns
	Observed RYT	Predicted RYT	0.370	9	0.327ns
Nutrient accumulation	Observed TLO	Predicted TLO	0.955	120	<0.001
	Observed RLO	Predicted RLO	0.416	24	0.043*
	Observed RYT	Predicted RYT	0.528	24	0.008*
Dry biomass and agronomic productivity	Predicted RYT	Predicted RLO	0.955	24	<0.001*
	Predicted RYT	Predicted TLO	0.144	24	0.501ns
	Predicted RLO	Predicted TLO	-0.008	24	0.972ns

[1]Pooled results for both years, and pooled for both fertility treatments if significant yield-density regressions were obtained at both fertility levels.

6.3.2 Indices of intercrop performance: dry biomass and agronomic yields

Predicted RLO and TLO estimates for total dry matter production in the two seasons (1994 and 1995), at each population density combination represented in this study, are presented in Figs. 6.3 and 6.4, and in Appendix 6. These, and most of the subsequent results, are for the high fertility regime only, because significant density-dependence seldom occurred at low fertility (Chapters 3 and 4). The results suggest that yield advantages occurred when beans and beets were intercropped, since mixture RLO values exceeded 1.00 (Fig. 6.3). The advantages were not large, ranging from about 8% to 12% and tending to increase with increasing species densities. The advantages were greater in 1995 than in 1994. Total land output (TLO) was dominated by beet, which was the more productive species (Fig. 6.4).
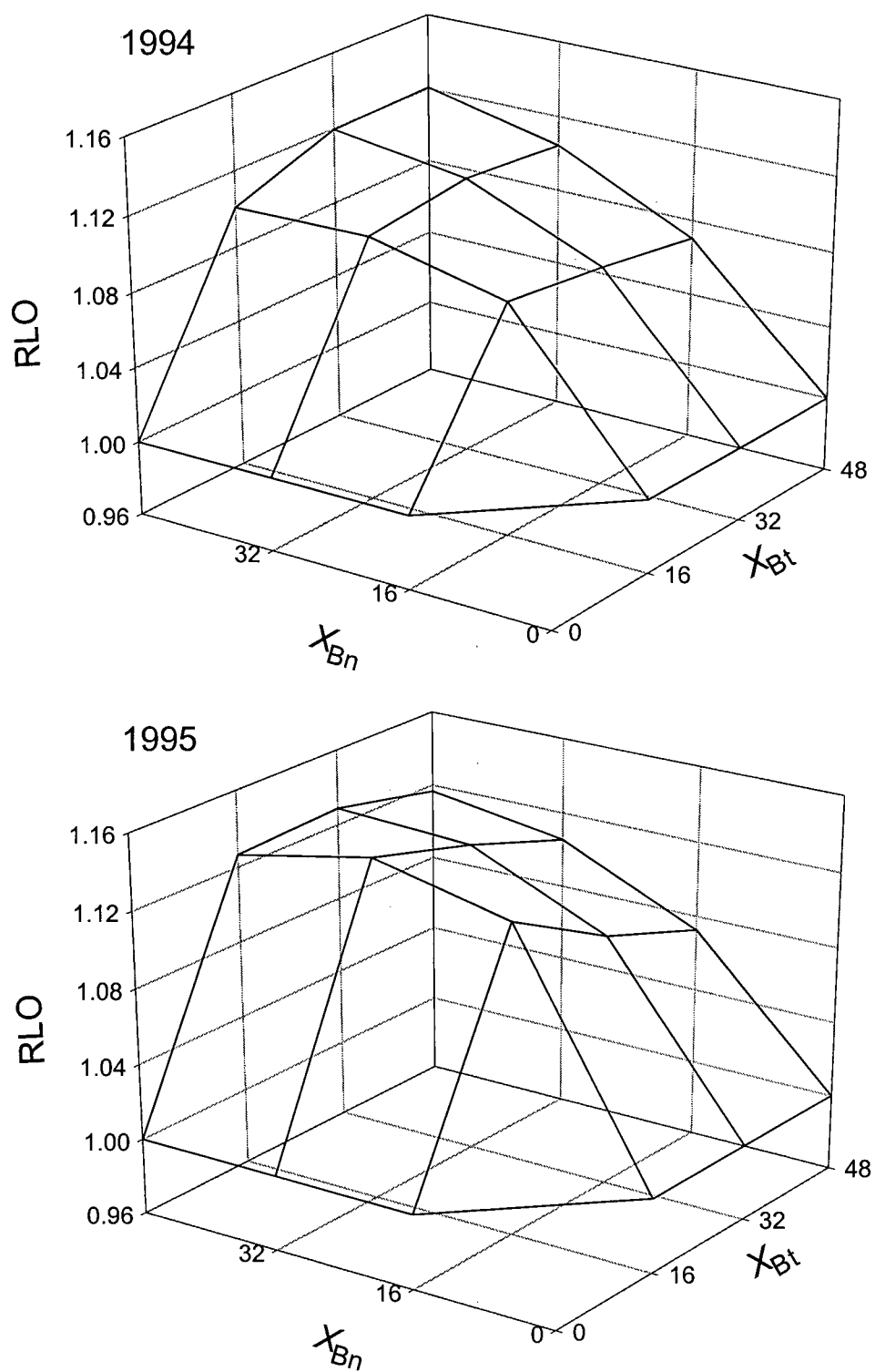
Figure 6.3. Relative Land Outputs for dry mass formation per unit land area in 1994 (top panel) and 1995 (bottom panel) estimated from yield-density relationships at each of the population density combinations represented in these studies, in the fertilized plots.
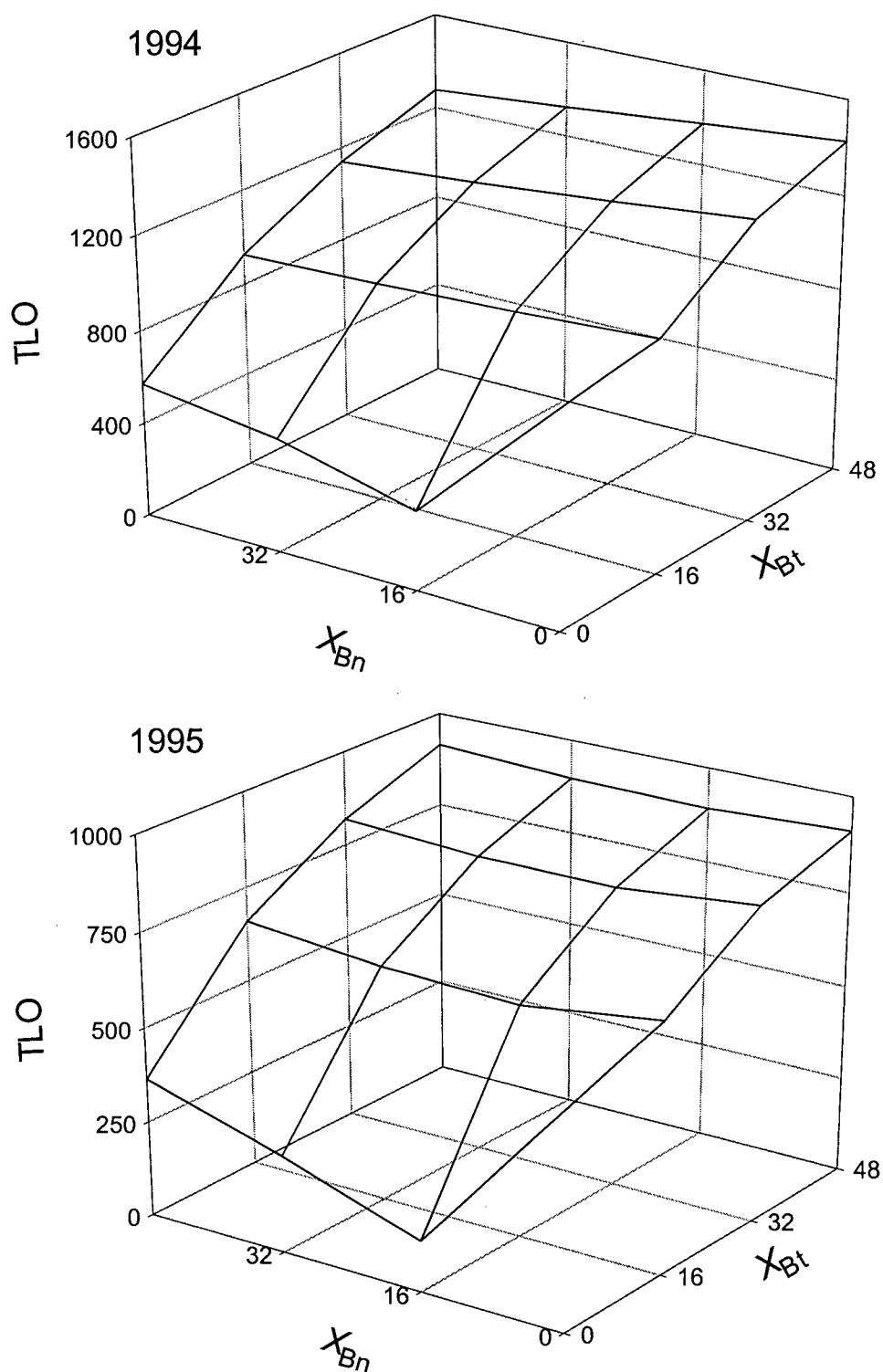
Figure 6.4. Total Land Outputs for dry mass formation per unit land area in 1994 (top panel) and 1995 (bottom panel) estimated from yield-density relationships at each of the population density combinations represented in these studies, in the fertilized plots.

Agronomic yields involved dry mass of bean pods and beet storage roots. These constituents involved significant proportions of total plant dry mass (Chapters 3 and 5), so it is not surprising that they produced patterns of behaviour for RLO and TLO which resembled those shown for biomass productivity (Figs. 6.5 and 6.6). Again, the RLO results suggested the occurrence of yield advantages in mixtures, ranging from 4 to 24% greater than that of corresponding pure stands (Fig. 6.5). Again, TLO was highest in dense beet populations (Fig. 6.6).

Comparison of the RLO and TLO results shows little relationship between these indices. For example, RLO values were higher for agronomic yield in 1995 than in 1994, while TLO was lower in 1995 than in 1994 (Figs 6.5 and 6.6). The patterns of density-dependence differed between the two indices, and RLO and TLO were not significantly correlated (Table 6.2).

6.3.3 Indices of intercrop performance: nutrient capture

Usually, the results for the relative and total indices of productivity pertaining to nutrient capture (Figs. 6.7 to 6.16) were similar to those just described for dry matter and agronomic yields. Non-significant regressions prevented estimates being made for N in 1994 and Ca in 1995, but otherwise RLO and TLO could be calculated in both years for the five nutrient elements and the higher fertility level.

