The effect of plant traits and resource supply characteristics on plant competition: a mechanistic model.

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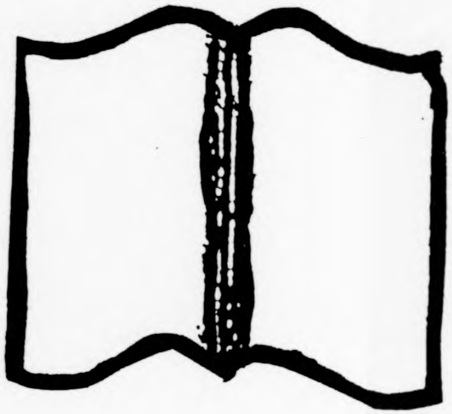


Abstract

An individual-based, spatially explicit model of herbaceous plants is presented in an attempt to investigate some of the predictions made by the CSR model (Grime 1979) and the Resource Ratio and R^* hypotheses (Tilman 1982, 1988). The model simulates early growth of herbaceous individuals and competition between these individuals for light and soil nutrients (nitrogen and phosphorus), along a nutrient gradient. Various model plant species are constructed to investigate the effect of plant traits on competition.

High allocation to root is predicted to confer a slight advantage in habitats with low nutrient availability, and conversely high allocation to shoots is predicted to confer a competitive advantage in habitats with high nutrient availability. A plastic response to the availability of resources in the allocation of growth between root and shoot is predicted to confer a competitive advantage in all habitats, though the bias of the plasticity (*e.g.* consistently greater allocation to root than shoot would be a root biased allocation pattern) may affect this. Growth uncoupled from resource acquisition is predicted to be advantageous in nutrient poor habitats, while growth coupled to resource acquisition is predicted to be advantageous in nutrient rich habitats.

Above- and below-ground inter-specific competition along nutrient gradients is examined for these species. Below-ground competition intensity for a soil resource in the absence of light competition is predicted to be higher for a highly mobile resource than for a relatively immobile resource, but competition for light is predicted to be greater for the more mobile resource. Competition intensity for soil nutrients is predicted to be maximal at low nutrient availability, and the intensity of light competition is predicted to be greatest in nutrient rich habitats.

The implications for current plant competition theories are discussed.

Contents

Chapter 1. The theories of Grime and Tilman

Chapter 2. An Individual-Based Plant Competition Model

Chapter 3. Simulation Runs

Chapter 4. Model validation

Chapter 5. Discussion

Appendix

List of Tables

List of Figures

Chapter 1

The Theories of Grime and Tilman

1.1 Introduction

1.1.1 Competition and plant communities

The factors determining the spatial and temporal arrangement of plant species have been ascribed to many different processes. One such process, which has generated considerable attention from plant ecologists, is resource competition. That plants may affect each other's performance either indirectly (*e.g.* influencing the availability of a common resource) or directly (*e.g.* allelopathy) is not in question as many studies have demonstrated negative effects of neighbours (see Harper 1977, Connell 1983, Schoener 1983), but there exists much debate as to the magnitude of these interactions, how they may influence vegetation distribution and succession, and the evolutionary role played by such forces. Despite the sheer volume of work concerning plant competition, ecologists have discovered few general principles and laws; one notable critic has suggested that the understanding of plant competition has hardly increased since the seminal work of Clements in 1929 (Keddy 1991).

1.1.2 Plant competition theories

The primary role of competition theories is to present a conceptual framework within which observations and experimental results may be organized in a way as to be ecologically meaningful. A secondary role is prediction, which may be tested by further observation or experiment to reveal the predictive value of a theory, though it is appreciated that there tends to be a trade-off between the generality and precision of an ecological theory (Peters 1991, Sharpe & Rykiel 1991). Prediction of vegetation dynamics is now the goal of many plant ecologists, but prediction requires testable theories.

Direct resource competition has been demonstrated to be a real phenomenon affecting the relative performance of vascular terrestrial plants (see Connell 1983, Schoener 1983) and consequentially much attention has focused on the possible influence of competition on the population and community structure of vegetation. However, attempts to determine the precise role and mechanisms of competition (either by observation or experiment) have yielded few clear general patterns, partly due to differences in methodology, definitions and emphasis, and scientific laws linking competition to habitat and community organization are still missing.

Generally speaking, competition may influence vegetation at two extreme time scales: at the evolutionary scale (the significance of competition as a selective force; *e.g.* evolution of plant trait syndromes) and at the ecological scale (mechanisms of competition and population dynamics). Thus, a mature theory of plant competition must operate at both of these time scales. Several theories attempt to address these issues: both the CSR model (Grime 1979) and the Resource Ratio hypothesis (Tilman 1982, 1988) make several important predictions concerning the mechanisms and properties of resource competition, while the Habitat Template model (Taylor *et al.* 1990) deals only with the evolutionary significance of competition. All of these theories invoke a concept of competition intensity (CI), and all but the Resource Ratio hypothesis identify habitats where competition is intense and is the predominant factor governing community assembly.

1.1.3 Context and principal aims of thesis

The context of this thesis is limited mainly to the mechanisms of interspecific competition at the ecological level because of the temporal structure of the model presented (see chapter 2), therefore only the theories of Grime (CSR model; section 1.2) and Tilman (Resource Ratio hypothesis and R* theory; section 1.3) are considered in detail. The principal aims of this thesis were:

(1) to review the Grime vs. Tilman debate with the aim of reconciliation, and to initiate a synthesis of the CSR model and Resource Ratio / R* hypotheses where possible and suggest tests which may distinguish between the models;

(2) to develop a mathematical model that simulates plant competition for resources which could be used to investigate the hypotheses of Grime and Tilman.

Construction of the model prompted insights into resource competition (*e.g.* the possible significance of resource supply properties and plastic allocation of biomass) and assisted greatly in placing the two theories into a common context.

1.2 CSR model

1.2.1 Introduction

Grime's CSR-strategy theory (or triangular model of plant strategies; Grime 1979) is constructed on the assumption that vegetation is influenced by two primary environmental processes, *stress* and *disturbance*, and that these two processes have influenced the evolution of terrestrial plants to such an extent that herbaceous vegetation is now differentiated along a stress/disturbance gradient. This differentiation, according to Grime (1979), is evident in distinct patterns of plant strategies (Grime's term), which are syndromes of certain morphological, physiological and life-history characteristics. Grime (1979) also identifies another process, *competition*, which emerges as a consequence of neighbouring plants making similar demands upon a limited local resource, and has also influenced the evolution of vegetation most strongly in habitats where Grime predicts competition to be most 'intense'.

1.2.2 Definitions of concepts

Grime (1979) defines stress as "the external constraints which limit the rate of dry matter production of all or part of the vegetation" (Grime 1979:21) and includes all environmental factors affecting habitat productivity (biomass per-unit area) such as temperature, water, nutrient availability and light intensity. Thus an unproductive habitat would be deemed a very 'stressful' environment while a productive habitat would be less 'stressful'. Disturbance is defined as "mechanisms which limit the plant biomass by causing its partial or total destruction" (Grime 1979:39) and includes grazing, senescence, fire, wind and frost.

Grime's concept of competition is defined as "the tendency of neighbouring plants to utilize the same quantum of light, ion of a mineral, molecule of water, or volume of space" (Grime 1979:8). Definitions of competition are discussed in sections 1.4.2 and 1.5.2.

The concepts of stress and disturbance have been criticized for lack of precision and the validity of such generalized concepts has been questioned (Grubb 1985). Grime does not offer operational definitions with which to measure the stress or disturbance level of a habitat, though as Grime's concept of stress is effectively an inverse function of productivity, the clarity of the CSR model would benefit from replacing stress with a concept of productivity (Grubb 1985).

1.2.3 CSR strategies

The CSR model assumes that all herbaceous species may be ordinated according to their inherent ability to compete, reproduce and tolerate stress and that there is a direct trade-off between these three abilities. These assumptions lead to the prediction of three primary plant 'strategies' (called Competitors, Ruderals and Stress-Tolerators by Grime) which are syndromes of associated physiological, morphological and life-history traits corresponding to the above abilities and to the three extreme corners of the Stress/Disturbance/Competition template (Grime 1974). Triangular ordination requires this assumed direct trade-off as three dimensions (ability to compete, reproduce and tolerate stress) are reduced to two: the third axis is determined by the other two. Without this assumed trade-off this reduction of dimensions may distort data or result in information loss (Loehle 1988) so any test of the assumed trade-off must measure each ability independently. An important point is that Grime's classification model uses a closed system with axis variables bounded at both ends by minimum and maximum limits (*i.e.* a point lying outside of the triangle is theoretically impossible), yet Grime's tests of the model use open-ended continuous variables (*e.g.* RGR, plant height, seed mass) or discrete classes, *e.g.* life-history and life-form classes (Grime 1979:Fig.19). The CSR model also predicts that *any* stress will result in the same adaptive traits, even though the cause of stress may be very different (*e.g.* low resource availability and high temperature): this prediction has been criticised by Tilman (1987).

1.2.4 Competitive ability

Grime (1979) perceives competitive ability as an *absolute* measure of a species's ability to compete for *all* resources — this derives from the assumption of a positive correlation between an organism's ability to compete for different resources (Grime 1979:16) and a definition of competition based on acquisition. Thus, Grime presumes that species may be ranked by their competitive abilities and predicts the order of ranking will not change along a productivity gradient. Grime uses intrinsic plant traits to construct an index of competitive ability, though use of certain traits, such as RGR_{max}, may not provide an accurate estimation of a plant's overall competitive ability *per se*, but may reflect competitive ability for light more than for soil resources (Newman 1973). The validity of overall competitive ability as a concept depends on whether competitive ability is positively correlated for all resources at all points along a resource gradient: the CSR model demands that this is true (see section 1.4.3). Nevertheless, the choice of trait is likely to influence conclusions concerning the importance and intensity of competition along a stress gradient based on such observations.

1.2.5 Competition intensity

Grime predicts that "competition ... declines in importance and intensity in vegetation with increasing intensities of stress ... and disturbance" (Campbell & Grime 1992:15). Changes in the intensity of competition along a productivity gradient are central to the CSR-strategy theory as many of its predictions and explanations require the intensity of competition to be greatest in undisturbed, productive (and therefore unstressed, sensu Grime) habitats. Using an operational definition based on the absolute reduction in plant performance due to competition (Campbell *et al.* 1991), Campbell and Grime (1992) demonstrated that competition intensity is indeed maximal when nutrient stress is minimal (nutrient availability is maximal), though by using an alternative definition based on the relative reduction in plant performance Campbell and Grime

(1992) also demonstrated that competition intensity does not vary significantly with habitat stress (see section 1.4.4). As Welden and Slauson (1986) have pointed out, intensity and importance of competition are very different ways of describing the effect of competition on populations, while the use of either word is meaningless without an accompanying explicit operational definition (Grace 1991, Peters 1991; see sections 1.4.2 and 1.5.2). Following Welden and Slauson's comments, Grime and Hodgson (1987) predict that competition will be maximally 'intense' *and* 'important' in habitats where competitive pressure has resulted in a monoculture.