Except for Mg in 1995, where there was no advantage (Fig. 6.11), the RLO estimates for nutrient uptake suggested that there was more mineral uptake when beans and beets were intercropped, compared to their corresponding pure stands (Figs. 6.7 to 6.11). Again, RLO values for nutrient uptake were density dependent, with higher values being recorded at high density combinations. The highest values for RLO were for P in 1995, which exceeded 1.5 in the highest density mixtures. Total nutrient uptake (TLO) was again dominated by beets (Figs. 6.12 to 6.16). Also once again, RLO and TLO behaved differently. For example, RLO showed yield advantages even when TLO values were low, such as in the 1995 data (e. g. Figs 6.8 and 6.13).
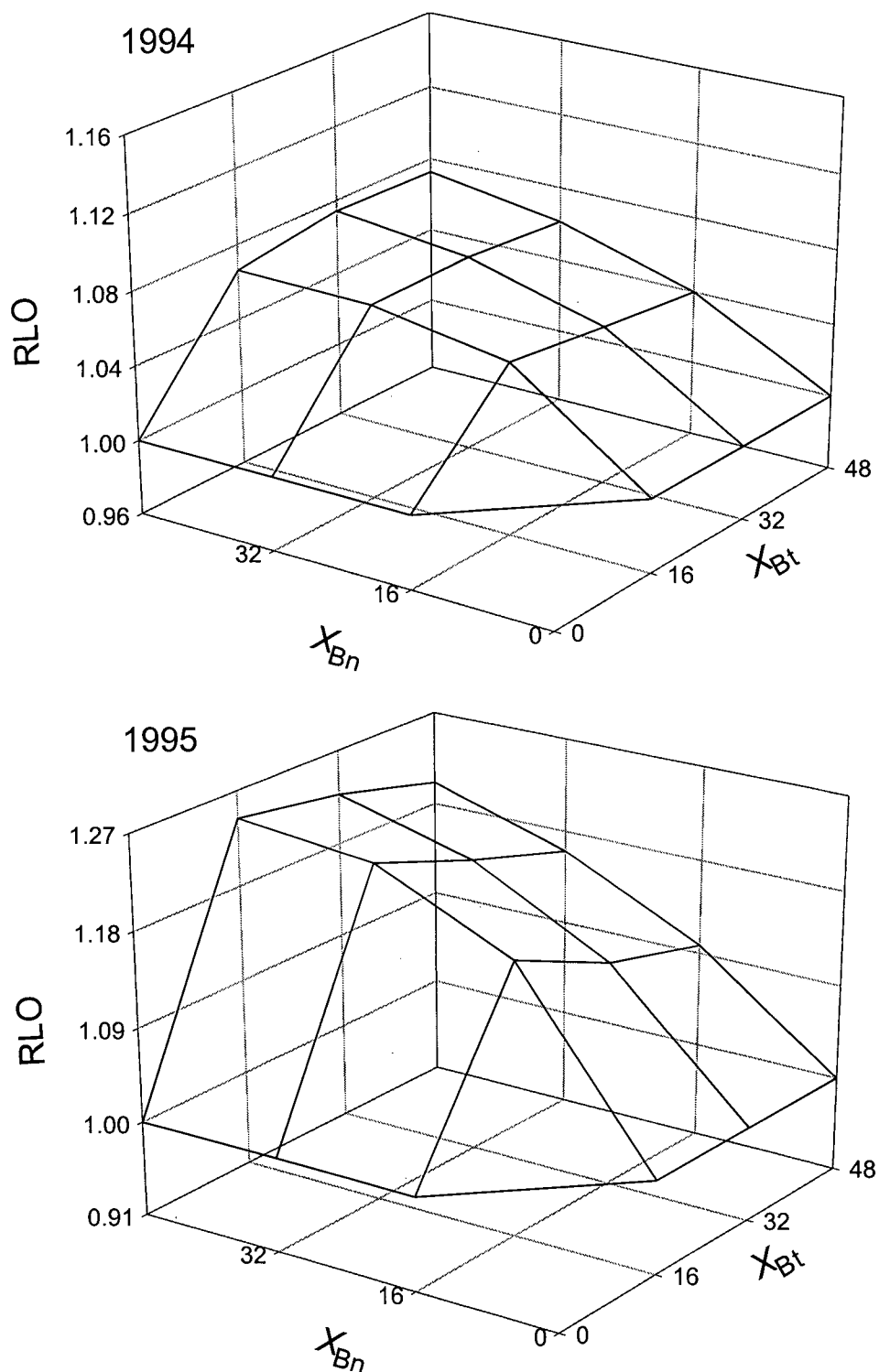
Figure 6.5. Relative Land Outputs for dry mass of agronomic yield per unit land area in 1994 (top panel) and 1995 (bottom panel) estimated from yield-density relationships at each of the population density combinations represented in these studies, in the fertilized plots.
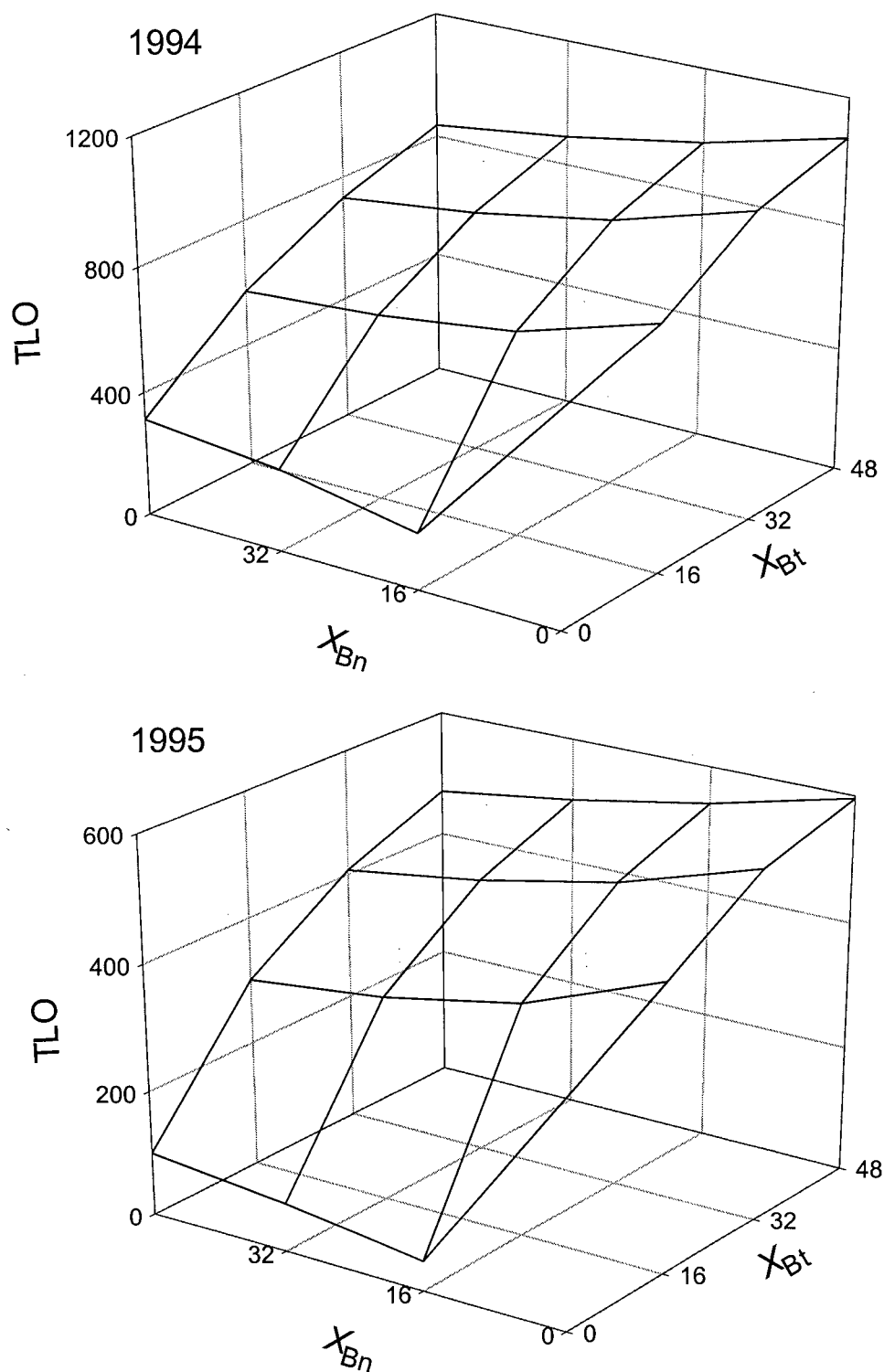
Figure 6.6. Total Land Outputs for dry mass of agronomic yield per unit land area in 1994 (top panel) and 1995 (bottom panel) estimated from yield-density relationships at each of the population density combinations represented in these studies, in the fertilized plots.
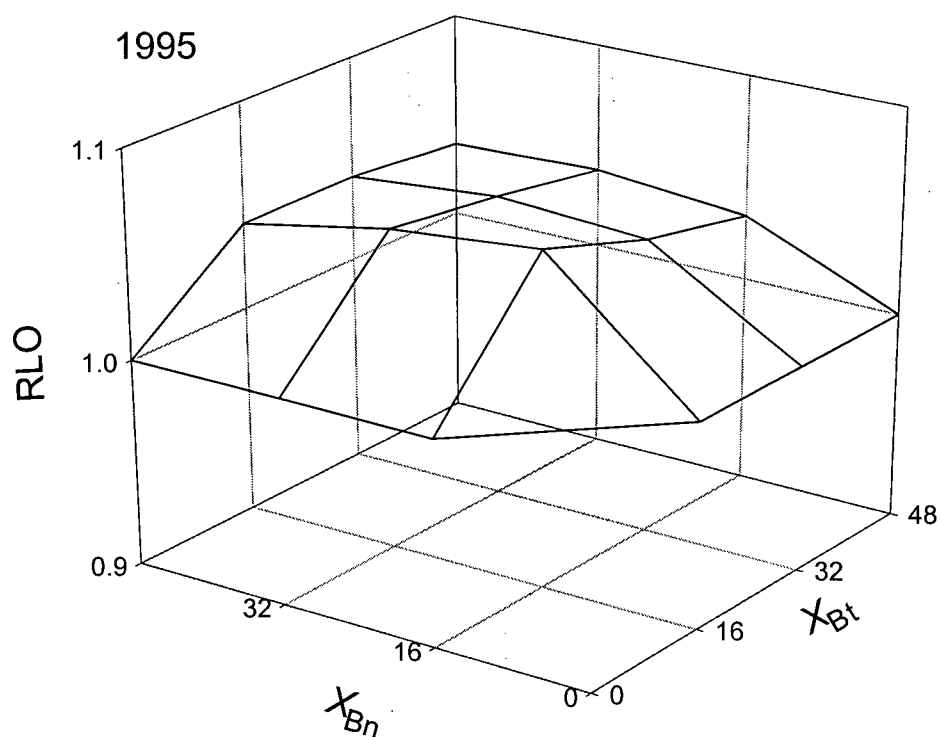
Figure 6.7. Relative Land Outputs for N accumulation per unit land area in 1995 estimated from yield-density relationships at each of the population density combinations represented in these studies, in the fertilized plots.
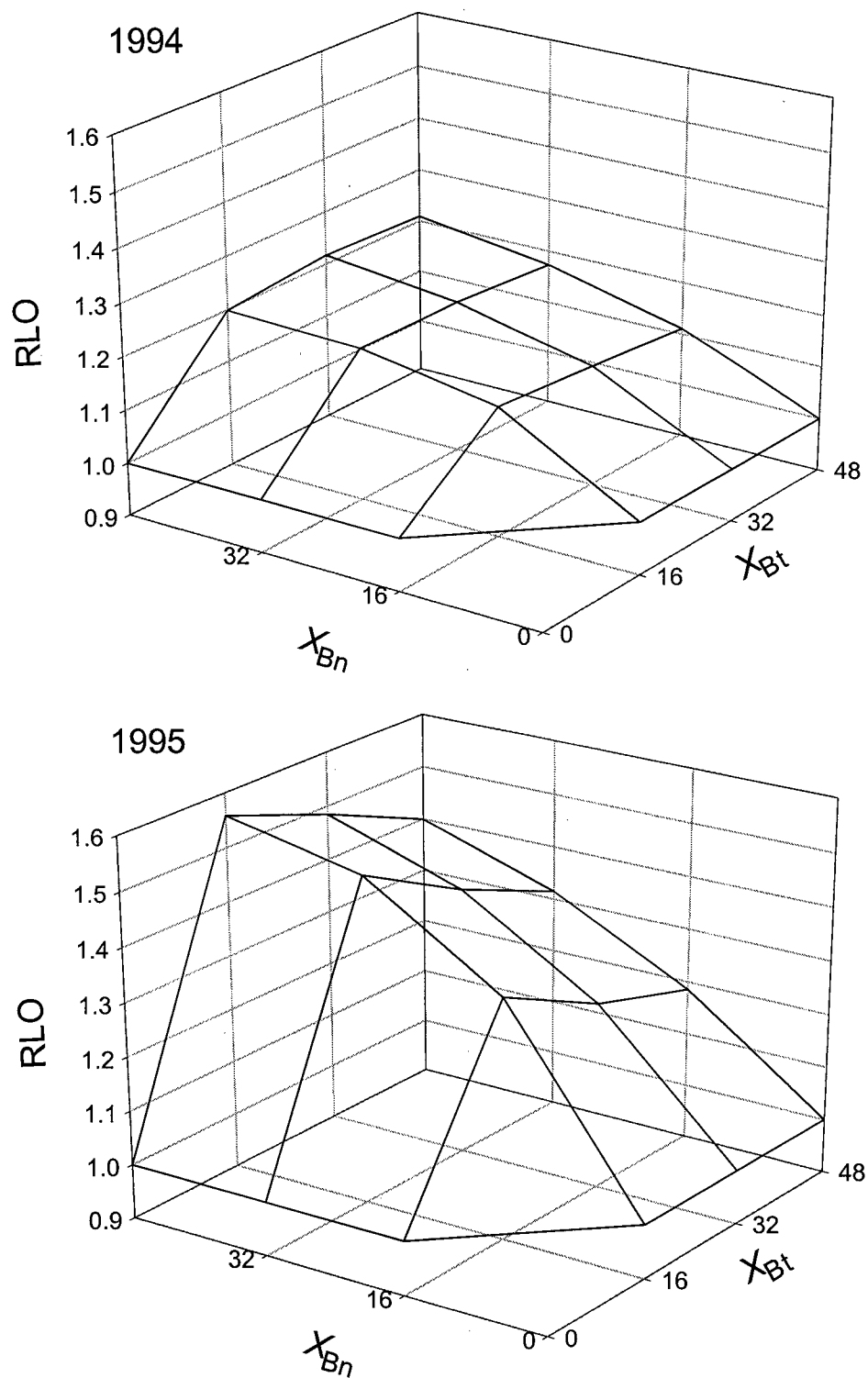
Figure 6.8. Relative Land Outputs for P accumulation per unit land area in 1994 (top panel) and 1995 (bottom panel) estimated from yield-density relationships at each of the population density combinations represented in these studies, in the fertilized plots.
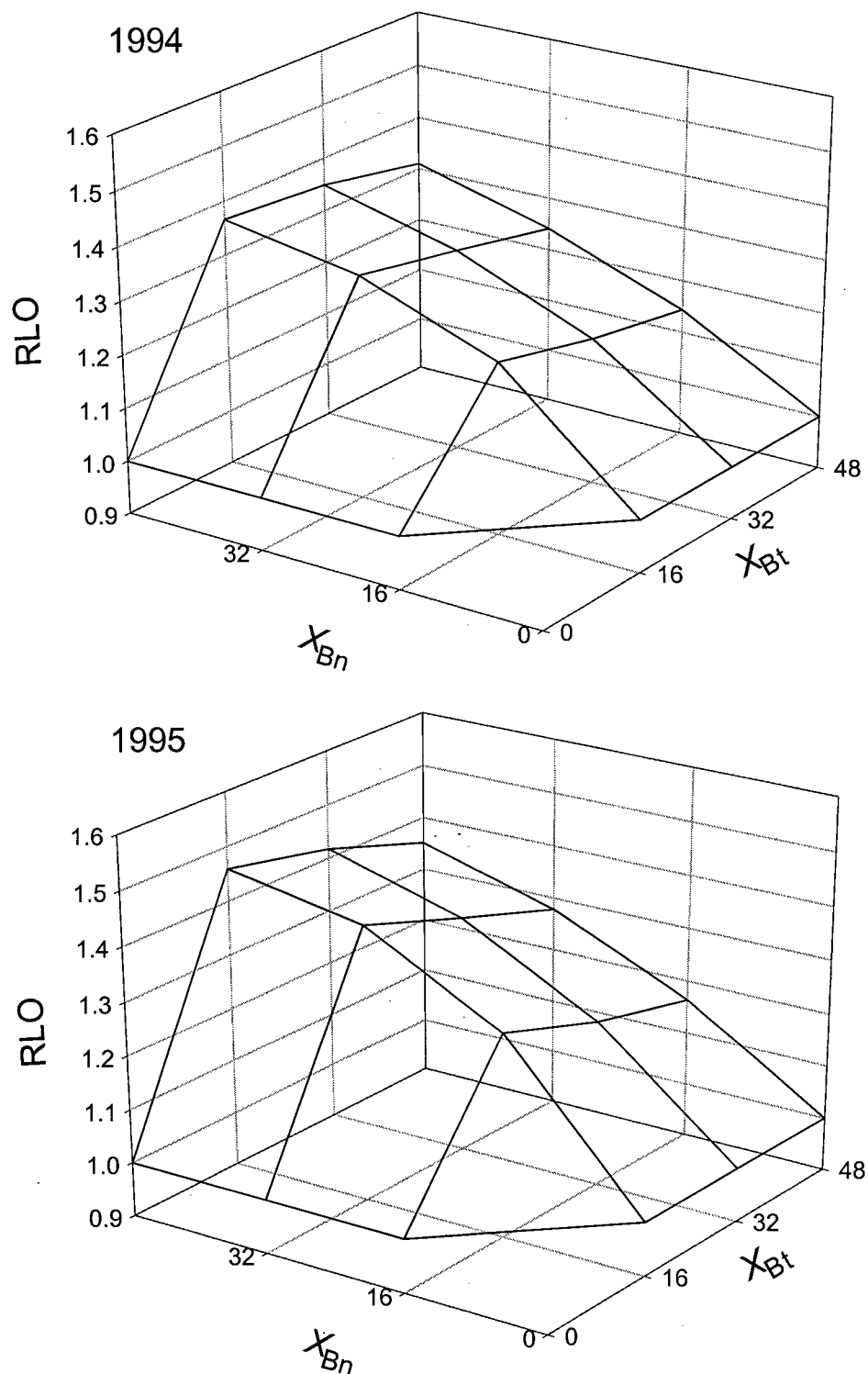
Figure 6.9. Relative Land Outputs for K accumulation per unit land area in 1994 (top panel) and 1995 (bottom panel) estimated from yield-density relationships at each of the population density combinations represented in these studies, in the fertilized plots.
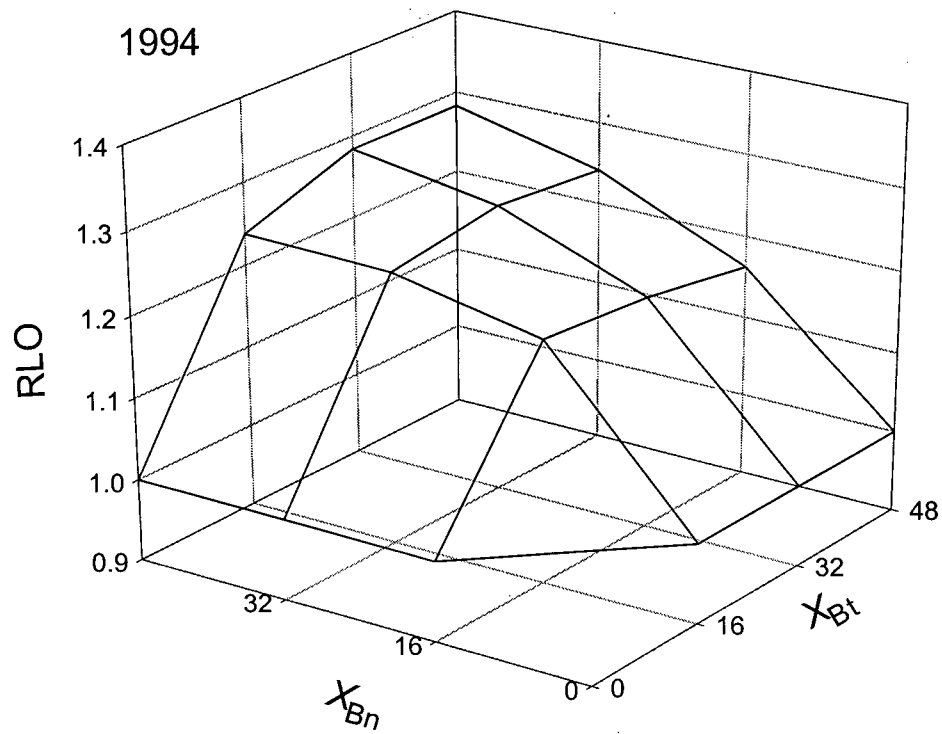
Figure 6.10. Relative Land Outputs for Ca accumulation per unit land area in 1994 estimated from yield-density relationships at each of the population density combinations represented in these studies, in the fertilized plots.
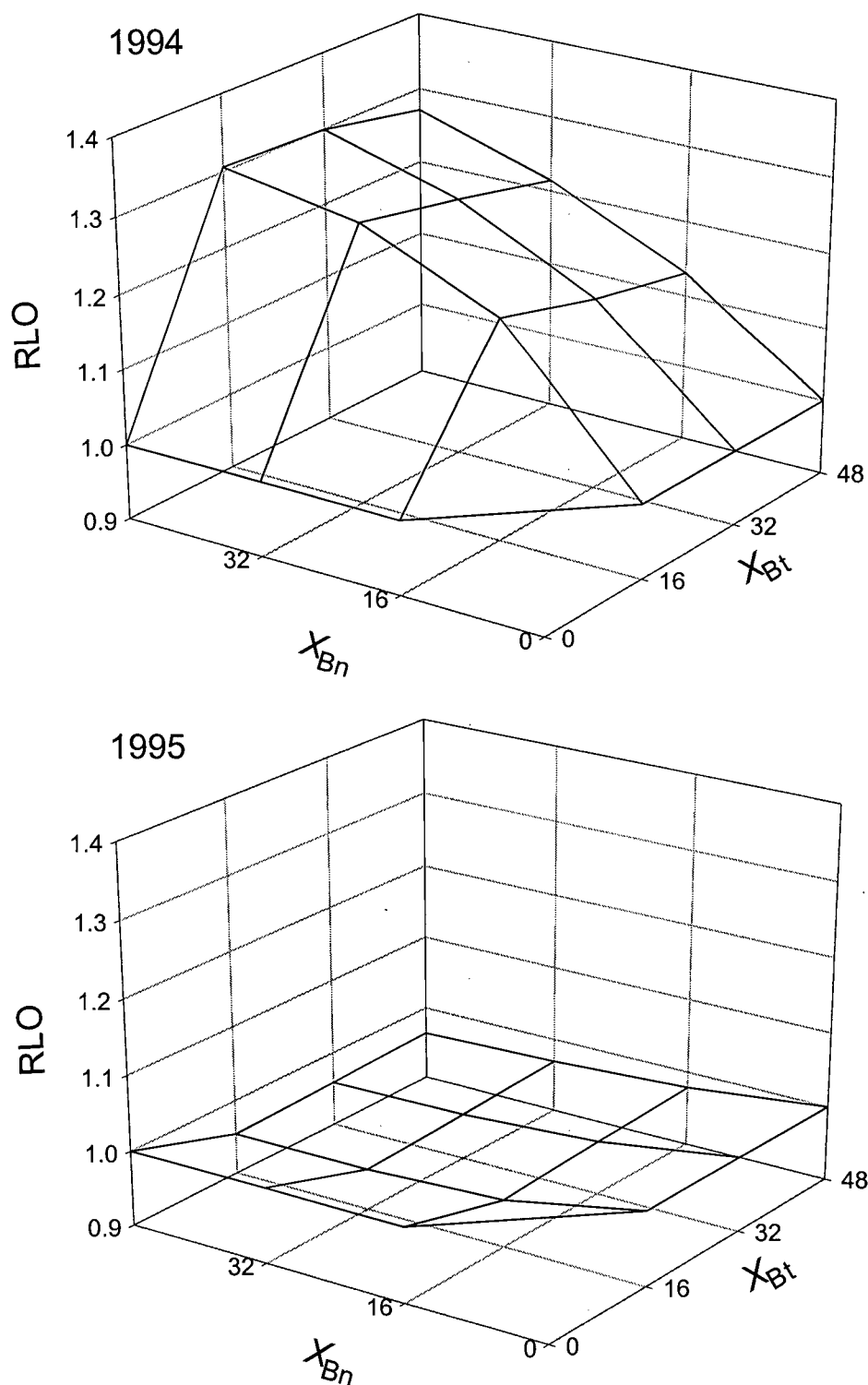
Figure 6.11. Relative Land Outputs for Mg accumulation per unit land area in 1994 (top panel) and 1995 (bottom panel) estimated from yield-density relationships at each of the population density combinations represented in these studies, in the fertilized plots.
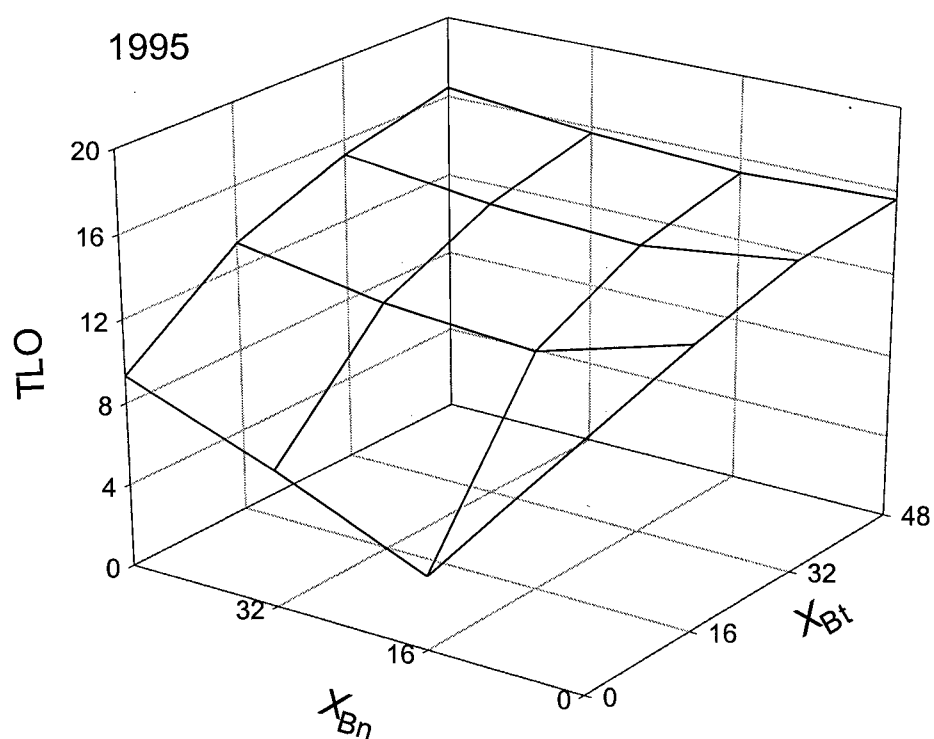
Figure 6.12. Total Land Outputs for N accumulation per unit land area in 1995 estimated from yield-density relationships at each of the population density combinations represented in these studies, in the fertilized plots.
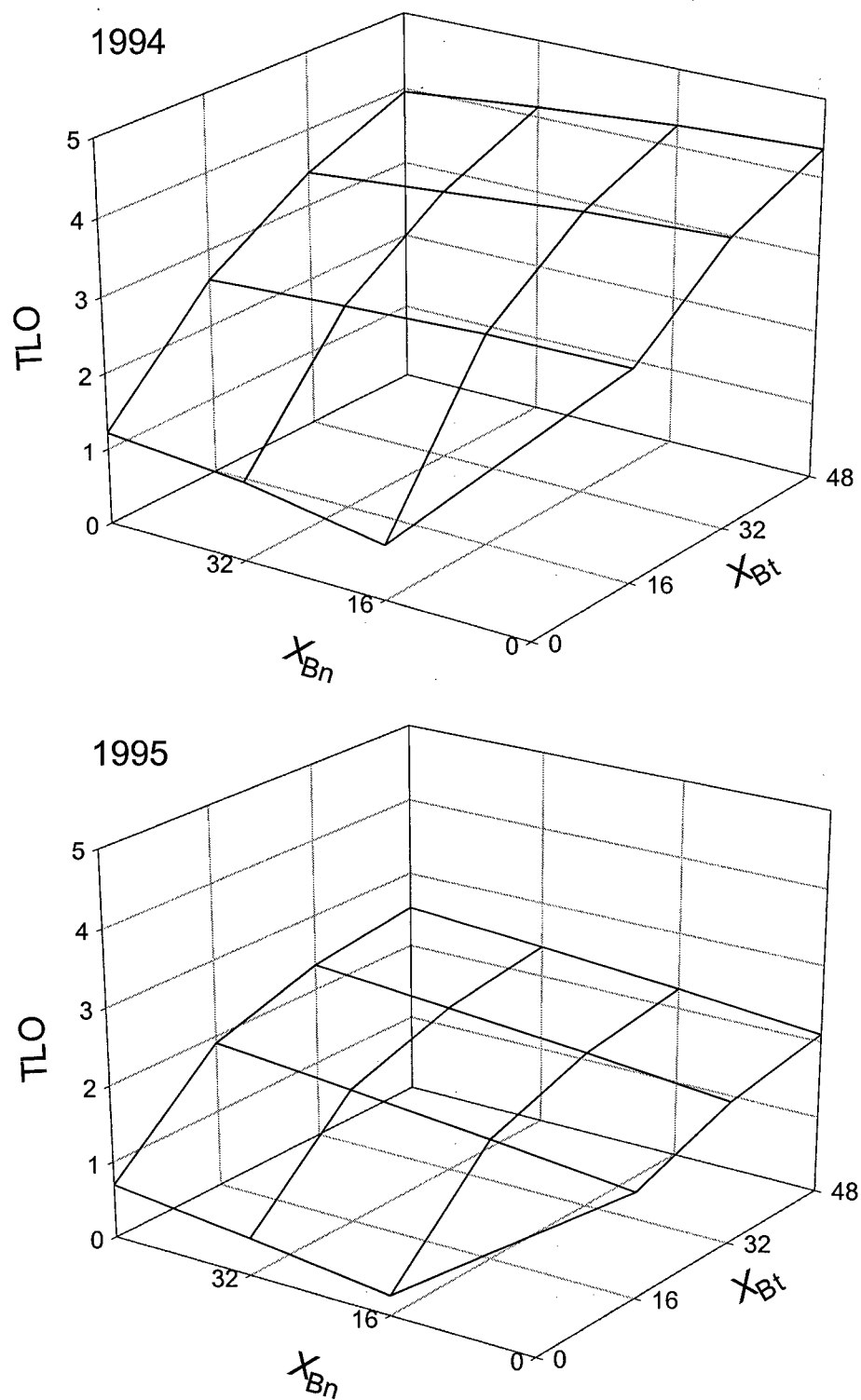
Figure 6.13. Total Land Outputs for P accumulation per unit land area in 1994 (top panel) and 1995 (bottom panel) estimated from yield-density relationships at each of the population density combinations represented in these studies, in the fertilized plots.
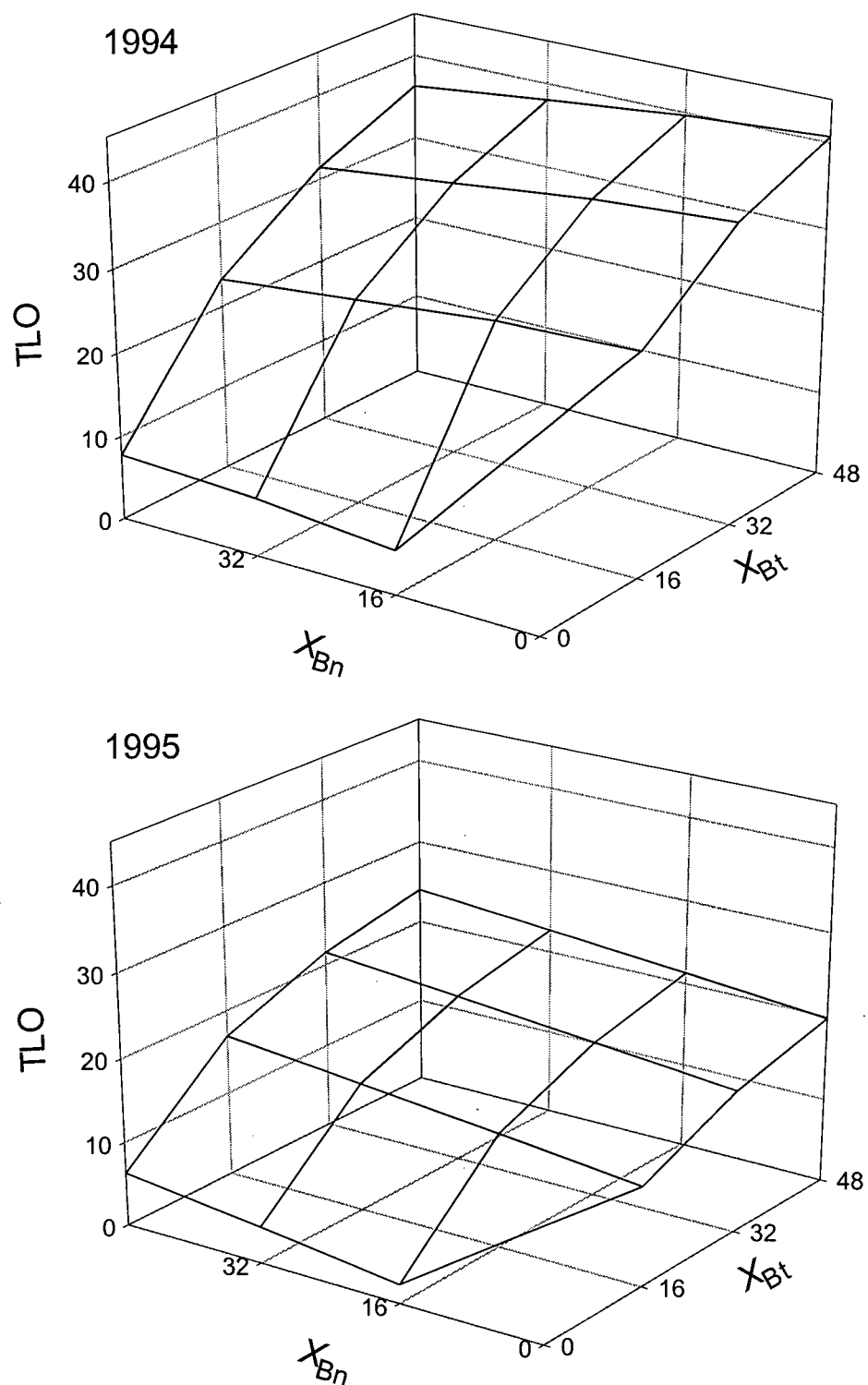
Figure 6.14. Total Land Outputs for K accumulation per unit land area in 1994 (top panel) and 1995 (bottom panel) estimated from yield-density relationships at each of the population density combinations represented in these studies, in the fertilized plots.
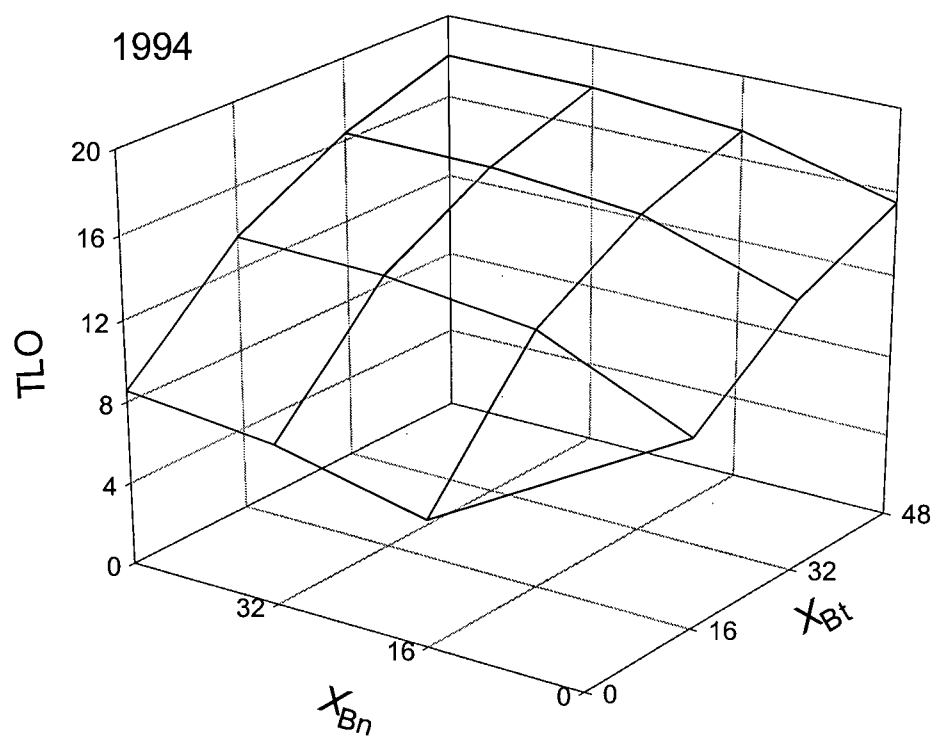
Figure 6.15. Total Land Outputs for Ca accumulation per unit land area in 1994 estimated from yield-density relationships at each of the population density combinations represented in these studies, in the fertilized plots.
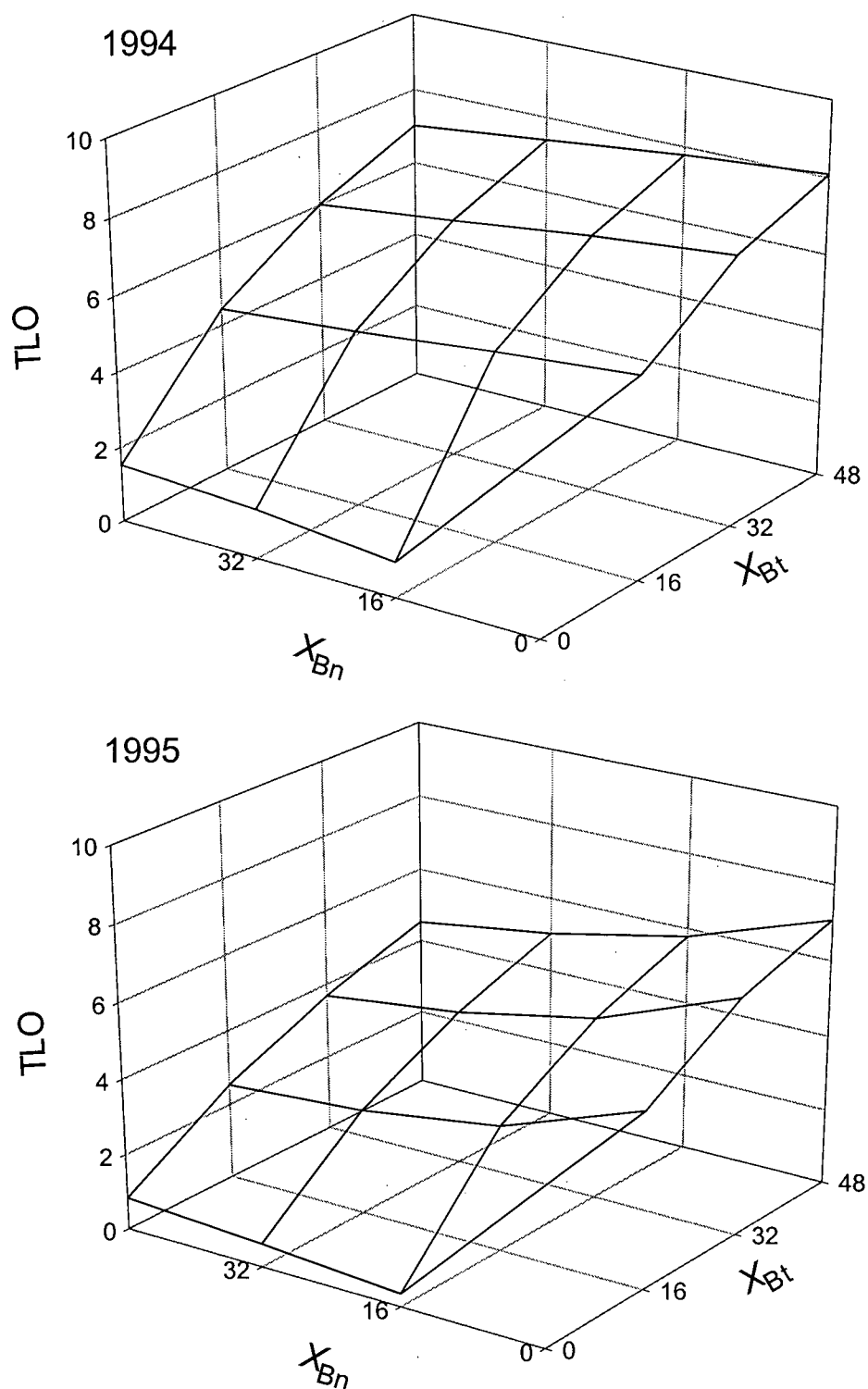
Figure 6.16. Total Land Outputs for Mg accumulation per unit land area in 1994 (top panel) and 1995 (bottom panel) estimated from yield-density relationships at each of the population density combinations represented in these studies, in the fertilized plots.