1.2.6 Adapted plant traits

Allocation of acquired resources

Although the CSR model does not describe allocation patterns of acquired resources explicitly (*cf.* Tilman's ALLOCATE model), the theory does make some general and tacit assumptions. Based on the premise that plants adapted to a resource-rich habitat possess traits which confer a greater ability to "tap the surplus of resources above and below ground and to maximize dry matter production" (Grime 1979:20), Competitors are predicted to rapidly allocate a high proportion of captured resources to vegetative growth, thereby increasing the plant's capacity for resource acquisition. Competitors are also predicted to allocate resources to perennial structures and storage of 'growth' for the following growing season (Grime *et al.* 1986:7).

In contrast is the allocation 'strategy' of Stress-Tolerators which are predicted to allocate the majority of resources to storage systems, while Ruderals are predicted, over a growing season, to initially allocate mainly to vegetative growth (in a similar way to Competitors) and then mainly to reproductive structures (Grime *et al.* 1986:7).

Allocation between root and shoot

Although it has been widely acknowledged that plants from unproductive habitats tend to have greater root:shoot ratios than plants from productive habitats (Chapin 1980), the CSR model does not include any predictions concerning overall root:shoot ratio, only predictions concerning the relative plasticity between root and shoot allocation (see below).

Plasticity of allocation between root and shoot

A non-constant response to the environment is referred to as a plastic response, one example of which is variation in the root:shoot ratio of a plant species depending on the light and nutrient conditions experienced by the individual. Laboratory experiments prompted the general observation that species from productive habitats (Competitors, sensu Grime) exhibit a greater response, in terms of root:shoot ratio, to environmental changes in nutrient availability than species characteristic of unproductive habitats (Stress-Tolerators) (Rorison 1987). This is consistent with the predictions of the CSR model: a Competitor's response to vegetation-induced 'stress' (resource reduction due to competition) will involve "large and rapid changes in root:shoot ratio, leaf area, and root surface area", while the response of Stress-Tolerators is characterized by less rapid changes in morphology which are "often small in magnitude" (Grime 1979:50).

Grime also asserts that the maximizing of production realised by Competitors is achieved by plastic allocation *within* above- and below-ground structures, *e.g.* root growth is promoted in areas of relatively high nutrient availability: this mechanism has been called 'active foraging' (Grime *et al.* 1986, 1991). Confusingly, Grime also refers to this as a Competitor's response to stress (Grime & Campbell 1991), *i.e.* resource reduction by competition. Thus, plants from productive habitats (Competitors) are predicted to have a high degree of morphological plasticity at the whole plant level (allocation between root and shoot) and at the level of the organ (allocation within root and shoot systems), while plants from unproductive habitats (Stress-Tolerators) are predicted to exhibit a low degree of morphological plasticity.

Growth and storage

The CSR model proposes that the effect of stress as an evolutionary pressure has resulted in differences in RGR (specifically RGR_{max}) between plants of high and low stress habitats: Competitors have higher potential growth rates than Stress-Tolerators. As mentioned above, Competitors are predicted to direct almost all resources acquired into vegetative growth while Stress-Tolerators are predicted to direct relatively more resources into storage, effectively uncoupling growth from resource capture resulting in 'luxury consumption' (where acquisition exceeds demand, Chapin 1980) and reduced potential RGR_{max} (Chapin 1980, Grime 1979; though for an alternative explanation see Garnier 1991, Poorter 1990). As the CSR model relates competitive ability to the *rate* of resource acquisition, a fast growing plant is predicted to be a superior competitor compared to a slow growing plant, all else being equal (*e.g.* initial sizes, per-unit size acquisition rates).

The storage of potential growth is predicted to be advantageous in stressful (unproductive) habitats by insuring the individual plant against temporal variations in resource availability which may otherwise prove lethal (Chapin 1980). Stored growth, in the form of energy and nutrient reserves, may also facilitate high rates of acquisition in special circumstances of resource supply (*e.g.* rapid growth with increased resource availability (resource flush); Grime & Campbell 1991), though this highlights an inconsistency with the CSR classification system as such species could be identified as both Stress-Tolerators (during resource 'stress') and Competitors (during resource flush).

1.3 Resource Ratio hypothesis and R^* theory

1.3.1 Introduction

Tilman (1977, 1980) first developed the Resource Ratio hypothesis and R^* theory of competition during experiments with algal communities in the early 1980's and shortly afterwards developed the theory for terrestrial plants based upon graphical models of competition and the ALLOCATE model of plant competition (Tilman 1982, 1988). This has been the most important contribution to plant competition theory in the last 15 years, and has stimulated much discussion and experiment.

1.3.2 Resource ratio hypothesis

Tilman's Resource Ratio hypothesis provides a possible explanation for the coexistence of directly competing species. This is in contrast to the 'competitive exclusion principle' in that species coexist because they have inherent differences in their resource requirements, specifically the ratio of resources acquired.

The theory assumes that each plant species requires a specific ratio of the supply of resources for optimum performance (Tilman 1982); the supply ratio may be mediated by the environment or by the effect of vegetation upon the environmental availability of the resources. In association with the other assumptions of this theory (mainly that resource availability and vegetation biomass achieve an equilibrium), Tilman (1982) demonstrates that this simple mechanism may permit different species to coexist at equilibrium, but only the same number of species as different resources and the consumption vectors of each species must be unique. Tilman has also proposed that the same mechanism may drive succession due to changes in the relative availability of different resources mediated by resource consumption by the vegetation present (Tilman 1985). Spatial factors are not explicitly considered within this concept, though the introduction of resource heterogeneity (in time or space) is predicted to increase the number of coexisting species (see Tilman 1982, 1985 and section 1.3.6).