6.3.4 Effects of soil fertility on indices of intercrop performance

Comparisons of indices of intercrop productivity, between higher and lower soil fertility levels, were limited because yield-density relationships under low soil fertility were seldom significant. Significant regressions occurred for fresh mass of marketable pods and storage roots (FWMP and FWMSR) in 1994 and 1995, and WP and WSR in 1995 (Chapter 3). Fresh mass can be poorly related to other measures of productivity, because of fluctuations that can occur in plant water content. For that reason, the 1995 results for WP and WSR were used to compare intercrop performance at the two soil fertility levels.

As described earlier (Fig. 6.5) RLO for agronomic yield behaved like the majority of other measures, suggesting the occurrence of yield advantage in mixtures (Fig. 6.17). At low fertility, however, no yield advantage occurred (Fig. 6.17). Higher fertility resulted in greater TLO, with the highest total productivity being obtained at high beet densities at both fertility levels (Fig. 6.17).
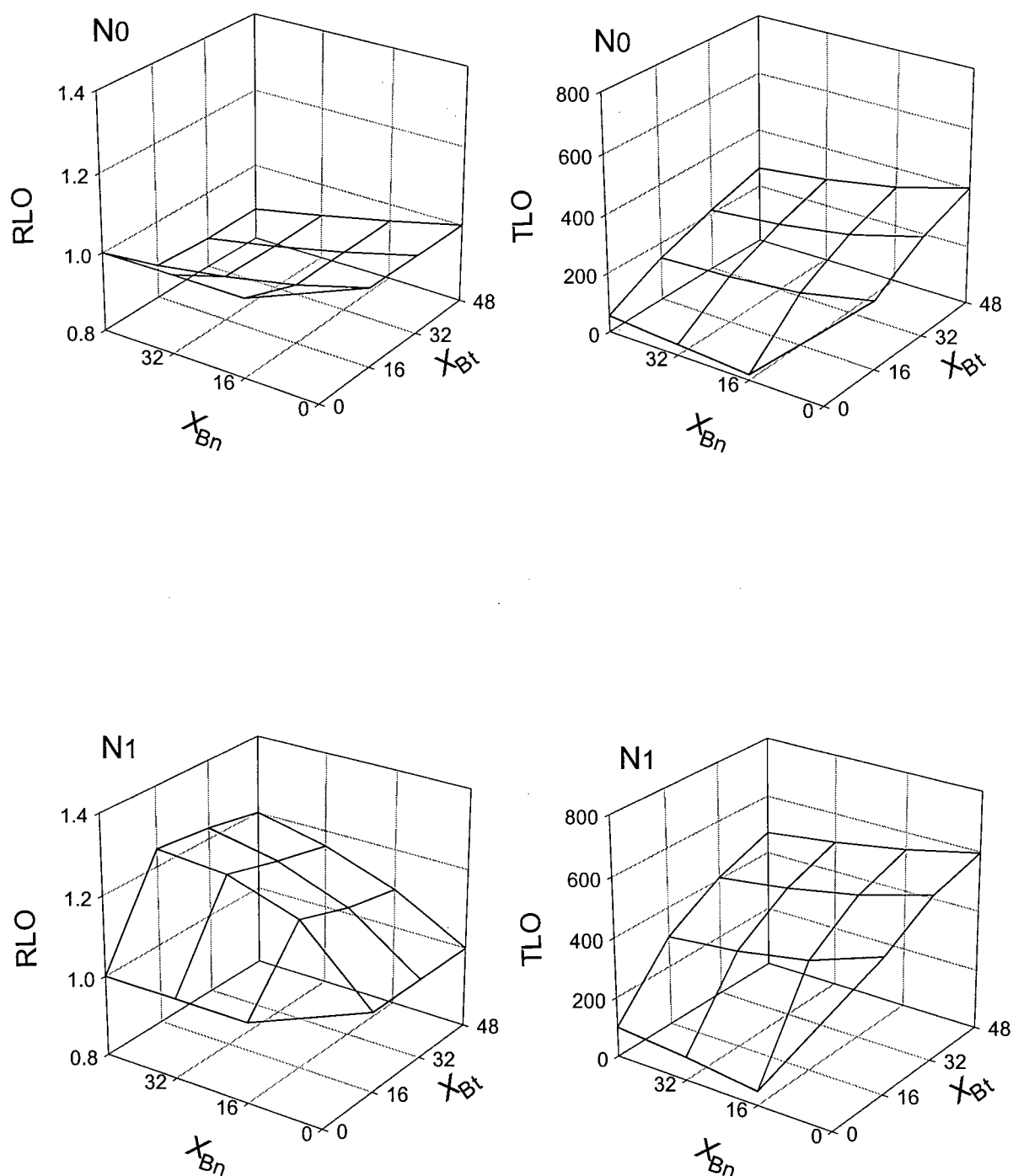
Figure 6.17. Relative Land Outputs (left panels) and Total Land Outputs (right panels) for dry mass of agronomic yield per unit land area in 1995 in the unfertilized (top panels) and fertilized plots (bottom panels) estimated from yield-density relationships at each of the population density combinations represented in these studies.

6.4 Discussion

The issue of whether yield advantages or disadvantages occur in mixtures is complicated, since it is open to a number of experimental approaches and methods of evaluation. Furthermore, complications may arise from aspects of experimental design, the conditions under which the experiments are conducted, and the spatial and temporal arrangements of the associated species. Some authors argue that single-density replacement series are inadequate (Jolliffe *et al.* 1984, Connolly 1986, Snaydon 1991) since it has been used to make inappropriate yield comparisons and is dependent on the arbitrary choice of plant population densities. Rodriguez (1997) felt that replacement series approach is appropriate, since the effects of changing species proportions can be examined at constant total planting density. The issue of plant proportions, however, may be moot since extensive work with yield-density relationships indicates the occurrence of independent effects of the associated species (Jolliffe 1997). For studies involving weed competition with a crop Cousens *et al.* (1991) felt that an additive series, where the recommended density of the crop is kept constant and the density of weed is varied, is an adequate approach. Snaydon (1991) suggested the use of a bivariate factorial design. Shainsky and Randosevich (1991) also used bivariate factorial design in their study in red alder and Douglas-fir plant competition. A bivariate factorial design was used in the research reported in this thesis. This design is amenable to conventional techniques of statistical analysis, such as ANOVA and multiple regression.

The literature contains a number of indices which have been used to evaluate the productive performance of species. The consideration of the combined absolute productivity of the species, here indicated as TLO, dates from early work in this field of interest (de Wit 1961). Relative indices, such as RYT (de Wit and Van den Bergh 1965) and LER (Willey 1979) were introduced later, as measures to compare the relative productivity of mixtures and pure stands. These are the most widely used indices for that purpose, but over the intervening years since their introduction, these indices have been subject to some criticisms. For example, Fisher (1979) argued that land equivalent ratios (LER) were not suitable to use since they involve the addition of ratios. If species proportions are unbalanced, bias should be introduced in the estimation of RYT or LER. Connolly (1987) felt that RYT was inappropriate, since it was density-dependent, which reflected his underlying concern with

the single-density replacement series from which RYT was calculated. Compared with RYT, which has a consistent definition and basis of calculation, LER has a more flexible meaning (Huxley and Maingu 1978, Mead and Willey 1980, Willey 1985, Pilbeam *et al.* 1994). For example, Ahmed and Rao (1982), Cummins (1973), Fisher (1977), Pogue and Arnold (1979) added together the densities used in pure stands in mixtures, making the overall intercrop population greater than the average pure stand densities. By so doing, since pure stand densities are lower than the densities of their mixture counterparts, a yield advantage might be apparent, merely because of the differences in the densities of mixtures as compared to their respective pure stands (Putnam *et al.* 1985). Different measures of monoculture performance have been used in calculating LER, but this creates a problem of inconsistency of meaning among different investigations. A problem with both RYT and LER is that they require different land areas, or amounts of plant material, between the monocultures and mixtures. i. e. the monocultures and mixtures are not operational alternatives since they cannot be done with the same amount of land and plant material (Jolliffe 1997). RLO was introduced to overcome this problem (Jolliffe 1997), and it is a generalization of an index earlier introduced by Wilson (1988). While it can be argued that RLO is a more appropriate index of relative mixture performance than RYT (or LER), the distinction may not be very consequential, since RLO and RYT are highly positively correlated.

For the reasons given earlier, this study used the fitted yield-density relationships to calculate RLO and TLO. This allowed the visualization of species population density effects. As argued previously in this chapter, RLO is more appropriate than RYT or LER as a measure of the relative performance of mixtures vs. pure stands because it is derived from the same population sizes inhabiting the same land areas. RLO has only been used in one previous publication (Jolliffe 1997). Here it has demonstrated a density-dependence which, as far as relative (LER or RYT) mixture performance is concerned, has only occasionally been addressed in previous research (Connolly 1987, Bulson *et al.* 1997). In agreement with Bulson *et al.* (1997), relative mixture performance was usually found to increase with increasing population densities.

Taking into account the diversity of plant measures and both years (1994 and 1995 summer climatic data for the Totem Park Field Station can be accessed at the Department of

Soil Science, Faculty of Agriculture, of the University of British Columbia, Vancouver, Canada.). of the study, the preponderance of cases assessed in this research has suggested the occurrence of yield advantages when bean and beet were grown in mixed association. The advantages were not always large, although in a number of cases RLO exceeded 1.25. I conclude that, compared to corresponding pure stands the bean/beet associations did achieve higher productivity, especially at high densities. Other research, sometimes using different indices of performance, has also detected yield improvements in mixed associations. Using land equivalent ratios (LER) and total biomass Mchaina (1991) found relative yield advantages in bean/beet intercrops. Muli (1995), also using LER, found no yield advantages in bean/beet intercrops grown at different light intensities. Cases where other binary mixtures had yield advantages over their respective monocultures have been reported (Trenbath 1974, Trenbath 1976, Schultz, et al. 1982, Wilson and Newman 1987, Pilbeam et al. 1994, Jolliffe 1997). Other researchers have reported yield disadvantages, e. g. Willey and Osiru (1972), Finlay (1975), Fisher (1979), Pilbeam et al. (1994), while in some cases, yield advantages were recorded only at very high densities (Bulson et al. 1997).