1.3.3 R^* theory

For a single limiting resource, Tilman's theory predicts that the species with the lowest R^* value will competitively displace all other species as equilibrium is approached. Tilman defines R^* as "the resource level at which the net rate of population change for a species is zero" (Tilman 1988:20); this is also referred to by Tilman (1982) as the zero net growth isocline of the species. Equilibrium, in this case, occurs when resource supply equals resource consumption and reproduction equals mortality (*i.e.* no net change in the population size or biomass).

Thus, among organisms competing for the same limiting resource, the species with the lowest R^* value is predicted to be the superior competitor and to eventually displace all other species, but only with the assumption that all species have identical colonization abilities (Tilman 1994). Indeed, evidence suggests a trade-off between colonization ability and R^*, which at least in the initial stages of secondary succession contradicts the Resource Ratio hypothesis of succession as colonization ability seems to be responsible for initial dominance rather than competitive ability (Tilman & Wedin 1991*b*).

Tilman also identifies plant traits that are likely to be associated with a low R^* value: low RGR_{max}, longevity of roots and leaves, high efficiency of nutrient use, low maximal nutrient uptake rate and high affinity of nutrient uptake (low I_{max} and low K_m value respectively, *cf.* equation 2.8 in chapter 2) and high investment in defense against herbivory (Tilman 1990).

1.3.4 Competition intensity (CI) along a resource gradient

Tilman's theory makes several predictions concerning the intensity of competition experienced by competitors and habitat productivity, derived from a hypothesis linking above- and below-ground competition intensities to 'total' competition intensity, where competition for above- and below-ground resources occur simultaneously (Wilson & Tilman 1991; see sections 1.4.4 and 1.5.2). Total CI is assumed to represent the combined effects of above- and below-ground competition, and may show no quantitative change along a productivity gradient, but "there may be an important qualitative change, with plants mainly competing for soil resources in unproductive habitats and mainly competing for light in more productive areas" (Wilson & Tilman 1991:1051; see section 3.4). Tilman's ALLOCATE model also predicts that total CI will be independent of habitat productivity, though only competition is considered within the model (Grace 1991).

Wilson and Tilman (1991) propose that the intensity of competition for an above-ground resource (light) is greatest under conditions where there is greatest above-ground biomass (*i.e.* within a productive habitat), while competition for a below-ground resource is more intense than for light under conditions where that resource is most limiting (*i.e.* within an unproductive habitat).

Tilman's predictions, therefore, are that total competition intensity (*i.e.* CI experienced by the subject individual or population in unmanipulated vegetation) will remain constant along a soil resource gradient (Wilson & Tilman 1991, 1993), while along the same gradient, CI for the soil resource will decrease, in the absence of light competition, and CI for light will increase, in the absence of soil resource competition (Wilson & Tilman 1991, 1993).

1.3.5 The ALLOCATE model

The ALLOCATE model of plant competition (Tilman 1988) is principally concerned with allocation patterns of growth between an individual's resource acquiring organs and how an individual's competitive ability may be affected by allocation characteristics. A brief description of this model is included in section 2.1.2. Three important predictions of the model are that:

> (1) a plant with higher allocation to photosynthetic tissue will have a higher RGR_{max} than a plant with lower allocation to photosynthetic tissue all else being equal.
>
> (2) the ability of an individual to compete for a resource is influenced by its ability to allocate biomass to tissues conferring a high acquisition rate of that resource (*e.g.* allocation to either leaf or stem may increase the light intensity experienced by an individual). It follows that there will be a negative correlation between the competitive ability of a species for different resources, due to allocational trade-offs.
>
> (3) allocation patterns of resident vegetation will change along a productivity gradient such that root allocation will be maximal in low productivity habitats, stem allocation will be maximal in high productivity habitats, while leaf allocation will be maximal at a level of intermediate productivity.

Prediction #1 was disputed by Shipley and Peters (1990, 1991) as they found no significant negative correlation between RGR_{max} and root:shoot ratio of 68 herbaceous wetland plants. However, their experiment was subsequently criticised by Poorter and

Lambers (1991) who also objected to the assumption within ALLOCATE that all species have identical per-unit mass photosynthesis and respiration rates. The assumptions of the ALLOCATE model are discussed in section 2.1.2.

1.3.6 Resource heterogeneity in time and space

Further elaboration of Tilman's theory incorporating resource heterogeneity proved necessary in an attempt to explain the well recognized 'apparent' paradox of the number of plant species being much greater than the number of different resources available (Tilman 1988). Spatial factors are not explicitly considered within Tilman's resource ratio or R^* theory, though the introduction of resource heterogeneity (in time or space) is predicted to increase the number of coexisting species (Tilman 1982, 1985, 1994; Tilman & Pacala 1993). Further consideration of space as a resource has led Tilman (1994) to predict that coexistence of competing species requires limiting similarity between allocation patterns (the only interspecific difference between Tilman's simulation species) and "two-way or three-way interspecific trade-offs among competitive ability, colonization ability, and longevity" (Tilman 1994:2; *cf.* CSR model), but "it is uncertain if there must be a trade-off between longevity and competitive ability" (Tilman 1994:11). It is not clear whether such heterogeneity could be considered compatible with the resource and biomass equilibrium requirements of the Resource Ratio and R^* hypotheses, mentioned above.

1.4 Comparison of the theories of Grime and Tilman

1.4.1 Introduction

The major difference between the two theories is their respective treatment of the elements of competition. Grime attempts to distinguish between resource acquisition (the mechanism of competition, *sensu* Grime) and conservation of acquired resources (tolerance, *sensu* Grime), while Tilman's concept of competition includes characteristics of both acquisition and tolerance.

Emphasis

Grime's CSR model is mainly concerned with above-ground effects and response, and attributes great emphasis to competition for light. This is understandable given that Grime assumes competition to be most intense and important in productive, undisturbed habitats, where the majority of competition is likely to be for light (Wilson & Tilman 1991; see section 3.4 on the relative intensity of below- and above-ground competition), for example in the work of Campbell and Grime (1992) neither below-ground biomass or soil processes were quantified. Tilman gives greater emphasis to below-ground processes and they form an integral component of Resource Ratio hypothesis and R^* theory: in most of Tilman's experimental work below-ground mechanisms are consistently investigated.

Temporal framework

The CSR model and the Resource Ratio hypothesis are contained within slightly different temporal frameworks for competition processes. The CSR model describes competition over a single growing period for established plants and while it comments on the immediate effect of vegetation on resource availability (*e.g.* prediction of morphological plasticity in Competitors), the CSR model does not explicitly describe resource availability as a function of vegetation, time or competition. R^* theory predicts the outcome of competition only when vegetation and resource levels have achieved equilibrium: in a natural habitat, resource equilibrium (where the availability of an environmental resource is constant through time) is likely to occur only towards the end of succession, after many generations. Therefore, the competitive outcome is predicted by the CSR model after one or two growing seasons, and after many growing seasons by the R^* theory. As the R^* theory requires equilibrium conditions of resource levels, Tilman's work applies greater emphasis to the overall reduction of resources down to these critical levels and the ability of plants to tolerate such levels. Tilman considers the end result of competition to be largely independent of the rate of reduction. Tilman does, however, emphasize that the short-term effects of competition may be entirely different to the longer-term effects (see Tilman 1988:chapter 6).

Explicitness

Grime has never presented theories in terms of explicit mathematical models, relying instead on verbal description; the majority of Tilman's theory is presented graphically (R^* theory) and mathematically (ALLOCATE model) and as such has not been open to the same misinterpretation as Grime's theories. Formal mathematics may not be the most convenient form of expression, but it does not suffer from the ambiguity associated with language: the CSR model could only benefit if expressed in such a way (Grace 1990).

1.4.2 Competition

Grime has been criticized by Tilman (1987) for restricting competition to only 'Competitors' (by Grime's definition only species occupying productive, undisturbed habitats) implying that 'Stress-Tolerators' do not compete at all, though Grime in reply (Thompson & Grime 1988) pointed out that this was a misinterpretation. Grace (1990) suggested that the extreme strategy identified as the 'Competitor' syndrome by Grime should be re-termed 'Exploiter' to avoid further confusion. Grime elaborated further by proposing that "competition ... declines in importance and intensity in vegetation with increasing stress (constraints on production) and disturbance (destruction of biomass)" (Campbell & Grime 1992:15). Tilman (1988), in contrast, proposed that competition should be experienced by all individuals in all habitats. These differences in opinion as to where and when competition is of ecological significance stem from the differences in definitions, discussed below.

Conceptual definitions of competition

Definitions of plant competition have always proved problematic. Harper (1961) recommended suspension of the use of the word 'competition' because of the ambiguity of currently available definitions and the lack of a universally accepted (and practised) definition, and subsequently introduced yet another term to plant ecology, 'interference', which did not become widely accepted. Over thirty years on and the word 'competition' is still used to describe the indirect influence of plants on each other via a common resource, and various definitions are *still* causing confusion and misinterpretation. Grace (1991) observed that semantics, especially when defining terms and concepts, had caused apparent contradictions between the theories of Grime and Tilman. This is exemplified most by the differences in their respective definitions of competition: Tilman's definition of competition is based on the "net negative relationship between the abundances of competing species that involves both resource capture and tolerance to low resource levels" (Grace 1990), while Grime's definition of competition is based solely on capacity for acquisition of resources (*cf.* definition in section 1.2.2 above). Grime's theory segregates the concept of tolerance from the concept of competition, while Tilman's definition of competition incorporates both. See section 1.5.2 for the conceptual definition of competition used within this thesis.

Operational definitions of competition

Operational definitions of competition assume that competition reduces the 'performance' of an individual or species, compared to the performance achieved in the absence of competition. This is not a complete operational definition: 'performance' requires a definition and is usually based on final yield or growth rate. Two sets of experiments are required to determine if competition is occurring: with and without the suspected source of competition. The lack of distinction between competition at the individual and species level may be important, considering that competition occurs between individuals and not between species *per se*.

The differences in operational definition of competition have been discussed by Grace (1990, 1991, 1993, 1995*a*). Grime used absolute reduction in plant performance by competition as an operational definition of the intensity of competition (Campbell & Grime 1992) while Tilman used the relative reduction of plant performance by competition (Wilson & Tilman 1991, 1993). Grace (1995*a*) concluded that the relative measure (CIr) is a better expression of the intensity of competition than the absolute measure (CIa), CIr not being subject to size related differences between the competing individuals or species.