Seasonal variations in RLO (and RYT) were detected in these studies, reflecting the seasonal differences in the underlying yield-density relationships noted earlier (Chapters 3 and 4). For example, in 1994, RLO and RYT based on total biomass were generally higher than those based on agronomic yield, but in 1995 this was reversed (Figs 6.3 to 6.6). This may be due to the plastic adjustment of plant proportions, especially in beets, in response to the impacts of competition. As reported earlier (Chapters 3 to 5), in 1994, beets responded strongly to competition from beans, thereby reducing its agronomic yield, but in 1995, beet was more dominant than the bean, and tended to respond less. Earlier studies have noted that agronomic yield (or reproductive yield) is often sensitive to competition among plant species (Harper 1961, 1977).

With few exceptions (notably Mg in 1995), the results of the nutritional analyses indicated that nutrient capture was enhanced by intercropping since the values of RLO (RYT) commonly exceeded 1.00 (Figs. 6.7 to 6.11). These results agree with the findings of Natarajan and Willey (1981) and Reddy and Willey (1981), who used LER to show that enhanced nutrient uptake occurred in sorghum/pigeon pea and pearl millet/groundnut

mixtures, respectively. In the case of Mg, its behaviour in 1995 may have been inconsistent with the patterns shown by other elements because of differences in relative rates of uptake, or partitioning into the harvested parts. Because of statistically insignificant yield-density regressions, only a limited amount of information was available to address the question of whether similar patterns of mixture performance occur at different levels of soil fertility. In the one case where this was assessed, RLO for dry agronomic yield behaved differently at the two fertility levels.

As is well known for monoculture productivity, TLO values varied between the seasons (1994 and 1995), increased with species population density, and were higher in fertilized treatments than in unfertilized treatments. Beet, which was quantitatively higher than bean in terms of its yield per unit land area at equivalent density, tended to dominate the behaviour of TLO. Indeed, beet monocultures at 48 plants m^{-2} were at least as productive as any of the mixtures (Fig. 6.6), and if TLO is the criterion used, then to obtain highest productivity they are the best system found in this study. Other aspects of production, however, are also important, and nutritional or ecological considerations could lead to different conclusions. It is important to note that RLO or RYT were ineffective in indicating TLO, since they were uncorrelated with TLO and showed different patterns of behaviour with respect to seasons (1994 and 1995), population density and fertility level. Much of the literature has used RYT or LER to search for the most productive associations (i. e. highest TLO). It is an original result of the present research that such an approach may be futile. For example, high RLO can be obtained under circumstances where TLO is low. It is also suggested from these findings that there is a danger of reporting relative yield advantages without showing the level of productivity at which the relative yield advantages were obtained.

The results in Chapters 3 and 4 indicated the regular occurrence of competition within- and between the associated species, at high fertility. Here, in terms of productivity per unit land area, this does not imply that bean/beet intercrops were antagonistic under high soil fertility levels. Relative yield advantages were also regularly found. The quantitative connections between competitive relationships and productivity have not yet been formally

worked out, and are complex (eqn. 2.14 to 2.16). These connections are being followed up in additional work, which is outside the scope of this thesis.

In conclusion, the common occurrence of relative yield advantage in the mixed associations suggests productive complementarity of the mixed species despite the presence of competition between the species. In reaching this conclusion, inverse yield-density models were helpful because they were found to describe crop yields per unit land area. Relative Land Output seems to provide similar assessments of mixture productivity as those given by Relative Yield Total. Relative indices of intercrop performance (RYT and RLO) were not good indicators of absolute levels of biomass productivity, agronomic output or nutrient capture.

7. General Discussion

7.1 Main themes

The research described in this thesis characterized competition, growth and productivity when common beans (*Phaseolus vulgaris* L.) and table beets (*Beta vulgaris* L.) were intercropped at two soil fertility levels. The study touches on a broad range of issues, which can largely be considered in relation to the following main themes:

(1) quantifying within- and between-species components of interference in associations of bean and beet, in order to determine if interference is consistent for a number of different measures of plant growth, at different soil fertility levels, and for different seasons (1994 and 1995) (Chapter 3),

(2) quantifying within- and between-species components of interference in associations of bean and beet, focusing on foliar nutrient accumulation and shoot canopy light interception, in order to determine if competition for nutrients and/or light is consistent for different soil fertility levels and for different seasons (1994 and 1995) (Chapter 4),

(3) detailing further the impacts of interference, soil fertility and seasons (1994 and 1995) on plant growth, using methods of plant growth analysis, allometric analysis and yield component analysis (Chapter 5), and

(4) evaluating the productivity and nutrient uptake of intercropped beans and beets to test whether the mixed associations are more productive than their corresponding pure stands, and whether these assessments of productivity are influenced by soil fertility and seasons (1994 and 1995) (Chapter 6),

As discussed in the following sections, these themes are pertinent to mixed crop ecology, growth and productivity.

7.2 Crop ecology

Competition among associated plants is considered to be an important influence in shaping the structure and controlling the dynamics of plant communities (Tilman 1990a). It is challenging, however, to investigate competition in natural associations, which usually involve considerable complexity in species composition and are spatially non-uniform. The present studies have explored competition in agronomic situations where a number of experimental factors were controlled and/or manipulated. These included genotypes, population densities, time of plant establishment, spatial arrangement of the plants, and soil fertility. Such studies can be helpful in investigating some of the simpler aspects of plant competition, and they may lead to more rapid advances in understanding those aspects than can be achieved in natural ecosystems. Such studies, however, may not be particularly useful in addressing some complex aspects of mixed species ecology, such as successional patterns. In the present work, competitive balances within- and between-species were found to be highly variable, with competition changing with seasons (1994 and 1995), soil fertility level, and response variables observed.

These findings were reached by use of inverse yield-density regression models to quantify competition. At low population densities plants grow as if they are in isolation, hence they experience minimal or no interference from each other (Spitters 1983). As plant population density increases, interference among neighbouring plants intensifies (Firbank and Watkinson 1985). Inverse yield-density models describe the decline in yield per plant as population densities increase (Jolliffe 1997). Their parameters are useful indices of biological and agricultural aspects of plant interference (Jolliffe 1988). The Y-intercept, $1/a_{i0}$ or $1/a_{j0}$ of the inverse yield-density models measures the performance of species i or j in the absence of neighbors. This parameter is however, not necessarily well estimated from experimental data, probably due to the asymptotic nature at the Y-axis of the yield per plant vs. density curve, from which the inverse models are derived (Spitters 1983). Model parameters a_{ii} and a_{jj} quantify the intensity of within-species interference, while parameters a_{ij} and a_{ji} give a measure of the intensity of between-species interference in mixture associations, when the reciprocal of yield per plant of species i or j is the dependent variable. Competitive balances are directly indicated through the ratios of the parameters, a_{ij}/a_{ii} or a_{ji}/a_{jj}, referred to as

substitution rates (Spitters 1983). This thesis also introduced the index Relative Competitive Response (RCR), which can be calculated from the model parameters, and which allows competitive responses to be compared between response variables that have different scales of measurement. The RCR result showed that the various nutrient elements were competed for with approximately the same strengths.

For all the variables measured for the two species, values of $1/a_{10}$ or $1/a_{20}$ particularly from fertilized treatments, indicated that beets might potentially perform better than beans in the absence of competitors. Values of a_{12}/a_{11} and a_{21}/a_{22} usually indicated that beans were better competitors than beets in 1994, while in 1995, beets were stronger competitors. The 1994 findings agree with Mchaina's (1991) that beans were stronger competitors than beets, This can be attributed to the poor establishment of beets in the 1994 experiment. The 1995 findings agree with Muli's (1995) observations, suggesting that given a better chance for early emergence, beets have the potential of being a stronger competitor than beans when the two are intercropped. The variation in the strength of competition of the two species over the two years also shows that between-species plant competition can be modified, by among other things, establishment, seasonal variations and variation in soil factors. Connolly *et al.* (1990), observed similar trends in their studies on *Poa* and *Stellaria* species, while Suehiro and Ogawa (1980) observed altered competitive balances under different soil salinity levels.

In this research, inverse yield-density models were used for the first time to quantify within- and between-species competitive balances for specific nutrient elements, namely nitrogen, phosphorous, potassium, calcium and magnesium. Since competition is for environmental resources, the finding that these models can be used to quantify competition for an individual element is important. It has the potential to help us elucidate how competition governs the performance of plant species.

The types of interference detailed in the present studies were deemed to be competitive interference, although other forms of interference cannot be ruled out. Under low soil fertility, yield-density regressions were often not significant, but regressions were commonly significant with reasonably high R^2 values and significant slopes, where fertilizer was applied. This finding implies that competition for resources was more important and

intense (Welden and Slauson 1986) under higher soil fertility than under low soil fertility, agreeing with Grime's (1977) perspective.

During the course of crop growth, there may have been some competition for light (PAR) between the associated species since the shoot canopy was closed after about the first half of July. The substitution rates for light interception, however, did not match those found for dry matter formation or nutrient accumulation. This suggests that competition for soil resources may have been predominant. This agrees with the distinct response of plant growth to soil fertilization. As discussed in Chapter 4, the lack of significance for the yield-density models at low soil fertility does not mean that there was no competition for resources under that condition. Low fertility may have depressed plant responsiveness to population density treatments, and the statistical method employed for analysis may not have been sufficiently sensitive to detect the competition which was occurring. Experiments have been performed by others that have provided evidence of plant competition under low soil fertility (Fowler 1981, Fowler and Antonovics 1981, Tilman and Wedin 1993, Theodose, *et al.* 1996).

7.3 Crop physiological aspects

At the establishment stage during the seasons (1994 and 1995) of 1994, beet seedlings germinated very slowly, which culminated in low germination rate for beets (about 70%). This seemed to be due to excessive sowing depth in relation to seed size, surface sealing due to high silt content observed at the 1994 experimental site, and soil compaction. Beets had over 90% germination rate in 1995 season, since there was minimal soil compaction and surface sealing at the 1995 site. Beets were also sown at very shallow depth, (from the experience of 1994 experiment). Beans on the other hand, were not as affected by the soil factors in both 1994 and 1995, although there were cases of broken hypocotyls due to the surface sealing in the 1994 site. Both plant species showed good health and growth vigor, under fertilized treatments, but stunted growth under unfertilized treatments. In the treatments that received fertilizer, plants from densely populated subplots appeared slender and taller than plants from less densely populated subplots.

Analysis of variance (ANOVA) results indicated a decrease in mean yield per plant of the various primary measures, for each species, with increasing population density of the two

species, for most of the variables tested in both years. Mchaina (1991) and Muli found similar trends in bean/beet mixtures. The finding that yield per plant decreased with increase in species population density agrees with the evidence from plant interference studies (Holliday 1960, Willey and Heath 1969, Potdar 1986, Gaye 1990, Gaye and Jolliffe 1995, Jolliffe 1988).

Several methods of analysis were used to detail plant responses to the various sources of variation, when beans and beets were intercropped. Some similarities and differences were found in the behaviour of the two species. Analysis of variance results indicated that for both species, specific leaf area increased with increasing population density. Leaf area index increased with the increase in the density of the target species, but decreased with increase in the population density of the companion species. In bean, harvest index decreased with increase in beet population density, and dry mass per pod (WP/PN) decreased with increase in population densities of the two species. In beet increasing beet population density decreased leaf area ratio, leaf weight ratio and harvest index, while bean population density decreased leaf weight ratio and leaf area ratio.

Allometry in plants can be described as quantitative relationships existing among different measures of plant parts as growth proceeds (Jolliffe et al. 1988). The procedure of Jolliffe et al. (1988) was employed to assess the effects of fertilizer application and bean and beet species population density on yield. When experimental treatments were taken into account, strong allometric relations between total harvested biomass W, and other primary measures were observed in both species. These allometric relationships in both species were significantly (P<0.05) influenced by species population density treatments, and sometimes by fertilizer treatment. This observation agrees with finding of other researchers in higher plants. (Weiner and Thomas 1992, Weiner and Fishman 1994 McLachlan et al. 1995). Population density and fertilizer treatment also affected W non-allometrically.

Yield component analysis by two dimensional partitioning (Eaton et al. 1986) indicated that leaf area index was the major contributor to the total variation in both beans and beets yield per unit land area. Leaf area index was also the yield component for which most treatment effects were significant (Tables 5.3 and 5.6). Leaf area index is an important property in connection with canopy light interception, since interception tends to be

proportional to LAI, but the yield component analysis results do not necessarily suggest that competition for light was controlling crop performance. Leaf area index is the product of target species leaf area per plant and its population density, so it is to be expected that LAI and X_{target} should be correlated. Also, leaf area per plant was found to respond to companion species population densities (Chapter 3), so effects of the companion species on LAI do not necessarily indicate the occurrence of competition for light. The yield component analysis also detected other major sources of variation in yield: specific leaf weight and dry weight per pod for beans, and leaf weight ratio and harvest index in beets. The present results extend the findings of previous investigations (Jolliffe *et al.* 1990, Jolliffe and Gaye 1995, Mchaina 1991) which found significant density effects on yield components, using the two-dimensional partitioning technique.

7.4 Intercrop productivity

The productive performance of the intercropped associations of bean and beet was assessed using the inverse yield-density relationships that had also been used for the analysis of competition. This was made possible by the fact that those relationships were also found to describe yield per unit land area.

A common theme in the scientific study of intercropping has been the expectation that mixed species associations may be more productive than their pure stand counterparts. This result might occur, for example, if one species facilitates the growth of the other, or if there are compatible competitive balances between the species. Quantitatively, this expectation is evaluated through the use of relative indices, such as Relative Land Output (RLO) or Relative Yield Total (RYT). As noted in Chapter 2, there may be other advantages of crop mixtures beyond that of increased relative productivity, including: diversity of diet and income source, stability of production, reduced pest and disease incidences, efficient use of family labor, and intensive production with limited land resource (FAO 1991, Francis *et al.* 1976).

Using both RLO and RYT, the intercrops of beans and beets tended to exhibit higher productivity than their corresponding monocultures. This occurred for most measures of productivity, including total dry biomass, agronomic yields, and mineral nutrient capture, although the mixture yield advantages were not always large. An interesting result was that

increases in relative productivity tended to occur with increasing population densities, a relationship which has not been well-defined in the earlier literature. The occurrence of relative yield advantages in intercrops has often been reported in the literature (Willey and Osiru 1972, Trenbath 1974, Willey 1979, Natarajan and Willey 1980, Ofori and Stern 1987, Snaydon and Satorre 1989, Yunusa 1989, Pilbeam, *et al.* 1994, Tilman, *et al.* 1996, Bulson, *et al.* 1997, Jolliffe 1997), but it is not an inevitable result (Jolliffe 1997).

Using land equivalent ratios (LER) and total biomass Mchaina (1991) found relative yield advantages in bean/beet intercrops. Muli (1995) also using LER, found no yield advantages in bean/beet intercrops. Such variations among investigations using the same species mixtures may reflect the variations in competitive relationships that can occur, as illustrated by the results in Chapters 3 and 4. Here, it is shown that relative yield advantages can occur in intercrops in which both species are competing with each other. Also, the RYT and RLO results for nutrient capture, indicated that there was more uptake when beans and beets were intercropped than when they were grown in their respective pure stands. This agrees with the findings of Natarajan and Willey (1980), and Reddy and Willey (1981) in legume/non-legume intercrops.

The relative performance of mixtures compared with pure stands is of ecological interest, but is not necessarily of agronomic importance. A farmer is more interested in the overall output (TLO) of the land than in RYT or RLO. For example, both the agronomic and total biomass results indicated that bean/beet intercrops showed yield advantages (RLO or RYT >1.0) even where TLO productivity was low. i. e. there is a possibility of reporting mixture yield advantages at low levels of agricultural productivity. This is a serious problem since much of the literature (Trenbath 1974, 1976, Schultz, *et al.* 1982, Wilson and Newman 1987, Mchaina 1991, Bulson *et al.* 1997) has reported intercrop yields using relative indices of mixture performance, without indicating at what level of production the yield advantages were achieved. This might lead the farmers to practice the intercropping based on the researchers' finding, only to achieve low absolute production. The present work did not find any correlation of the relative indices with TLO. In terms of TLO, the highest levels of productivity observed in these studies were obtained at the higher soil fertility level with dense beet populations.

8. Conclusions

Based on the objectives described in Chapter 1, the following conclusions were reached:

(1) A distinctive feature of this research was that it evaluated competition through a broad range of plant assessments. From these evaluations, it is concluded that the occurence of interference was commonly expressed by many different measures of plant growth. However, the particular balances of within-species and between species competition varied among different measures of plant growth. Although it has been predicted that competition might be severe at low fertility, this study found that at low fertility levels competition was poorly detected due to the suppression of plant growth. In addition, there were differences in competitive balances between growing seasons. Bean was the stronger competitor (based on dry weights of the various primary measures) in 1994, and beet was the stronger competitor than the bean in 1995 (Chapter 3). These findings extend the limited body of previous knowledge by highlighting the flexibility of competition as the same species grow in association under different environmental conditions.

(2) This research evaluated within- and between-species competitive balances for individual nutrient elements, which has not been done previously. Coefficients used to measure competition varied for the nutrient elements tested, for the different soil fertility levels, and for the two different seasons (1994 and 1995). Bean was the stronger competitor for all the mineral nutrients in 1994, while beet was the stronger competitor in 1995. A scale-independent index, Relative Competitive Response, showed that the nutrient elements were competed for with approximately the same strength. The ability of the two species to compete for photosynthetically active radiation was also directly assessed. Beets were found to intercept more PAR than beans, but interception did not appear to be the determinant of competitive performance in these associations.

(3) On the basis of growth analysis of the growth indices, allometric analysis and yield component analysis using TDP, the following conclusions were reached concerning plant growth responses to competition:

(a) Leaf area index was an important determinant of yield variation for both species and was found to significantly increase with the increase in the population density of the test

species, but decreased with the population density of the companion species. In bean, specific leaf weight and pod dry weight per pod number were also found to be the major contributors to variation in pod yields; while in beets, leaf weight ratio and harvest index were other major contributors to overall variation in the storage root yield per land area. Both fertilizer and plant population treatments were found to induce yield variation in both beans and beets.

(b) Species growth responses differed from each other and also differed between different experimental treatments. Bean population density had no significant effect on the bean indices specific leaf area, leaf area ratio, leaf weight ratio and harvest index, but increasing beet population density significantly decreased specific leaf area, leaf weight ratio stem weight ratio and harvest index of beans in 1995. Beet population density significantly decreased the leaf area ratio, leaf weight ratio and harvest index of beets, while bean population density significantly decreased leaf area ratio and leaf weight ratio, but had no effect on specific leaf area and harvest index of beets.

(c) Dry matter partitioning was also affected by experimental treatments. In beans in 1994 the ranking of dry matter allocation was: pods>stem>leaves, while in 1995, the pattern was: stem>pods>leaves. The pattern of dry matter partitioning in beets in both 1994 and 1995, was: storage roots>leaves. In beets, allocation of the dry matter to the storage roots decreased, while allocation to the leaves increased, with increase in the beans population density. Beet population density had no effect on dry matter allocation in beets.

(d) There were allometric and non-allometric influences of experimental treatments on combined dry mass per plant of both beans and beets. Much of the variation in combined dry mass per plant was related to adjustments in allometry, although direct, *i. e.* non-allometric, experimental influences on dry mass per plant were also detected.

(4) The productive performance of the species mixtures was evaluated using a new measure of intercrop performance, relative land output (RLO), as well as by total yield per unit land area. These assessments were applied to a broader range of measures of productivity than has been done in previous research. These studies showed that

(a) there was complementarity in bean/beet mixture associations compared to their corresponding pure stands. This conclusion is on the basis that predicted RYT and RLO

values showed yield advantages (RYT or RLO values greater than 1.00) in the bean/beet intercrops under high fertility regime. These relative indices varied for different measures of yield, with total biomass giving higher values in 1994 than those based on the agronomic yields, whereas in 1995, relative indices based on total biomass was lower than those based on agronomic yields.

(b) for most elements and under most experimental circumstances there was also greater nutrient uptake in bean/beet mixture associations than the uptake in their respective pure stands. This type of assessment has not previously been done.

(c) Relative productivity of mixtures (RLO) showed yield advantages even where total productivity (TLO) values were low. Overall, relative and total measures of intercrop productivity were not correlated. Much previous research has attempted to identify the most productive associations through the use of relative measures of productivity (e. g. RYT and LER, which are highly correlated with RLO). A key finding of the present investigations is that such attempts are not likely to succeed.

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10. Appendices

Appendix 1a. Soil analysis prior to planting in 1994 and 1995.

Year	Nutrients (ppm)						pH	Org. Matter (%)	Texture (%) (Hydrometer)		
	N	P	K	Ca	Mg	S			Sand	Silt	Clay
1994	15 (def)	190 (opt)	75 (def)	817 (opt)	190 (mar)	0.3 (def)	5.9	4.0	68	28	4
1995	37 (mar)	71 (def)	124 (mar)	1090 (opt)	69 (def)	1.0 (def)	5.6	4.0	77	19	4

def:- Deficient
mar:- Marginal
opt:- Optimum

Appendix 1b. Mean values and standard errors for growth observations[1]

Bean - 1994 Data

Fert.	X_{Bn}	X_{Bt}		PN	LA	WL	WS	WP	W	LAI	SLA	LWR	LAR	HI
0	16	0	mean	5.65	279.5	1.61	2.13	5.73	9.47	0.45	174.7	0.177	30.9	0.589
			±s. e.	0.52	25.8	0.15	0.21	0.70	1.02	0.04	2.6	0.008	1.4	0.018
0	32	0	mean	4.20	217.3	1.20	1.65	3.69	6.54	0.70	180.7	0.182	32.9	0.560
			±s. e.	0.34	17.0	0.09	0.08	0.25	0.37	0.05	3.1	0.007	1.4	0.013
0	48	0	mean	3.60	202.8	1.08	1.52	2.90	5.50	0.97	181.5	0.199	36.3	0.521
			±s. e.	0.27	25.0	0.11	0.17	0.34	0.58	0.12	6.5	0.008	2.3	0.019
0	16	16	mean	5.70	266.7	1.53	2.11	5.37	9.01	0.43	179.2	0.167	29.7	0.582
			±s. e.	0.67	22.2	0.15	0.12	0.48	0.66	0.04	4.0	0.010	1.6	0.022
0	32	16	mean	3.75	47.1	0.91	1.23	2.71	4.85	0.15	96.6	0.180	15.4	0.512
			±s. e.	0.50	5.5	0.15	0.12	0.48	0.72	0.02	17.8	0.012	2.8	0.022
0	48	16	mean	4.30	72.4	1.09	1.40	3.44	5.93	0.35	107.9	0.190	20.4	0.538
			±s. e.	0.45	10.0	0.14	0.11	0.53	0.75	0.05	19.8	0.013	4.4	0.025
0	16	32	mean	4.05	211.0	1.21	1.53	4.10	6.84	0.34	175.2	0.179	31.2	0.587
			±s. e.	0.42	17.0	0.10	0.10	0.37	0.52	0.03	3.9	0.007	1.3	0.017
0	32	32	mean	5.50	208.6	1.54	2.22	5.21	8.97	0.67	147.6	0.164	23.7	0.569
			±s. e.	0.52	27.4	0.19	0.16	0.56	0.86	0.09	10.6	0.007	1.7	0.013
0	48	32	mean	4.60	317.3	1.37	1.72	4.47	7.56	1.52	212.7	0.184	39.0	0.570
			±s. e.	0.59	59.3	0.18	0.20	0.69	1.02	0.28	12.5	0.006	2.5	0.016

0	16	48	mean	3.80	190.8	1.29	1.71	3.96	6.95	0.31	188.9	0.155	28.0	0.588
			±s. e.	0.51	29.3	0.42	0.41	0.55	1.30	0.05	7.6	0.010	1.1	0.020
0	32	48	mean	4.05	262.9	1.29	1.64	4.07	6.99	0.84	200.1	0.190	38.0	0.555
			±s. e.	0.37	33.2	0.13	0.12	0.52	0.76	0.11	10.1	0.007	2.3	0.018
0	48	48	mean	4.40	247.1	1.25	1.68	3.91	6.84	1.19	194.4	0.167	32.2	0.555
			±s. e.	0.78	58.2	0.29	0.32	0.72	1.27	0.28	7.1	0.009	1.8	0.020
1	16	0	mean	16.55	1230.9	5.90	6.15	17.46	29.51	1.97	215.9	0.197	40.3	0.599
			±s. e.	1.71	167.7	0.81	0.89	1.89	3.32	0.27	22.4	0.010	3.0	0.018
1	32	0	mean	9.35	607.0	3.07	4.98	11.76	19.81	1.94	199.1	0.156	30.7	0.597
			±s. e.	0.55	39.6	0.19	0.40	0.61	1.07	0.13	6.3	0.006	1.2	0.011
1	48	0	mean	4.75	275.8	2.15	2.94	6.72	11.81	1.32	123.7	0.180	21.9	0.575
			±s. e.	0.28	47.3	0.17	0.25	0.36	0.73	0.23	16.5	0.006	2.9	0.011
1	16	16	mean	10.00	528.0	2.70	3.54	7.13	13.37	0.84	195.4	0.201	39.2	0.529
			±s. e.	1.03	57.1	0.29	0.36	0.80	1.35	0.09	3.7	0.007	1.5	0.018
1	32	16	mean	7.55	611.7	2.84	4.20	7.43	14.48	1.96	216.1	0.200	42.8	0.512
			±s. e.	0.71	49.2	0.24	0.38	0.62	1.16	0.16	4.5	0.009	1.7	0.014
1	48	16	mean	5.65	444.5	2.07	3.60	5.87	11.54	2.13	212.1	0.181	38.2	0.507
			±s. e.	0.41	38.8	0.16	0.29	0.49	0.86	0.19	5.3	0.006	1.4	0.014
1	16	32	mean	6.30	422.6	2.21	3.28	5.78	11.27	0.68	192.7	0.201	38.0	0.509
			±s. e.	0.42	27.9	0.14	0.30	0.46	0.82	0.04	5.8	0.009	1.2	0.012
1	32	32	mean	5.35	380.4	1.86	3.18	5.75	10.79	1.22	208.3	0.170	35.1	0.528
			±s. e.	0.37	27.6	0.14	0.19	0.39	0.62	0.09	5.5	0.008	1.6	0.016
1	48	32	mean	5.10	295.4	1.44	2.44	4.48	8.36	1.42	204.7	0.174	35.4	0.530
			±s. e.	0.41	27.8	0.12	0.20	0.41	0.67	0.13	6.6	0.009	1.8	0.017

1	16	48	mean	6.50	566.9	2.89	4.61	7.79	15.30	0.91	192.4	0.190	36.4	0.519
			±s. e.	0.70	74.3	0.34	0.65	0.85	1.79	0.12	4.1	0.005	1.0	0.013
1	32	48	mean	6.05	381.8	2.08	3.57	5.74	11.39	1.22	181.8	0.183	32.8	0.504
			±s. e.	0.42	36.4	0.14	0.31	0.41	0.74	0.12	9.6	0.006	1.5	0.013
1	48	48	mean	4.20	283.3	1.50	2.49	4.72	8.71	1.36	187.3	0.180	34.1	0.535
			±s. e.	0.31	23.2	0.09	0.22	0.39	0.64	0.11	9.0	0.009	2.9	0.017

Bean 1995 Data

Fert.	X_{Bn}	X_{Bt}		PN	LA	WL	WS	WP	W	LAI	SLA	LWR	LAR	HI
0	16	0	mean	7.75	307.7	1.84	3.14	2.66	7.63	0.49	165.2	0.248	40.8	0.314
			±s. e.	0.80	42.5	0.24	0.35	0.44	0.99	0.07	3.4	0.008	1.3	0.018
0	32	0	mean	5.65	204.7	1.27	2.34	1.58	5.18	0.66	157.8	0.250	39.1	0.302
			±s. e.	0.51	23.7	0.13	0.27	0.18	0.54	0.08	4.6	0.010	1.6	0.013
0	48	0	mean	4.65	170.8	1.08	1.64	1.33	4.05	0.82	159.0	0.270	42.6	0.305
			±s. e.	0.39	14.4	0.09	0.09	0.18	0.35	0.07	3.5	0.009	1.2	0.017
0	16	16	mean	2.70	96.1	0.54	1.35	0.53	2.42	0.15	179.0	0.226	40.4	0.226
			±s. e.	0.21	5.2	0.03	0.11	0.03	0.14	0.01	4.8	0.008	1.6	0.011
0	32	16	mean	3.80	144.2	0.73	1.90	0.81	3.44	0.46	202.3	0.205	41.1	0.238
			±s. e.	0.43	19.9	0.11	0.19	0.09	0.37	0.06	6.6	0.007	1.5	0.012
0	48	16	mean	4.60	164.0	0.83	2.38	0.90	4.11	0.79	197.1	0.201	39.9	0.224
			±s. e.	0.42	21.5	0.10	0.25	0.08	0.40	0.10	9.0	0.011	3.0	0.010
0	16	32	mean	3.45	133.6	0.70	1.95	0.76	3.41	0.21	194.2	0.209	40.4	0.230
			±s. e.	0.40	18.8	0.10	0.27	0.09	0.45	0.03	4.9	0.009	1.8	0.009

0	32	32	mean	3.60	150.0	0.69	1.81	0.70	3.19	0.48	222.2	0.213	46.7	0.218
			±s. e.	0.24	13.5	0.06	0.14	0.06	0.23	0.04	9.7	0.012	2.7	0.010
0	48	32	mean	3.75	143.9	0.76	2.03	0.84	3.63	0.69	195.8	0.198	37.6	0.235
			±s. e.	0.32	20.2	0.11	0.19	0.08	0.37	0.10	10.7	0.012	2.1	0.007
0	16	48	mean	4.30	122.4	0.62	2.07	0.75	3.44	0.20	215.8	0.173	35.1	0.220
			±s. e.	0.44	17.0	0.10	0.24	0.10	0.40	0.03	11.3	0.015	2.1	0.013
0	32	48	mean	2.90	110.3	0.54	1.48	0.56	2.58	0.35	214.6	0.212	43.2	0.216
			±s. e.	0.20	7.0	0.04	0.11	0.05	0.15	0.02	14.0	0.013	1.8	0.014
0	48	48	mean	3.05	132.1	0.62	1.77	0.58	2.96	0.63	219.8	0.210	45.6	0.196
			±s. e.	0.23	7.7	0.04	0.11	0.04	0.16	0.04	9.8	0.010	2.5	0.010
1	16	0	mean	8.80	447.4	2.39	4.27	3.07	9.73	0.72	184.1	0.234	43.3	0.304
			±s. e.	0.82	59.8	0.30	0.34	0.38	0.98	0.10	6.8	0.009	2.4	0.013
1	32	0	mean	7.80	389.5	2.19	3.58	3.05	8.81	1.25	174.9	0.256	44.5	0.363
			±s. e.	0.50	40.8	0.20	0.50	0.24	0.90	0.13	3.6	0.009	1.3	0.015
1	48	0	mean	7.50	350.5	2.01	3.61	2.38	8.00	1.68	167.0	0.262	43.1	0.317
			±s. e.	0.54	42.0	0.20	0.52	0.23	0.87	0.20	7.3	0.010	1.7	0.019
1	16	16	mean	7.25	320.3	1.90	3.76	2.29	7.94	0.51	166.7	0.248	41.1	0.316
			±s. e.	0.72	39.3	0.22	0.60	0.21	0.98	0.06	3.5	0.008	1.3	0.018
1	32	16	mean	5.50	278.6	1.54	3.21	1.87	6.62	0.89	178.9	0.228	40.3	0.291
			±s. e.	0.53	38.6	0.20	0.42	0.22	0.82	0.12	5.7	0.008	1.3	0.012
1	48	16	mean	5.40	281.9	1.51	3.31	1.65	6.47	1.35	185.8	0.238	44.0	0.267
			±s. e.	0.38	28.1	0.14	0.43	0.14	0.67	0.13	4.3	0.008	1.4	0.013
1	16	32	mean	6.45	266.0	1.57	3.39	2.28	7.24	0.43	169.4	0.217	36.5	0.311
			±s. e.	0.31	17.9	0.10	0.18	0.18	0.37	0.03	4.1	0.008	1.3	0.013

Fert.	X_{Bn}	X_{Bt}												
1	32	32	mean	5.80	292.7	1.62	3.66	1.80	7.07	0.94	180.0	0.229	41.1	0.255
			±s. e.	0.44	20.8	0.10	0.21	0.11	0.38	0.07	2.7	0.007	1.3	0.009
1	48	32	mean	5.50	347.9	1.88	3.44	1.86	7.18	1.67	186.1	0.264	48.8	0.264
			±s. e.	0.41	26.9	0.15	0.32	0.13	0.55	0.13	4.7	0.009	1.5	0.009
1	16	48	mean	6.40	294.5	1.62	3.15	2.02	6.79	0.47	183.2	0.239	43.6	0.313
			±s. e.	0.67	36.7	0.20	0.42	0.22	0.81	0.06	8.5	0.008	2.4	0.012
1	32	48	mean	6.15	291.1	1.62	3.59	1.93	7.14	0.93	178.6	0.229	40.9	0.273
			±s. e.	0.53	33.1	0.18	0.43	0.21	0.79	0.11	4.1	0.006	1.3	0.011
1	48	48	mean	5.75	269.3	1.50	3.29	1.51	6.30	1.29	178.6	0.235	41.9	0.242
			±s. e.	0.42	25.3	0.13	0.26	0.12	0.48	0.12	4.6	0.007	1.5	0.010

Beet - 1994 Data

Fert.	X_{Bn}	X_{Bt}		LA	WL	WSR	W	LAI	SLA	LWR	LAR	HI
0	0	16	mean	683.7	7.32	16.5	23.81	1.09	94.7	0.325	30.1	0.675
			±s. e.	43.6	0.46	1.69	1.98	0.07	2.8	0.019	1.5	0.019
0	0	32	mean	438.0	4.71	6.93	11.64	1.4	96.9	0.417	39.9	0.583
			±s. e.	29.3	0.34	0.66	0.82	0.09	5.1	0.028	3.0	0.028
0	0	48	mean	284.6	3.06	9.54	12.6	1.37	92.3	0.257	23.1	0.743
			±s. e.	23.6	0.2	0.92	1.03	0.11	3.1	0.015	1.0	0.015
0	16	16	mean	507.8	4.9	12.49	17.39	0.81	104.4	0.285	29.5	0.715
			±s. e.	29.0	0.27	0.78	0.96	0.05	3.0	0.011	1.1	0.011
0	16	32	mean	405.7	4.08	11.84	15.92	1.3	100.3	0.254	25.2	0.746
			±s. e.	30.5	0.3	0.39	0.53	0.1	2.9	0.013	1.3	0.013

0	16	48	mean	457.8	3.91	10.11	14.02	2.2	117.6	0.284	33.0	0.716
			±s. e.	29.4	0.22	0.64	0.75	0.14	3.9	0.014	1.7	0.014
0	32	16	mean	594.8	5.57	9	14.57	0.95	108.6	0.414	44.9	0.586
			±s. e.	37.0	0.38	0.99	1.28	0.06	3.4	0.025	3.4	0.025
0	32	32	mean	411.1	3.68	8.01	11.69	1.32	127.3	0.319	36.3	0.681
			±s. e.	34.9	0.31	0.66	0.86	0.11	20.6	0.019	3.0	0.019
0	32	48	mean	442.9	4.1	10.79	14.9	2.13	108.1	0.289	31.1	0.711
			±s. e.	64.8	0.62	1.81	2.33	0.31	3.3	0.019	2.3	0.019
0	48	16	mean	477.9	4.4	8.59	12.99	0.76	106.9	0.361	38.2	0.639
			±s. e.	44.4	0.34	1.11	1.39	0.07	4.1	0.019	2.1	0.019
0	48	32	mean	370.7	3.2	6.23	9.43	1.19	117.2	0.358	41.4	0.642
			±s. e.	30.6	0.27	0.69	0.85	0.1	3.8	0.022	2.5	0.022
0	48	48	mean	490.9	4.75	11.87	16.62	2.36	105.8	0.301	30.5	0.699
			±s. e.	30.9	0.33	1.19	1.34	0.15	4.4	0.019	1.0	0.019
1	0	16	mean	1255.8	11.18	33.21	44.39	2.01	123.9	0.246	28.0	0.754
			±s. e.	96.7	1.08	1.81	2.43	0.15	10.2	0.016	1.2	0.016
1	0	32	mean	1014.1	10.26	32.64	42.9	3.25	100.5	0.239	23.8	0.761
			±s. e.	54.3	0.61	1.38	1.71	0.17	2.8	0.011	1.0	0.011
1	0	48	mean	797.3	7.91	28.1	36.01	3.83	101.7	0.226	22.7	0.774
			±s. e.	43.7	0.44	2.27	2.57	0.21	2.9	0.01	0.9	0.01
1	16	16	mean	983.5	9.87	26.86	36.72	1.57	100.8	0.274	27.5	0.726
			±s. e.	58.2	0.62	2.16	2.67	0.09	2.5	0.01	1.1	0.01
1	16	32	mean	645.4	6.5	17.23	23.72	2.07	101.2	0.276	27.8	0.724
			±s. e.	33.1	0.41	1.07	1.39	0.11	2.4	0.01	1.0	0.01

Fert.	X_{Bn}	X_{Bt}		LA	WL	WSR	W	LAI	SLA	LWR	LAR	HI
1	16	48	mean	645.4	7.96	21.6	29.56	3.1	89.0	0.263	22.6	0.737
			±s. e.	34.6	0.87	1.38	2.07	0.17	5.0	0.013	1.1	0.013
1	32	16	mean	751.2	7.31	17.76	25.07	1.2	103.9	0.298	30.6	0.702
			±s. e.	38.2	0.36	1.31	1.56	0.06	3.8	0.012	1.3	0.012
1	32	32	mean	702.6	6.82	22.59	29.41	2.25	104.9	0.235	24.3	0.765
			±s. e.	32.7	0.39	1.22	1.45	0.1	3.5	0.01	0.9	0.01
1	32	48	mean	508.0	5.18	13.94	19.12	2.44	99.4	0.279	27.7	0.721
			±s. e.	25.6	0.3	1.1	1.32	0.12	2.7	0.012	1.3	0.012
1	48	16	mean	981.5	9.91	22.25	32.16	1.57	99.6	0.314	31.1	0.686
			±s. e.	60.1	0.56	1.61	2.07	0.1	2.8	0.011	1.1	0.011
1	48	32	mean	693.7	5.91	18.86	24.77	2.22	117.6	0.256	29.8	0.744
			±s. e.	53.8	0.45	2.08	2.45	0.17	3.9	0.016	1.8	0.016
1	48	48	mean	492.3	4.87	11.16	16.02	2.36	101.5	0.311	31.0	0.689
			±s. e.	36.1	0.3	0.91	1.12	0.17	3.3	0.014	1.1	0.014

Beet - 1995 Data

Fert.	X_{Bn}	X_{Bt}		LA	WL	WSR	W	LAI	SLA	LWR	LAR	HI
0	0	16	mean	939.2	9.49	23.94	33.43	1.50	101.0	0.290	28.9	0.710
			±s. e.	60.8	0.73	1.86	2.41	0.10	3.0	0.014	1.3	0.014
0	0	32	mean	571.6	6.12	14.79	20.91	1.83	94.6	0.312	29.2	0.688
			±s. e.	29.0	0.34	1.53	1.78	0.09	2.3	0.017	1.5	0.017
0	0	48	mean	342.1	3.57	8.70	12.27	1.64	95.2	0.349	32.8	0.651
			±s. e.	32.0	0.30	1.40	1.69	0.15	2.6	0.027	2.4	0.027

0	16	16	mean	461.0	5.26	8.16	13.42	0.74	89.3	0.395	35.0	0.605
			±s. e.	19.8	0.28	0.48	0.65	0.03	2.8	0.014	1.4	0.014
0	16	32	mean	480.2	5.20	9.77	14.97	1.54	93.8	0.349	32.5	0.651
			±s. e.	31.9	0.37	0.61	0.84	0.10	2.7	0.018	1.8	0.018
0	16	48	mean	330.7	3.53	5.08	8.61	1.59	92.7	0.414	38.4	0.586
			±s. e.	26.5	0.23	0.33	0.47	0.13	3.7	0.018	2.4	0.018
0	32	16	mean	539.8	5.56	8.34	13.90	0.86	97.1	0.407	39.1	0.593
			±s. e.	35.9	0.31	0.58	0.70	0.06	2.7	0.020	1.9	0.020
0	32	32	mean	421.8	4.52	7.85	12.37	1.35	93.8	0.372	34.9	0.628
			±s. e.	23.5	0.22	0.51	0.55	0.08	2.8	0.018	2.2	0.018
0	32	48	mean	385.9	4.03	5.64	9.67	1.85	99.5	0.409	39.8	0.591
			±s. e.	28.7	0.37	0.31	0.53	0.14	4.8	0.020	1.9	0.020
0	48	16	mean	506.3	4.56	5.71	10.27	0.81	111.2	0.462	51.0	0.538
			±s. e.	36.4	0.31	0.59	0.82	0.06	2.9	0.021	2.5	0.021
0	48	32	mean	360.9	3.52	5.52	9.04	1.15	105.5	0.387	40.1	0.613
			±s. e.	23.2	0.27	0.30	0.42	0.07	4.1	0.022	2.0	0.022
0	48	48	mean	355.5	3.57	5.35	8.91	1.71	101.3	0.401	40.4	0.599
			±s. e.	19.7	0.23	0.32	0.47	0.09	2.2	0.015	1.5	0.015
1	0	16	mean	1433.0	16.39	28.67	45.06	2.29	87.6	0.363	31.9	0.637
			±s. e.	80.0	0.94	1.16	1.62	0.13	1.8	0.015	1.5	0.015
1	0	32	mean	1031.7	11.52	18.02	29.54	3.30	92.6	0.392	35.7	0.608
			±s. e.	40.2	0.58	0.89	1.07	0.13	4.2	0.017	1.9	0.017
1	0	48	mean	588.8	6.54	11.08	17.61	2.83	93.9	0.381	35.9	0.619
			±s. e.	57.1	0.79	1.50	2.23	0.27	2.7	0.012	1.7	0.012

1	16	16	mean	840.7	8.81		18.70	27.50	1.35	96.8	0.336	32.2	0.664
			±s. e.	39.0	0.47		1.68	1.99	0.06	3.0	0.016	1.5	0.016
1	16	32	mean	782.7	7.48		17.04	24.51	2.50	105.4	0.316	32.9	0.684
			±s. e.	37.8	0.38		1.26	1.42	0.12	2.3	0.017	1.5	0.017
1	16	48	mean	496.3	4.83		10.59	15.42	2.38	105.1	0.322	34.0	0.678
			±s. e.	32.8	0.37		0.81	0.89	0.16	3.3	0.022	2.7	0.022
1	32	16	mean	704.7	6.78		14.22	21.00	1.13	105.5	0.322	33.8	0.678
			±s. e.	38.3	0.41		0.72	1.06	0.06	2.9	0.009	1.0	0.009
1	32	32	mean	678.5	6.93		13.05	19.97	2.17	98.4	0.350	34.2	0.650
			±s. e.	51.4	0.52		0.86	1.20	0.16	2.5	0.019	1.7	0.019
1	32	48	mean	539.9	4.96		9.32	14.28	2.59	111.7	0.348	38.2	0.652
			±s. e.	40.1	0.43		0.68	0.94	0.19	3.8	0.021	2.0	0.021
1	48	16	mean	678.7	6.82		12.06	18.88	1.09	101.2	0.364	36.6	0.636
			±s. e.	38.8	0.43		0.77	1.02	0.06	3.2	0.016	1.8	0.016
1	48	32	mean	598.6	4.88		11.21	16.09	1.92	123.0	0.311	37.8	0.689
			±s. e.	42.6	0.30		0.96	1.19	0.14	4.7	0.012	1.6	0.012
1	48	48	mean	465.1	4.61		7.86	12.47	2.23	102.9	0.377	38.5	0.623
			±s. e.	21.9	0.27		0.53	0.64	0.11	3.3	0.021	2.2	0.021

[1]Results are pooled for the two blocks each year, providing 20 observations per mean value. Units of measurement: LA in cm^2, dry masses in g, SLA and LAR in $cm^2 \, g^{-1}$.