1.4.3 Mechanisms of competitive success

Competitive success within the CSR model is determined only by ability to acquire resources by individuals; no reference is made regarding the effect of reduction of resources by acquisition. Competitive ability is predicted to be positively correlated with rate of resource acquisition. R^* theory, on the other hand, predicts that competitive success will result from an ability to acquire resources and to tolerate low resource levels induced by acquisition. The tolerance aspect is especially important in the establishment of seedlings to maintain the population (Goldberg 1990). No temporal element is included: R^* is assumed to be independent of the *rate* of acquisition. Hence, R^* theory can only predict the eventually superior competing species. Also, R^* theory cannot predict the outcome if resource levels do not reach R^* values of competing populations or if equilibrium does not occur.

Plant traits conferring 'competitive ability'

Because of the differences in definition of competition between the two theories, predictions linking plant traits to competitive ability are not strictly comparable (Grace 1990, 1991). However, both theories make similar predictions concerning adaptive plant features and high rates of resource acquisition. Grime's 'superior competitor' possesses traits which confer high rates of resource acquisition ('Competitor', *sensu* Grime), whereas Tilman's 'superior competitor' possesses traits which confer tolerance properties ('Stress-Tolerator', *sensu* Grime).

Growth rate

High growth rate is predicted by both Tilman and Grime to confer high rates of resource acquisition, and both predict that high acquisition rates are likely to be favoured above tolerance traits in productive habitats; such plant traits correspond to Grime's Competitor syndrome. High growth rate is necessary for maintenance of high acquisition rates, because of the positive feedback loop between growth and acquisition (see section 3.3.4).

Both theories also predict species from unproductive habitats will have a lower

RGR_{max} than species from productive habitats, but they ascribe slightly different reasons. Grime stipulates that reduction of RGR_{max} is due to the uncoupling of growth from resource acquisition (*i.e.* non-allocation of 'growth' to resource acquiring tissue), while Tilman's explanation centres on resource allocation away from photosynthetic tissue to other organs of resource acquisition or support tissue. These are not contradictory explanations: both assume that allocation of acquired resources away from the growth of photosynthetic material will result in a lower RGR_{max}.

Allocation between root and shoot

While the Resource Ratio hypothesis makes explicit predictions concerning allocation and environment (productivity of habitat negatively correlated with root:shoot ratio of resident species), the CSR model largely ignores allocation between root and shoot other than describing morphological plasticity (see below).

Plasticity

Both theories incorporate plastic response of plants into their framework, but again emphasizing different aspects. The CSR model predicts a high degree of morphological plasticity *within* organs of resource acquisition where beneficial (restricted to Competitors, *i.e.* plants adapted to productive habitats), whereas Tilman's theory predicts plasticity to occur *between* organs of acquisition (*i.e.* root and shoot) and is expected to be advantageous in habitats with high soil resource and light levels (Tilman 1988). These concepts have been referred to as 'active' and 'optimal' foraging respectively (Grime *et al.* 1986, 1991; Iwasa & Roughgarden 1984; Tilman 1982, 1988).

Trade-offs associated with resource acquisition and utilization

Both Grime and Tilman assume a trade-off between a plant's ability to acquire resources and ability to 'tolerate' low resource availability (Grace 1991). This trade-off is more apparent in Grime's theory as it is the major justification for classification between Competitor and Stress- Tolerator plant syndromes. However, quantification of such assumed trade-offs is lacking; it would be interesting to see a plot of R^* against maximal uptake rate.

Competitive abilities for different resources

The CSR model predicts a positive correlation between competitive abilities for different resources, while Resource Ratio and R^* theories predict a negative correlation. Goldberg (1990) argued that both statements could be true given the different definitions of competitive ability, and that size asymmetry or symmetry of competition (which is expected to be different for light and nutrient competition) will affect the sign of the correlation. Thus, if competitive ability is based only on acquisition (Grime's definition) then a positive correlation is expected, if it is based on tolerance as well (Tilman's definition) then a negative correlation is expected. Neither Grime or Tilman present explicit operational definitions of 'competitive ability'.

Summary

The theories of Grime and Tilman both assume a trade-off between the ability to tolerate low resource levels and have high rates of resource acquisition. Hence, both theories predict that individuals with traits conferring tolerance to low resource levels have been selected in unproductive habitats while those with traits conferring high acquisition rates will have been selected in productive habitats; this has support from observations concerning the nutrient uptake capacity of species from unproductive habitats (Chapin 1980). The different emphasis on tolerance (Tilman) and acquisition (Grime) has resulted in different predictions concerning the mechanisms of competition and the 'importance' and intensity of competition in habitats of differing productivity. Tilman's superior competitor (species with lowest R^* value) corresponds to Grime's Stress-Tolerator syndrome. Tilman's theories also identify some traits predicted to be advantageous in a productive and therefore light-limited habitat (*e.g.* high RGR_{max}, tall, high shoot allocation to preempt competition for light under productive conditions, high resource acquisition rates); these traits correspond well to those possessed by Grime's Competitor syndrome.

1.4.4 Competition intensity (CI)

Grime predicts that the intensity of competition for a resource is maximal where that resource is in maximum abundance, and that the intensity is lowest when the resource is scarce (Campbell & Grime 1992). Grime assumes that within a particular habitat the intensity of competition is inversely proportional to the relative intensities of stress and disturbance present in the habitat; consequently Grime expects competition to be most intense for a resource in a habitat where it is in high abundance (minimum stress) and there is no disturbance (Campbell & Grime 1992).