Appendix 1c. Mean values of fresh and dry masses of marketable bean pods 1994 and 1995

Fert. level	X_{Bn}	X_{Bt}	1994		1995	
			Fresh mass (g plant^{-1})	Dry mass (g plant^{-1})	Fresh mass (g plant^{-1})	Dry mass (g plant^{-1})
0	16	0	5.17	1.20	25.1	1.92
0	16	16	4.37	1.27	8.05	0.640
0	16	32	4.73	1.17	7.33	0.580
0	16	48	3.290	0.965	7.87	0.640
0	32	0	8.46	2.00	28.2	2.22
0	32	16	4.62	1.25	9.33	0.74
0	32	32	8.72	2.41	9.16	0.710
0	32	48	7.57	2.12	6.07	0.490
0	48	0	10.5	2.83	18.5	1.42
0	48	16	8.33	2.30	12.9	1.00
0	48	32	10.3	2.86	10.3	0.810
0	48	48	8.96	2.37	10.7	0.810
1	16	0	13.2	3.42	45.0	3.61
1	16	16	6.64	1.68	31.8	2.44
1	16	32	6.42	1.66	34.0	2.61
1	16	48	5.00	1.30	32.7	2.57
1	32	0	13.7	4.03	43.7	3.42
1	32	16	10.9	2.61	29.2	2.29
1	32	32	11.0	3.11	35.9	2.74
1	32	48	9.41	2.49	24.8	1.89
1	48	0	15.28	4.51	32.1	2.48
1	48	16	16.0	4.26	30.9	2.43
1	48	32	11.4	2.76	31.1	2.51
1	48	48	10.6	2.63	26.4	1.99

Appendix 1d. Mean values of fresh and dry masses of marketable beet storage roots 1994 and 1995

Fert. level	X_{Bt}	X_{Bn}	1994		1995	
			Fresh mass (g plant^{-1})	Dry mass (g plant^{-1})	Fresh mass (g plant^{-1})	Dry mass (g plant^{-1})
0	16	0	13.1	1.98	107	17.30
0	16	16	16.8	2.66	50	8.13
0	16	32	4.69	0.705	40.7	6.98
0	16	48	2.48	0.400	29.4	4.59
0	32	0	14.4	2.26	67.6	11.6
0	32	16	17.8	3.08	36.7	6.41
0	32	32	25.4	3.02	37.8	6.35
0	32	48	13.5	2.13	24.8	4.37
0	48	0	18.9	3.31	37.8	6.72
0	48	16	25.7	4.18	37.7	6.47
0	48	32	18.3	2.96	31.9	5.47
0	48	48	19.1	3.19	24.8	4.26
1	16	0	30.1	4.30	177	25.82
1	16	16	26.2	4.01	95.8	15.6
1	16	32	18.8	2.81	64.1	10.4
1	16	48	10.6	1.55	60.9	10.5
1	32	0	42.8	6.63	101	14.8
1	32	16	27.3	4.26	66.8	10.9
1	32	32	25.8	4.18	75.7	13.1
1	32	48	32.5	5.09	68.8	10.6
1	48	0	37.2	6.38	80.1	12.4
1	48	16	46.9	7.57	60.5	10.5
1	48	32	34.1	5.38	67.6	11.2
1	48	48	33.9	5.21	52.6	8.64

Appendix 2. Mean values of elemental concentrations (%) and contents (grams plant^{-1})

Beans 1994

Fert. level	X_1	X_2	Concentration (%)					Content (g plant^{-1})				
			N	P	K	Ca	Mg	N	P	K	Ca	Mg
0	16	0	2.41	0.27	1.81	1.58	0.28	0.23	0.025	0.17	0.15	0.027
0	16	16	2.41	0.25	1.36	1.81	0.31	0.22	0.023	0.12	0.16	0.027
0	16	32	2.67	0.24	1.98	1.57	0.30	0.18	0.017	0.12	0.11	0.021
0	16	48	2.84	0.26	1.54	1.31	0.27	0.20	0.018	0.10	0.20	0.018
0	32	0	2.55	0.29	1.71	1.65	0.29	0.17	0.019	0.11	0.11	0.019
0	32	16	2.95	0.29	1.49	1.18	0.24	0.13	0.015	0.06	0.05	0.011
0	32	32	2.58	0.24	1.42	1.56	0.27	0.23	0.023	0.12	0.13	0.023
0	32	48	2.59	0.28	1.41	1.45	0.25	0.18	0.018	0.09	0.10	0.017
0	48	0	2.37	0.29	1.66	1.51	0.28	0.13	0.015	0.07	0.06	0.015
0	48	16	2.49	0.27	1.44	1.60	0.27	0.15	0.015	0.08	0.10	0.016
0	48	32	2.31	0.25	1.46	1.51	0.25	0.17	0.018	0.10	0.11	0.018
0	48	48	2.39	0.29	1.43	1.43	0.27	0.17	0.018	0.09	0.10	0.017
1	16	0	2.23	0.24	1.56	1.78	0.35	0.65	0.068	0.45	0.52	0.010
1	16	16	2.16	0.25	1.51	1.61	0.30	0.29	0.034	0.19	0.21	0.041
1	16	32	2.43	0.25	1.43	1.92	0.30	0.27	0.028	0.16	0.22	0.035
1	16	48	2.51	0.25	1.44	1.58	0.29	0.38	0.039	0.23	0.23	0.044
1	32	0	2.04	0.21	1.49	1.61	0.25	0.40	0.041	0.29	0.31	0.048
1	32	16	2.19	0.25	1.28	1.49	0.33	0.31	0.036	0.18	0.22	0.048
1	32	32	2.16	0.20	1.29	1.49	0.27	0.15	0.022	0.13	0.16	0.028

Fert. level	X_1	X_2	N	P	K	Ca	Mg	N	P	K	Ca	Mg
1	32	48	2.37	0.22	1.41	1.47	0.29	0.27	0.025	0.16	0.17	0.034
1	48	0	2.17	0.23	1.30	1.54	0.26	0.25	0.027	0.15	0.18	0.031
1	48	16	2.25	0.19	1.50	1.52	0.28	0.26	0.022	0.17	0.18	0.032
1	48	32	2.35	0.25	1.40	1.47	0.27	0.20	0.021	0.12	0.12	0.023
1	48	48	2.50	0.25	1.24	1.49	0.30	0.22	0.022	0.11	0.13	0.026

Beans 1995

Fert. level	X_1	X_2	Concentration (%)					Content (g plant^{-1})				
			N	P	K	Ca	Mg	N	P	K	Ca	Mg
0	16	0	4.04	0.18	1.52	1.34	0.27	0.27	0.014	0.13	0.011	0.019
0	16	16	4.83	0.16	1.22	1.06	0.29	0.12	0.0039	0.030	0.026	0.0069
0	16	32	4.83	0.16	1.22	0.96	0.29	0.16	0.0055	0.043	0.032	0.0095
0	16	48	4.45	0.16	1.24	1.00	0.28	0.15	0.0054	0.044	0.035	0.0094
0	32	0	3.82	0.17	1.53	1.27	0.27	0.19	0.0084	0.082	0.068	0.013
0	32	16	5.11	0.16	1.14	0.86	0.28	0.17	0.0055	0.040	0.030	0.0096
0	32	32	4.70	0.16	1.21	0.93	0.27	0.15	0.0050	0.039	0.29	0.0086
0	32	48	4.17	0.16	1.39	0.99	0.25	0.11	0.0040	0.036	0.025	0.0063
0	48	0	4.21	0.17	1.46	1.07	0.28	0.17	0.0069	0.058	0.042	0.011
0	48	16	4.24	0.18	1.31	1.00	0.29	0.17	0.0070	0.054	0.041	0.012
0	48	32	4.16	0.16	1.37	1.02	0.25	0.15	0.0057	0.050	0.037	0.0092
0	48	48	4.27	0.15	1.30	1.00	0.27	0.13	0.0044	0.038	0.029	0.0080
1	16	0	3.38	0.19	1.76	1.68	0.25	0.32	0.019	0.17	0.17	0.025
1	16	16	2.74	0.23	1.64	1.60	0.25	0.20	0.016	0.13	0.13	0.020
1	16	32	2.46	0.18	1.65	1.64	0.25	0.18	0.013	0.12	0.12	0.018

Fert. level	X2	X1	Concentration (%)					Content (g plant⁻¹)				
			N	P	K	Ca	Mg	N	P	K	Ca	Mg
1	16	48	2.55	0.20	1.62	1.62	0.24	0.17	0.011	0.10	0.11	0.017
1	32	0	2.41	0.22	1.75	1.68	0.23	0.21	0.018	0.15	0.15	0.020
1	32	16	2.84	0.19	1.60	1.52	0.25	0.17	0.012	0.10	0.11	0.017
1	32	32	2.59	0.16	1.56	1.63	0.25	0.18	0.011	0.11	0.11	0.017
1	32	48	2.57	0.18	1.56	1.49	0.24	0.17	0.012	0.11	0.11	0.017
1	48	0	2.95	0.21	1.75	1.52	0.23	0.21	0.015	0.14	0.12	0.018
1	48	16	2.59	0.20	1.86	1.63	0.23	0.17	0.012	0.12	0.10	0.015
1	48	32	2.24	0.20	1.50	1.89	0.23	0.16	0.013	0.11	0.14	0.016
1	48	48	2.59	0.17	1.70	1.50	0.23	0.16	0.011	0.11	0.10	0.015

Beets 1994

Fert. level	X2	X1	Concentration (%)					Content (g plant⁻¹)				
			N	P	K	Ca	Mg	N	P	K	Ca	Mg
0	16	0	1.97	0.35	3.18	2.29	0.76	0.46	0.087	0.77	0.49	0.17
0	16	16	1.07	0.32	2.91	1.66	0.65	0.18	0.055	0.51	0.31	0.085
0	16	32	2.73	0.39	4.04	2.18	0.94	0.40	0.056	0.59	0.32	0.14
0	16	48	1.75	0.23	2.92	1.98	0.69	0.23	0.030	0.38	0.26	0.090
0	32	0	2.32	0.28	3.43	3.09	0.86	0.27	0.033	0.40	0.36	0.10
0	32	16	1.32	0.30	2.75	1.48	0.60	0.21	0.048	0.44	0.23	0.094
0	32	32	1.61	0.31	3.31	1.73	0.64	0.19	0.036	0.39	0.19	0.075
0	32	48	1.71	0.34	3.66	1.33	0.59	0.16	0.032	0.35	0.12	0.053
0	48	0	1.43	0.34	2.71	1.58	0.53	0.18	0.042	0.33	0.17	0.060
0	48	16	1.62	0.30	3.38	1.44	0.55	0.23	0.041	0.48	0.20	0.076
0	48	32	1.67	0.36	3.52	1.43	0.56	0.26	0.054	0.56	0.17	0.077

0	48	48	1.82	0.29	4.02	1.35	0.59	0.30	0.048	0.67	0.21	0.096
1	16	0	2.15	0.30	3.65	1.83	0.80	0.97	0.13	1.60	0.86	0.36
1	16	16	1.65	0.35	3.45	1.13	0.58	0.62	0.13	1.28	0.41	0.21
1	16	32	2.05	0.35	3.17	1.31	0.69	0.51	0.090	0.81	0.32	0.17
1	16	48	1.86	0.37	3.97	1.47	0.69	0.73	0.17	1.77	0.55	0.30
1	32	0	1.73	0.32	3.06	1.52	0.70	0.74	0.14	1.31	0.66	0.30
1	32	16	1.77	0.35	3.05	1.15	0.61	0.43	0.081	0.72	0.28	0.15
1	32	32	1.51	0.26	2.97	1.05	0.54	0.44	0.077	0.88	0.31	0.16
1	32	48	1.61	0.26	3.32	1.46	0.64	0.41	0.063	0.83	0.31	0.15
1	48	0	1.67	0.32	3.32	1.17	0.67	0.61	0.10	1.09	0.38	0.22
1	48	16	1.58	0.35	3.45	1.13	0.56	0.47	0.11	1.01	0.32	0.16
1	48	32	1.67	0.32	2.84	1.27	0.66	0.32	0.062	0.56	0.23	0.12
1	48	48	1.91	0.39	3.91	1.79	0.78	0.30	0.065	0.65	0.27	0.12

Beets 1995

Fert. level	X2	X1	Concentration (%)					Content (g plant^{-1})				
			N	P	K	Ca	Mg	N	P	K	Ca	Mg
0	16	0	1.92	0.32	3.11	1.71	0.76	0.63	0.11	1.04	0.57	0.25
0	16	16	2.57	0.23	2.09	1.65	0.98	0.34	0.030	0.28	0.22	0.13
0	16	32	2.23	0.18	2.01	1.61	0.81	0.31	0.025	0.28	0.22	0.11
0	16	48	2.57	0.18	2.19	2.15	1.21	0.26	0.018	0.23	0.22	0.12
0	32	0	1.66	0.26	2.70	1.82	0.69	0.33	0.062	0.57	0.34	0.13
0	32	16	2.29	0.20	2.04	1.71	0.73	0.35	0.030	0.30	0.26	0.11
0	32	32	2.38	0.23	1.62	1.76	0.97	0.30	0.030	0.20	0.22	0.12

0	32	48	2.22	0.24	2.10	1.69	0.75	0.20	0.022	0.19	0.15	0.068
0	48	0	1.65	0.30	2.29	1.77	0.67	0.18	0.045	0.31	0.19	0.079
0	48	16	2.19	0.24	1.99	1.76	0.81	0.19	0.021	0.17	0.15	0.069
0	48	32	2.28	0.17	1.78	1.97	0.86	0.22	0.016	0.17	0.19	0.083
0	48	48	2.43	0.22	1.90	1.68	0.88	0.22	0.019	0.17	0.15	0.078
1	16	0	2.64	0.24	2.08	1.50	0.84	1.19	0.11	0.94	0.68	0.38
1	16	16	2.04	0.29	3.23	2.09	0.83	0.52	0.086	0.88	0.54	0.21
1	16	32	1.87	0.33	3.25	1.50	0.50	0.39	0.070	0.68	0.31	0.10
1	16	48	1.71	0.35	3.69	1.69	0.59	0.32	0.065	0.70	0.32	0.11
1	32	0	3.00	0.25	1.64	1.67	0.92	0.88	0.075	0.48	0.49	0.27
1	32	16	1.70	0.37	3.48	1.36	0.59	0.42	0.089	0.85	0.33	0.14
1	32	32	2.03	0.31	2.90	1.44	0.66	0.41	0.061	0.57	0.29	0.13
1	32	48	1.53	0.35	3.25	1.37	0.58	0.25	0.055	0.53	0.23	0.094
1	48	0	2.21	0.19	2.14	1.61	0.78	0.41	0.031	0.33	0.27	0.14
1	48	16	1.61	0.29	2.86	1.52	0.67	0.24	0.047	0.44	0.23	0.10
1	48	32	1.72	0.33	3.04	1.55	0.68	0.25	0.046	0.43	0.22	0.097
1	48	48	1.62	0.33	3.52	1.40	0.64	0.20	0.041	0.44	0.17	0.079

Appendix 3. Rationale for Relative Competitive Response

Use of inverse yield-density regression models was employed in Chapter 4 to quantify competition for the elements, N, P, K, Ca and Mg, where the reciprocal of the mean content of each element was used as the dependent variable in each case. However, It is well known that the average content of different nutrient elements in plants vary, depending on plant species, stage of growth or the organ. For example while N varies from about 2 to 5% of dry mass of plants, the average content of P in plants ranges between 0.3 and 0.5% (Marschner (1995). This is reflected by the different values for $1/a_{10}$ and $1/a_{20}$ obtained for the different elements (Tables 4.8 and 4.9). This suggests that the scales of the other parameters, a_{ii} ... a_{ji}, may be different for the different elements. This prevents the direct comparison of the values of parameters a_{ii} ... a_{ji} across the various elements. To bring competition for the nutrients to the same scale, a new parameter called Relative Competitive Response (RCR) was calculated using the formula given below (Eqn 4.1). RCR values made it possible to compare at the same scale, the strengths with which the nutrient elements were competed for by the two plant species. The RCR values helped to realize that the nutrient elements were competed for with almost the same strength (Table 4.7).

$$RCR_1 = 100/"Y" \; d"Y"/dX = 100(a_{11}+a_{12})/a_{10}+(a_{11}+a_{12})x24 \qquad \text{or}$$

$$RCR_2 = 100(a_{22}+a_{21})/a_{20}+(a_{22}+a_{21})x24 \qquad\qquad (4.1)$$

Appendix 4. Allometry for bean monocultures

Appendix 4a. Parameters and statistics for the best subset multiple regression models of the allometric relationship between W and LA in beans (pure stands).

Potential independent variable	Parameter	Parameter estimates		Standard regression coefficients	partial
		1994	1995	1994	1995
Intercept	$\ln(\alpha`)$	-	-3.18*	-	
		-	(0.240)	-	
ln (LA)	β_0	-	0.900*	-	0.989
Nln(LA)	β_1	-	-	-	-
X_1ln(LA)	β_2	-	-	-	-
X_2ln(LA)	β_3	-	-	-	-
NX_1ln(LA)	β_4	-	-	-	-
NX_2ln (LA)	β_5	-	-	-	-
X_1X_2ln(LA)	β_6	-	-	-	-
NX_1X_2ln(LA)	β_7	-	-	-	-
ln(N)	γ_1	-	-	-	-
$\ln(X_1)$	γ_2	-	-	-	-
$\ln(X_2)$	γ_3	-	-	-	-
$\ln(NX_1)$	γ_4	-	-	-	-
$\ln(NX_2)$	γ_5	-	-	-	-
$\ln(X_1X_2)$	γ_6	-	-	-	-
$\ln(NX_1X_2)$	γ_7	-	-	-	-
R^2		-	0.98	-	0.98
P(reg)		-	<0.001	-	<0.001

*Regression parameters significantly different from zero according to a T-test (P>0.05). Values in brackets are the standard errors of the parameter estimates.