Tilman predicts that overall intensity of competition along a productivity gradient should remain constant regardless of the abundance of the resource, but that the intensity of above- and below-ground resource competition differ in such a way as the net competition intensity remains constant (Wilson & Tilman 1991; see section 1.3.4).

These seemingly contradictory predictions have recently been shown to be compatible when the operational definitions of CI are considered (Grace 1993). Campbell and Grime (1992) used absolute reduction in performance caused by the presence of a competitor as a measure of the intensity of competition (absolute competition intensity, CIa) for the species while Tilman used relative reduction in performance (relative competition intensity, CIr) for the individual (Wilson & Tilman 1991, 1993).

1.5 Conceptual and Operational Definitions

1.5.1 The necessity of rigorous definitions

The confusion arising from different definitions being used for identical terms has detracted from real disagreements between the two theories, but has demanded that a more rigorous approach be taken when using definitions, in particular operational definitions (Grace 1991). In light of this, I present below the following definitions for key terms used in this thesis.

1.5.2 Competition

Conceptual definition

All references made in this thesis to competition are concerned only with direct competition for limiting and essential resources. Processes such as allelopathy, which are sometimes included in definitions of competition but do not mediate an effect via resource availability, are not considered as competitive processes. The conceptual definition of competition within this thesis is defined as

> **the interception of a unit of resource by an individual, where in the absence of that individual the unit of resource would be intercepted by another individual.**

This is *not* the same as 'sharing' of resources (*sensu* Grime's definition of competition, section 1.2.2).

Operational definition

The above definition of competition is not operational as it describes competition for a single individual, so competition must be measured at the species level, where competitive effects at the individual level may be summarized (*i.e.* the effect of competition on the *average* individual, or on the total yield of the species). Thus, the operational definition of competition would be a reduction in species performance (based on total yield, individual number or a function of both, or other factors such as total resource acquired) due to the additional presence of individuals of another species: this is identical to the definition of relative competition intensity proposed by Grace (1993, 1995*a*) and is describe in section 1.5.3 .

However, problems arise from this definition as to how and when performance is measured, and whether a particular measure of performance is suitable for different species. Within the work presented here total biomass yield per-unit time of a species has been used as a measure of the performance of that species, and mean plant size (total yield biomass / number of surviving individuals) per-unit time has been used as a measure of the performance of individuals (see chapter 3). Biomass is an appropriate measure of performance within the context of the simulation model (see chapter 2) for plants with growth coupled to acquired resources (see section 3.3.4), as it is closely linked to the total limiting resource acquired. However, for plants with growth uncoupled from resource acquisition (see section 3.3.4), while total biomass yield is appropriate as an expression of species performance, the use of mean plant size to measure performance may be misleading as any effect of internally stored resources (and not incorporated into biomass) on performance are excluded.

1.5.3 Competition intensity

Following Grace (1993, 1995*a*), the relative reduction in performance is used throughout as a measure of competition intensity, rather than the absolute reduction (CIa) as used by Campbell and Grime (1992) . This is referred to as CIr, and is defined as

$$\textit{relative Competition Intensity (CIr)} = \frac{P_{mono} - P_{mix}}{P_{mono}} \qquad (1.1)$$

where P_{mono} is the performance of the species or individual in the absence of competitors and P_{mix} is the performance of the species or individual is the presence of competitors, following an additive design for the mixture rather than a replacement design (see Snaydon 1991, 1994). This definition is consistent with the conceptual definition of competition stated above in section 1.5.2 . Thus the CIr experienced by species X in competition with species Y (i.e. the CIr exerted by species Y in competition with species X) is given by

$$CIr[X_{XY}] = \frac{P[X_X] - P[X_{XY}]}{P[X_X]} \qquad (1.2)$$

where $P[X_X]$ is the performance of species X in monoculture (species Y absent), $P[X_{XY}]$ is the performance of species X in mixture (species Y present), and the density of individuals in mixture (XY) is sum of the densities of individuals in each monoculture

(*X* and *Y*), *i.e.* additive design (Harper 1977).

As stated above (section 1.5.2), performance may be expressed by a variety of plant characters. Both Reader *et al.* (1994) and Wilson and Tilman (1993) used RGR as a measure of performance, to account for initial differences in size between individuals, though this method does make implicit assumptions about the growth of the individuals, *i.e.* growth assumed to be exponential and not logistic (J.B. Grace, *pers. comm.*). All competing individuals of the simulation runs in chapter 3 have identical initial sizes. Final yield and mean plant size are used for all the CIr calculations made in this thesis, for the reasons given above. These two measures give slightly different interpretations of competition intensity: yield-based CIr measures the CI of the population as a whole, whereas size-base CIr estimates the average CI experienced by the surviving individuals within that population.

1.5.4 Competitive ability

Competitive ability is a useful concept when considering the relative abilities of two individuals to compete for an essential resource but is plagued by the same difficulties in definition as competition. One method of gauging competitive ability between species is to compare performance of a reference species, when each species is grown in competition with the reference species under identical conditions (Gaudet & Keddy 1988). This comparative approach has been combined with the definition of competition given in section 1.5.3 such that the competitive ability of a species is based upon the intensity of competition exerted by that species when in competition with a reference or standard species.