Appendix 4b Parameters and statistics for the best subset multiple regression
models of the allometric relationship between W and WL in beans (pure stands).

Potential independent variable	Parameter	Parameter estimates		Standard partial regression coefficients	
		1994	1995	1994	1995
Intercept	$\ln(\alpha')$	1.70*	1.34*		
		(0.0497)	(0.0350)		
$\ln(WL)$	β_0	1.01*	1.07	0.987	0.988
		(0.0523)	(0.0523)		
$N\ln(WL)$	β_1	-	-	-	-
$X_1\ln(WL)$	β_2	-	-	-	-
$X_2\ln(WL)$	β_3	-	-	-	-
$NX_1\ln(WL)$	β_4	-	-	-	-
$NX_2\ln(WL)$	β_5	-	-	-	-
$X_1X_2\ln(WL)$	β_6	-	-	-	-
$NX_1X_2\ln(WL)$	β_7	-	-	-	-
$\ln(N)$	γ_1	-	-	-	-
$\ln(X_1)$	γ_2	-	-	-	-
$\ln(X_2)$	γ_3	-	-	-	-
$\ln(NX_1)$	γ_4	-	-	-	-
$\ln(NX_2)$	γ_5	-	-	-	-
$\ln(X_1X_2)$	γ_6	-	-	-	-
$\ln(NX_1X_2)$	γ_7	-	-	-	-
R^2		0.97	0.98	0.97	0.98
P(reg)		<0.001	<0.001	<0.001	<0.001

*Regression parameters significantly different from zero according to a T-test ($P<0.05$). Values in brackets are
the standard errors of the parameter estimates.

Appendix 4c Parameters and statistics for the best subset multiple regression

models of the allometric relationship between W and WS in beans (pure stands).

.Potential independent variable	Parameter	Parameter estimates		Standard partial regression coefficients	
		1994	1995	1994	1995
Intercept	$\ln(\alpha^{`})$	1.44*	0.969*		
		(0.0360)	(0.0968)		
$\ln(WS)$	β_0	1.04*	0.897*	0.985	0.957
		(0.0483)			
$N\ln(WS)$	β_1	-	-	-	-
$X_1\ln(WS)$	β_2	-	-	-	-
$X_2\ln(WS)$	β_3	-	-	-	-
$NX_1\ln(WS)$	β_4	-0.00440*	-	-0.283	-
		(0.000883)	-		-
$NX_2\ln(WS)$	β_5	-	-	-	-
$X_1X_2\ln(WS)$	β_6	-	-	-	-
$NX_1X_2\ln(WS)$	β_7	-	-	-	-
$\ln(N)$	γ_1	0.497*	-	0.266	-
		(0.117)	-		-
$\ln(X_1)$	γ_2	-	-	-	-
$\ln(X_2)$	γ_3	-	-	-	-
$\ln(NX_1)$	γ_4	-	-	-	-
$\ln(NX_2)$	γ_5	-	-	-	-
$\ln(X_1X_2)$	γ_6	-	-	-	-
$\ln(NX_1X_2)$	γ_7	-	-	-	-
R^2		0.99	0.92	0.99	0.92
P(reg)		<0.001	<0.001	<0.001	<0.001

*Regression parameters significantly different from zero according to a T-test (P<0.05). Values in brackets are the standard errors of the parameter estimates.

Appendix 4d Parameters and statistics for the best subset multiple regression
models of the allometric relationship between W and PN in beans (pure stands).

Potential independent variable	Parameter	Parameter estimates		Standard partial regression coefficients	
		1994	1995	1994	1995
Intercept	$\ln(\alpha^{\cdot})$	0.642*	-0.669*		
		(0.161)	(0.175)		
$\ln(PN)$	β_0	0.864*	1.34*	0.750	0.977
		(0.102)	(0.0914)		
$N\ln(PN)$	β_1	-	-		-
$X_1\ln(PN)$	β_2	-	-		-
		-	-		-
$X_2\ln(PN)$	β_3	-	-		-
$NX_1\ln(PN)$	β_4	-	-		-
$NX_2\ln(PN)$	β_5	-	-		-
$X_1X_2\ln(PN)$	β_6	-	-		-
$NX_1X_2\ln(PN)$	β_7	-	-		-
$\ln(N)$	γ_1	0.580*	-	0.310	-
		(0.165)	-		-
$\ln(X_1)$	γ_2		-		-
$\ln(X_2)$	γ_3		-		-
$\ln(NX_1)$	γ_4		-		-
$\ln(NX_2)$	γ_5		-		-
$\ln(X_1X_2)$	γ_6		-		-
$\ln(NX_1X_2)$	γ_7		-		-
R^2		0.96	0.96	0.96	0.96
P(reg)		<0.001	<0.001	<0.001	<0.001

*Regression parameters significantly different from zero according to a T-test ($P<0.05$). Values in brackets are
the standard errors of the parameter estimates.

Appendix 4e. Parameters and statistics for the best subset multiple regression models of the allometric relationship between W and WP in beans (pure stands).

Potential independent variable	Parameter	Parameter estimates		Standard regression	partial coefficients
		1994	1995	1994	1995
Intercept	$\ln(\alpha`)$	0.631*	1.24*		
		(0.0394)	(0.0737)		
$\ln(WP)$	β_0	0.959*	0.871*	0.998	0.959
		(0.0199)	(0.0817)		
$N\ln(WP)$	β_1	-	-	-	-
$X_1\ln(WP)$	β_2	-	-	-	-
		-	-	-	-
$X_2\ln(WP)$	β_3	-	-	-	-
$NX_1\ln(WP)$	β_4	-	-	-	-
$NX_2\ln(WP)$	β_5	-	-	-	-
$X_1X_2\ln(WP)$	β_6	-	-	-	-
$NX_1X_2\ln(WP)$	β_7	-	-	-	-
$\ln(N)$	γ_1	-	-	-	-
$\ln(X_1)$	γ_2	-	-	-	-
$\ln(X_2)$	γ_3	-	-	-	-
$\ln(NX_1)$	γ_4	-	-	-	-
$\ln(NX_2)$	γ_5	-	-	-	-
$\ln(X_1X_2)$	γ_6	-	-	-	-
$\ln(NX_1X_2)$	γ_7	-	-	-	-
R^2		0.99	0.92	0.99	0.92
P(reg)		<0.001	<0.001	<0.001	<0.001

*Regression parameters significantly different from zero according to a T-test (P<0.05). Values in brackets are the standard errors of the parameter estimates.

Appendix 5. Allometry for beet monocultures

Appendix 5a . Parameters and statistics for the best subset multiple regression

models of the allometric relationship between W and LA in beets (pure stands).

Potential independent variable	Parameter	Parameter estimates 1994	Parameter estimates 1995	Standard partial regression coefficients 1994	Standard partial regression coefficients 1995
Intercept	$\ln(\alpha`)$	-3.28*	-4.20*		
		(0.616)	(0.656)		
$\ln(LA)$	β_0	0.964*	1.28*	0.884	1.15
		(0.0973)	(0.104)		
$N\ln(LA)$	β_1	-	-	-	-
$X_1\ln(LA)$	β_2	-	-	-	-
$X_2\ln(LA)$	β_3	-	0.00430*	-	0.530
		-	(0.00137)	-	
$NX_1\ln(LA)$	β_4	-	-	-	-
$NX_2\ln(LA)$	β_5	0.000715*	-	0.221	-
$X_1X_2\ln(LA)$	β_6	-	-	-	-
$NX_1X_2\ln(LA)$	β_7	-	-	-	-
$\ln(N)$	γ_1	-	-	-	-
$\ln(X_1)$	γ_2	-	-	-	-
$\ln(X_2)$	γ_3	-	-	-	-
$\ln(NX_1)$	γ_4	-	-	-	-
$\ln(NX_2)$	γ_5	-	-0.530	-	-0.503
			(0.145)		
$\ln(X_1X_2)$	γ_6	-	-	-	-
$\ln(NX_1X_2)$	γ_7	-	-	-	-
R^2		0.93	0.97	0.93	0.97
$P(reg)$		<0.001	<0.001	<0.001	<0.001

*Regression parameters significantly different from zero according to a T-test ($P>0.05$). Values in brackets are the standard errors of the parameter estimates.

Appendix 5b. Parameters and statistics for the best subset multiple regression models of the allometric relationship between W and WL in beets (pure stands).

Potential independent variable	Parameter	Parameter estimates		Standard regression	partial coefficients
		1994	1995	1994	1995
Intercept	$\ln(\alpha')$	5.33* (0.684)	0.766* (0.189)		
$\ln(WL)$	β_0	-	1.40* (0.143)	-	1.31
$N\ln(WL)$	β_1	-	-0.155*	-	-0.427
$X_1\ln(WL)$	β_2	-	(0.0486)	-	
$X_2\ln(WL)$	β_3	0.0142* (0.00615)	-	0.577	-
$NX_1\ln(WL)$	β_4	-	-	-	-
$NX_2\ln(WL)$	β_5	-	-	-	-
$X_1X_2\ln(WL)$	β_6	-	-	-	-
$NX_1X_2\ln(WL)$	β_7	-	-	-	-
$\ln(N)$	γ_1	-	-	-	-
$\ln(X_1)$	γ_2	-	-	-	-
$\ln(X_2)$	γ_3	-1.86* (0.217)	-	-1.46	-
$\ln(NX_1)$	γ_4	-	-	-	-
$\ln(NX_2)$	γ_5	0.922* (0.286)	-	0.909	-
$\ln(X_1X_2)$	γ_6	-	-	-	-
$\ln(NX_1X_2)$	γ_7	-	-	-	-
R^2		0.91	0.95	0.91	0.95
P(reg)		<0.001	<0.001	<0.001	<0.001

*Regression parameters significantly different from zero according to a T-test ($P>0.05$). Values in brackets are the standard errors of the parameter estimates.

Appendix 5c. Parameters and statistics for the best subset multiple regression models of the allometric relationship between W and WSR in beets in monocultures.

Potential independent variable	Parameter	Parameter estimates		Standard partial regression coefficients	
		1994	1995	1994	1995
Intercept	$\ln(\alpha`)$	0.692* (0.123)	0.673* (0.0723)		
$\ln(WSR)$	β_0	0.876* (0.0419)	0.839* (0.0339)	0.989	0.900
$N\ln(WSR)$	β_1	-	0.0466* (0.0121)	-	0.140
$X_1\ln(WSR)$	β_2	-	-	-	-
$X_2\ln(WSR)$	β_3	-	-	-	-
$NX_1\ln(WSR)$	β_4	-	-	-	-
$NX_2\ln(WS)$	β_5	-	-	-	-
$X_1X_2\ln(WSR)$	β_6	-	-	-	-
$NX_1X_2\ln(WSR)$	β_7	-	-	-	-
$\ln(N)$	γ_1	-	-	-	-
$\ln(X_1)$	γ_2	-	-	-	-
$\ln(X_2)$	γ_3	-	-	-	-
$\ln(NX_1)$	γ_4	-	-	-	-
$\ln(NX_2)$	γ_5	-	-	-	-
$\ln(X_1X_2)$	γ_6	-	-	-	-
$\ln(NX_1X_2)$	γ_7	-	-	-	-
R^2		0.98	0.99	0.98	0.99
P(reg)		<0.001	<0.001	<0.001	<0.001

*Regression parameters significantly different from zero according to a T-test (P>0.05). Values in brackets are the standard errors of the parameter estimates.

Appendix 6. Relative and productivity measures for biomass and nutrient uptake in beans and beets 1994 and 1995

Appendix 6a. RYT, RLO and TLO, based on total biomass (W).

Total density	Beans:Beets	RYT		RLO		TLO (g m^{-2})	
		Observed	Predicted	Observed	Predicted	Observed	Predicted
1994 Low Soil Fertility (N$_0$)							
32	16:16	1.44	-	1.45	-	423	-
48	32:16	0.97	-	1.03	-	388	-
48	16:32	1.26	-	1.26	-	619	-
1994 High Soil Fertility (N$_1$)							
32	16:16	0.77	1.10	0.81	1.09	801	964
48	32:16	1.05	1.11	0.91	1.10	864	941
48	16:32	0.76	1.11	0.70	1.08	939	1,231
1995 Low Soil Fertility N$_0$							
32	16:16	0.55	-	0.61	-	253	-
48	32:16	0.94	-	1.02	-	332	-
48	16:32	1.09	-	1.17	-	534	-
1995 High Soil Fertility N$_1$							
32	16:16	0.92	1.08	0.92	1.12	567	612
48	32:16	0.95	1.08	1.02	1.14	548	624
48	16:32	1.23	1.07	1.30	1.09	900	797

Appendix 6b. RYT, RLO and TLO, based on agronomic yield (WP plus WSR).

Total density	Beans:Beets	RYT		RLO		TLO (g m^{-2})	
		Observed	Predicted	Observed	Predicted	Observed	Predicted
1994 Low Soil Fertility (N$_0$)							
32	16:16	1.63	-	1.68	-	286	-
48	32:16	0.94	-	0.94	-	231	-
48	16:32	1.30	-	1.26	-	444	-
1994 High Soil Fertility (N$_1$)							
32	16:16	0.71	1.07	0.77	1.05	544	659
48	32:16	0.95	1.07	0.79	1.07	522	604
48	16:32	0.70	1.07	0.64	1.05	644	858
1995 Low Soil Fertility (N$_0$)							
32	16:16	0.44	-	0.53	-	139	-
48	32:16	0.73	-	0.88	-	159	-
48	16:32	0.94	-	1.08	-	324	-
1995 High Soil Fertility (N$_1$)							
32	16:16	0.89	1.12	1.00	1.17	336	370
48	32:16	0.95	1.12	1.13	1.23	287	326
48	16:32	1.34	1.11	1.48	1.12	582	484

Appendix 6c. RYT and RLO for nutrient element uptake (1994).

Variable	Mixture densities (beans:beets)	RYT Observed	Predicted	RLO Observed	Predicted
		Low Soil Fertility (N$_0$)			
N	16:16	1.00	-	0.93	-
N	16:32	1.26	-	1.25	-
N	32:16	1.42	-	1.51	-
P	16:16	1.45	-	1.52	-
P	16:32	1.14	-	1.14	-
P	32:16	1.09	-	1.18	-
K	16:16	1.16	-	1.22	-
K	16:32	1.50	-	1.37	-
K	32:16	1.25	-	1.55	-
Ca	16:16	1.18	-	1.01	-
Ca	16:32	1.55	-	1.48	-
Ca	32:16	1.20	-	1.47	-
Mg	16:16	1.16	-	0.95	-
Mg	16:32	1.50	-	1.55	-
Mg	32:16	1.24	-	1.77	-
		High Soil Fertility (N$_1$)			
N	16:16	0.77	-	0.79	-
N	16:32	0.82	-	0.76	-
N	32:16	1.09	-	1.01	-
P	16:16	0.90	1.04	0.94	0.93
P	16:32	0.87	1.05	0.81	0.94
P	32:16	1.18	1.04	1.03	0.91
K	16:16	0.82	0.98	0.92	0.82
K	16:32	0.79	0.98	0.69	0.83
K	32:16	1.05	0.98	0.84	0.76
Ca	16:16	0.65	1.01	0.64	0.93
Ca	16:32	0.88	1.01	0.81	0.91
Ca	32:16	1.07	1.01	1.01	0.90
Mg	16:16	0.78	1.01	0.73	0.85
Mg	16:32	0.82	1.02	0.70	0.87
Mg	32:16	1.31	1.01	0.96	0.81

Appendix 6d. RYT and RLO for nutrient element uptake (1995).

| Variable	Mixture densities (beans:beets)	RYT Observed	RYT Predicted	RLO Observed	RLO Predicted
		Low Soil Fertility (N_0)			
N	16:16	0.83	-	0.89	-
N	32:16	1.62	-	1.63	-
N	16:32	1.26	-	1.27	-
P	16:32	1.01	-	1.10	-
P	16:16	2.22	-	2.50	-
P	32:16	1.28	-	1.55	-
K	32:16	1.33	-	1.59	-
K	16:32	2.00	-	2.25	-
K	16:16	1.18	-	1.46	-
Ca	16:16	1.00	-	1.04	-
Ca	32:16	1.17	-	1.31	-
Ca	16:32	1.01	-	1.04	-
Mg	16:32	0.89	-	0.95	-
Mg	16:16	1.19	-	1.34	-
Mg	32:16	1.04	-	1.30	-
		High Soil Fertility (N_1)			
N	16:16	0.76	0.93	0.66	0.90
N	32:16	0.95	0.94	0.97	0.93
N	16:32	0.84	0.94	0.87	0.91
P	16:32	0.47	0.74	0.48	0.59
P	16:16	0.72	0.67	0.69	0.57
P	32:16	0.72	0.75	0.62	0.48
K	32:16	0.42	0.78	0.43	0.66
K	16:32	0.90	0.72	0.96	0.65
K	16:16	0.76	0.78	0.85	0.56
Ca	16:16	0.51	-	0.61	-
Ca	32:16	1.14	-	1.18	-
Ca	16:32	0.96	-	0.86	-
Mg	16:32	0.79	1.04	0.76	1.04
Mg	16:16	1.02	1.05	1.04	1.04
Mg	32:16	0.85	1.05	0.77	1.06

10.7 Appendix 7. RYT Estimates
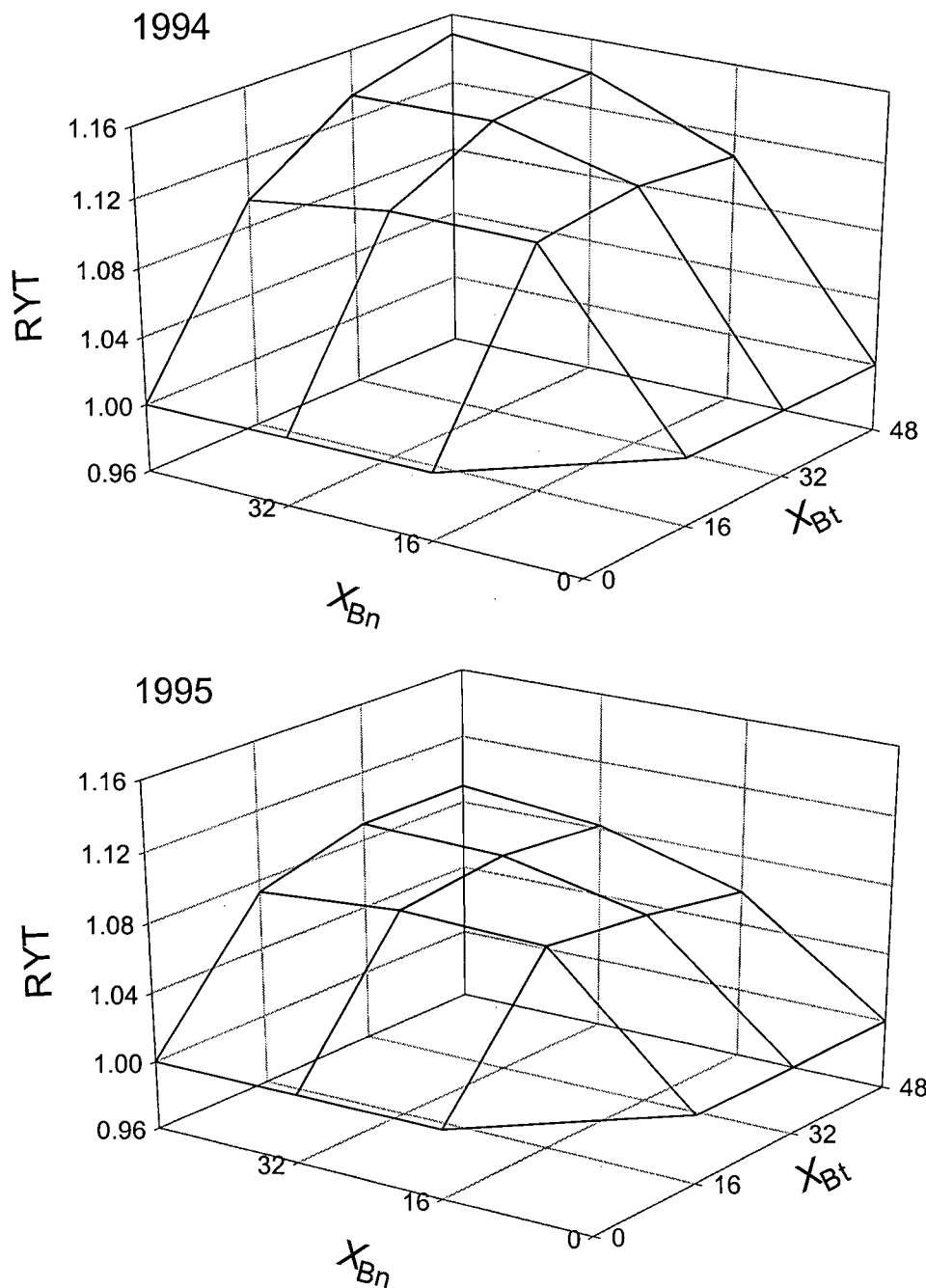
Figure 10.1. Relative Yield Totals for biomass production per unit land area in 1994 (top panel) and 1995 (bottom panel) estimated from yield-density relationships at each of the population density combinations represented in these studies
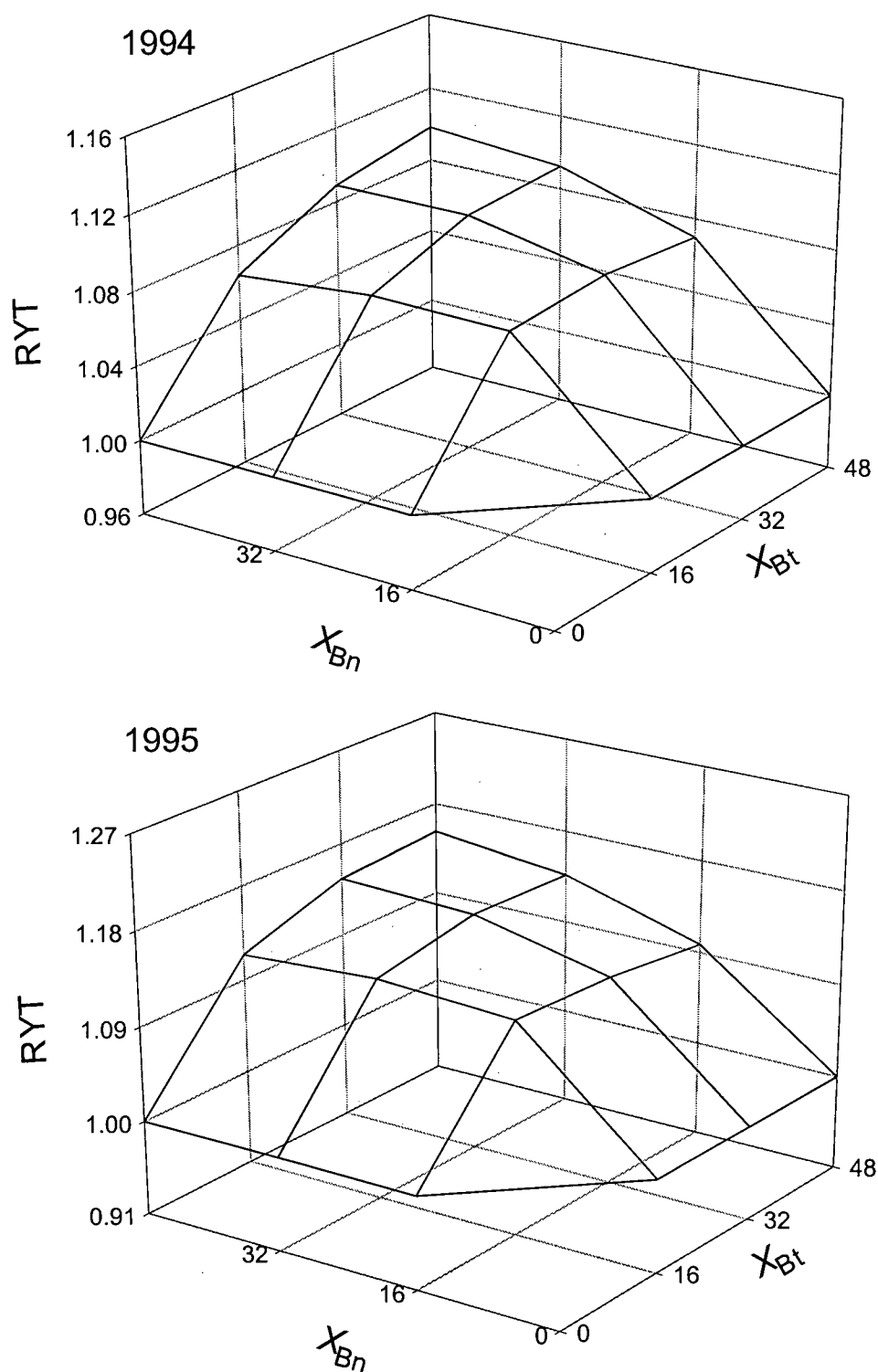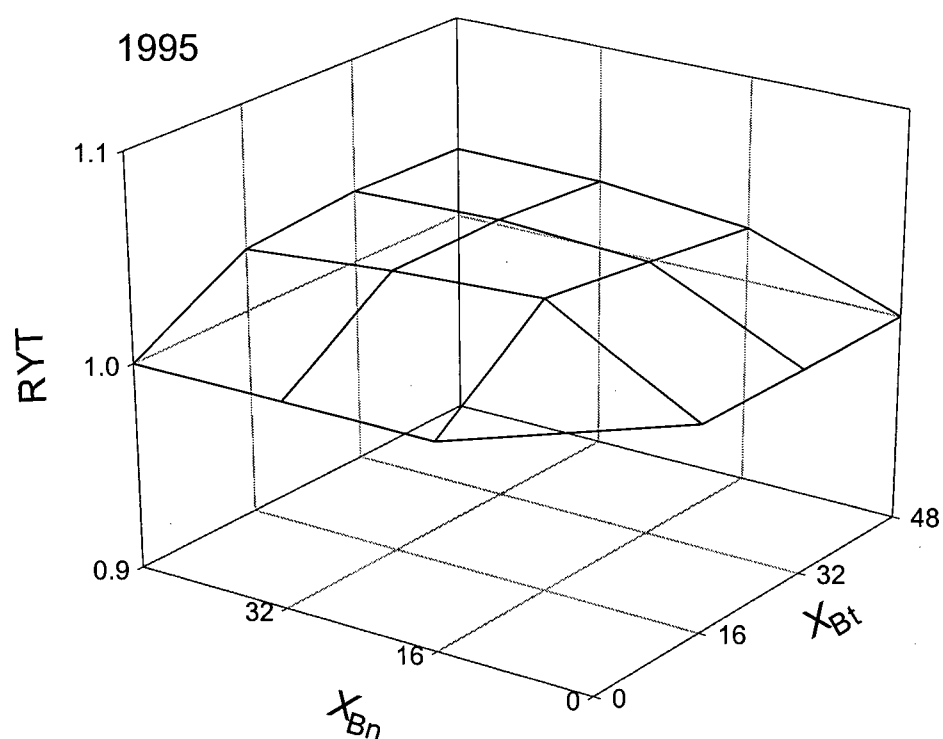
Figure 10.2. Relative Yield Totals for agronomic yield per unit land area in 1994 (top panel) and 1995 (bottom panel) estimated from yield-density relationships at each of the population density combinations represented in these studies

Figure 10.3. Relative Yield Totals for nitrogen accumulation per unit land area in 1995 estimated from yield-density relationships at each of the population density combinations represented in these studies
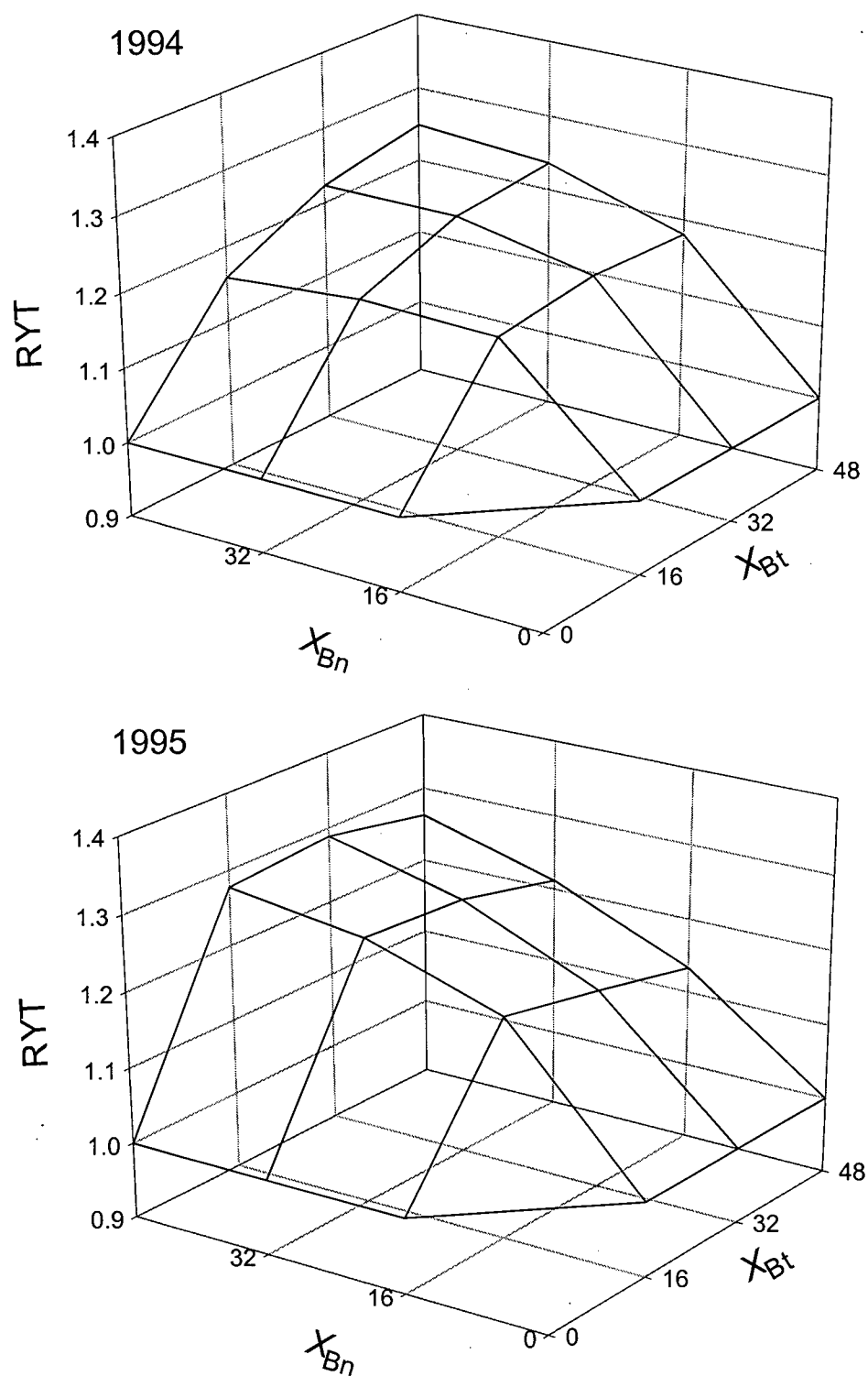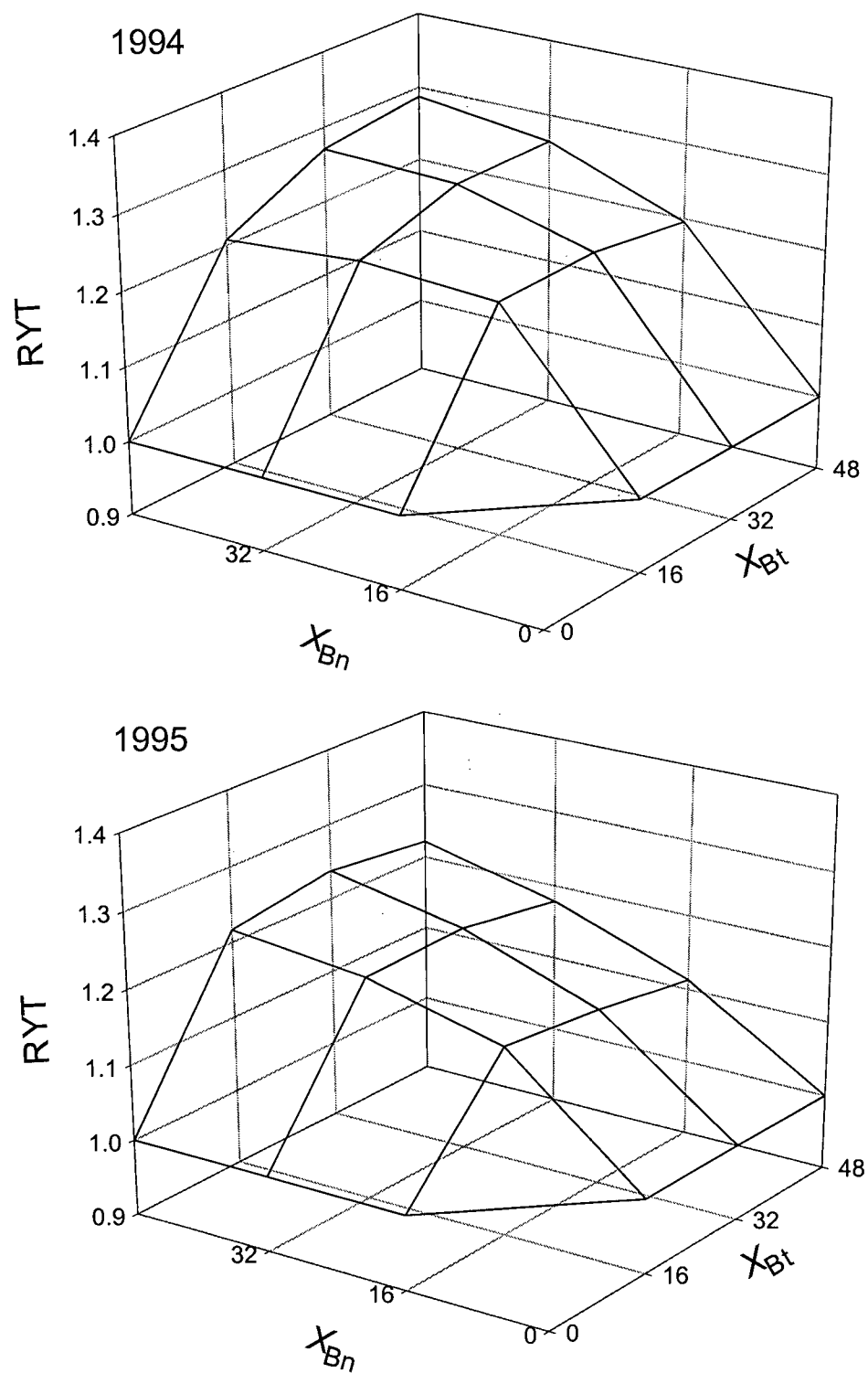
Figure 10.4. Relative Yield Totals for phosphorus accumulation per unit land area in 1994 (top panel) and 1995 (bottom panel) estimated from yield-density relationships at each of the population density combinations represented in these studies

Figure 10.5. Relative Yield Totals for potassium accumulation per unit land area in 1994 (top panel) and 1995 (bottom panel) estimated from yield-density relationships at each of the population density combinations represented in these studies
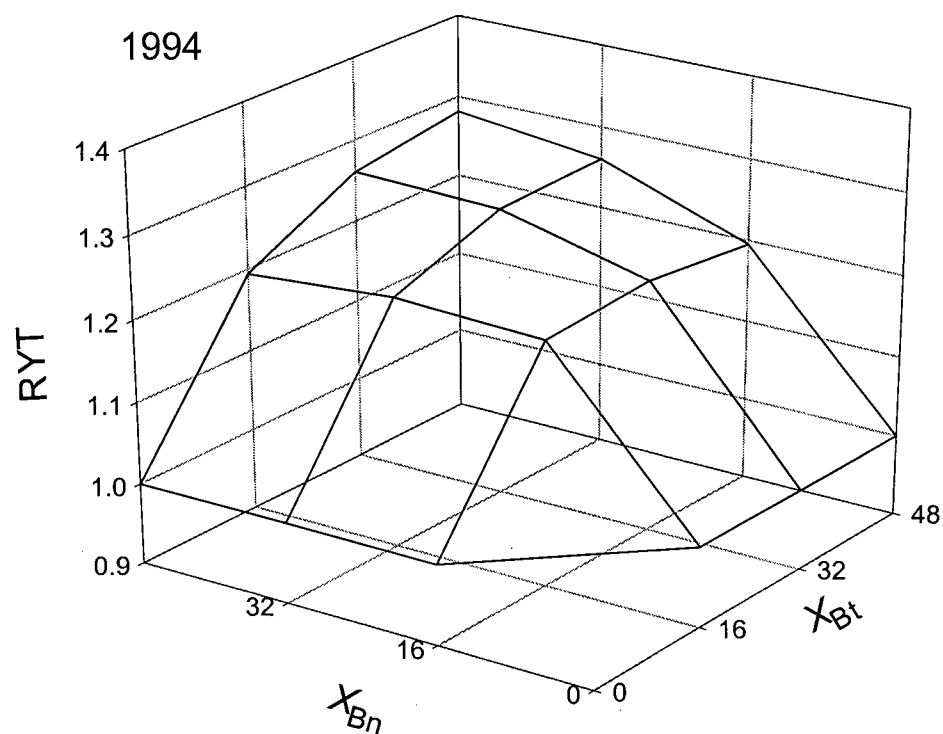
Figure 10.6. Relative Yield Totals for calcium accumulation per unit land area in 1994 estimated from yield-density relationships at each of the population density combinations represented in these studies
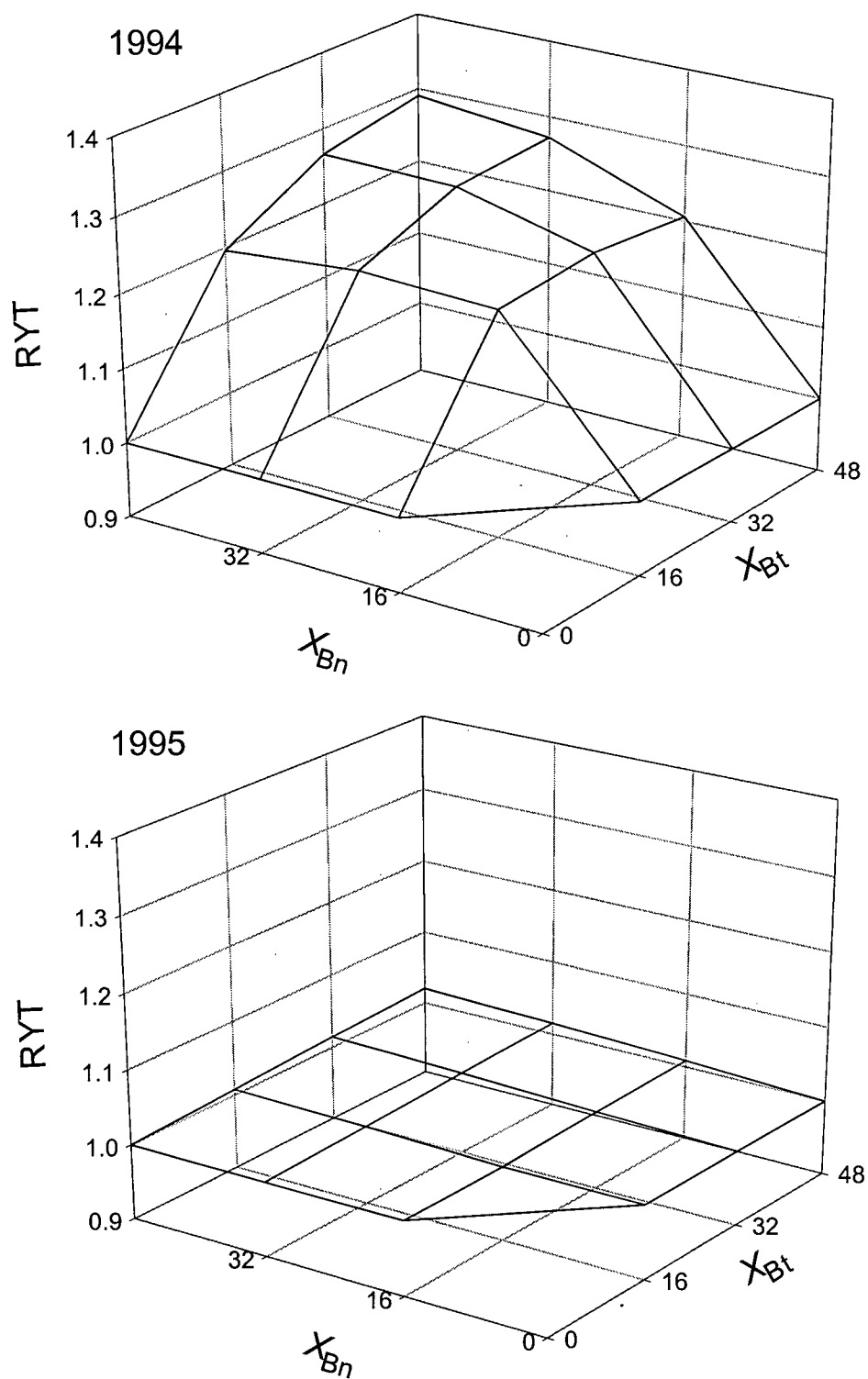
Figure 10.7. Relative Yield Totals for magnesium accumulation per unit land area in 1994 (top panel) and 1995 (bottom panel) estimated from yield-density relationships at each of the population density combinations represented in these studies