Calculation of competitive ability (CA)

CA of a subject species is determined by the CIr experienced by the reference species (species *a*; see section 3.1.7) when in competition with the subject species: however, the competitive ability of the reference species may change along environmental gradients, so the intra-specific CIr exerted by the reference species under identical environmental condition needs to be included into the calculation of the CA of the subject species. Therefore, the competitive ability of species X is given by the difference between the CIr experienced by species X in competition with species *a* and the CIr experienced by species *a* in competition with itself:

$$\begin{aligned} CA_X &= CIr[a_{aX}] - CIr[a_{aa}] \\ &= \frac{P[a_a] - P[a_{aX}]}{P[a_a]} - \frac{P[a_a] - P[a_{aa}]}{P[a_a]} \\ &= \frac{P[a_{aa}] - P[a_{aX}]}{P[a_a]} \end{aligned} \tag{1.3}$$

where $P[a_{aa}]$ is the performance of species *a* in competition with itself (double density monoculture), $P[a_{aX}]$ is the performance of species *a* in competition with species *X* and $P[a_a]$ is the performance of species *a* in monoculture (single density monoculture). Thus, if $CA_X=0$ then species *X* has identical CA to the reference species, if $CA_X>0$ species *X* has a greater CA than the reference species, and if $CA_X<0$ then species *X* has a lower CA than the reference species under the same environmental conditions (*i.e.* at the same resource availability level).

Chapter 2

An Individual–Based Plant Competition Model

2.1 Introduction

2.1.1 The use of mathematical models in ecology

The role of models within ecology can be either descriptive, predictive or investigative. The value of a predictive model is based solely on its accuracy of prediction; a descriptive model is usually employed to summarize what is known about the system under investigation and as such is limited by current knowledge, while an investigative model is a descriptive model up to a point, beyond which the processes and mechanisms described by the investigative model may not be supported by experimental evidence. The distinction between descriptive and investigative models is not always clear, but this approach to modelling can be extremely profitable by forcing the modeller to examine the precise nature of the interactions, even though little is known of the underlying processes. It is this aspect of modelling that can be most important as it demonstrates the extent of current knowledge and highlights the discrepancies.

Sharpe and Rykiel (1991) identify three distinct objectives for modelling: reality (the explicitness of causal or underlying processes), generality (the robustness of the model under varying situations) and precision (the accuracy of measurement or prediction). They suggest that any model is limited by approach and objective, and that compromise between the three above objectives determines the model type.

A model may describe processes in a phenomenological or a mechanistic manner (or a combination of both). There is growing concern within the field of ecology that phenomenological models fail to simulate processes to the same degree of accuracy or realism exhibited by functionally explicit mechanistic models. This is exemplified by the work of Armstrong (1993) which demonstrated the advantages of a mechanistic approach (pixel-based forest growth simulation) over the orthodox phenomenological approach (index-based forest growth simulation).

2.1.2 Plant competition models

The Lotka-Volterra competition equations

Based on the logistic equation, these equations are the 'building blocks' of several plant competition models; however the underlying assumptions concerning competitive interactions have been criticised (Tilman 1990). Each species is assigned competition coefficients, one for each other modelled species, which describe the competitive effect which that species has upon the appropriate competing species, given certain conditions. The coefficients are assumed to be constant through time, are specific only for a particular suite of environmental conditions, and it is assumed that individuals of both species described are of constant size. Thus, unless the coefficients for a particular suite of abiotic and biotic conditions are known explicitly from experimental study, the Lotka-Volterra competition model is ineffective. Therefore, to model competition along an environmental gradient using the Lotka-Volterra approach requires a complete experimentally determined knowledge of the competitive effect of each species on every other species at each point along the gradient, while to model competition along two or more simultaneous environmental gradients would require a prohibitive number of experiments.

The Aikman/Benjamin model of light competition between species.

Aikman and Benjamin (1994) presented a model of light competition between species, where growth rate is a function of the total light intercepted. In this model, individuals are not modelled *per se*, but the average individual for each species is described; all individuals have identical height and leaf area index, and equal spacing between individuals is assumed. In a slightly modified version of this model, the identical height assumption is relaxed, and different species (essentially cohorts of individuals) may differ in foliage height, though all individuals within that cohort are identical (Benjamin & Aikman 1995). While not strictly spatially explicit, the vertical (height) axis is modelled in some detail to describe the amount of light penetrating the canopy to reach the combined crown area of a species. One important feature of this model is that with sufficiently low biomass and average plant size, or at very low densities, no light competition is predicted to occur (*i.e.* open canopy structure). However, no competition for space or below-ground effects are included within the model, and while the model may be used to predict yields in mixtures using species specific parameter values gleaned from monoculture experiments (Benjamin & Aikman 1995), it cannot predict the outcome of competition in habitats of variable productivity (*e.g.* along a nutrient gradient) without extensive supporting experiments.

Baldwin's model of root competition for nutrients

Baldwin (1976) provided the first mechanistic model of individual plant competition. This model is primarily concerned with nutrient movement through the intervening soil between two individual plants. Movement is dependent upon several factors such as soil properties, nutrient uptake rates of the two plants, properties of the nutrient (diffusion and mass flow), and respective root mass and root characteristics. Included in his model are several features which have since become standard properties of individual plant growth models and are often incorporated into most physiological models of plant growth. Among these are the use of internal plant 'pools' of free nitrogen and soluble carbohydrate, as well as plastic allocation between root and shoot based on the relative quantities of the nitrogen and carbohydrate pools. Although the system modelled by Baldwin only included one-dimension (vertical) for water and nutrient flow (between two competing individuals), he was able to present a sensitivity analysis for various traits that could affect a plant's competitive ability. This paper of Baldwin (1976) has been overlooked in many plant competition studies.

Tilman's ALLOCATE model of plant population competition

The ALLOCATE model simulates competing populations over time: each species differs in the allocation pattern employed between individuals' root, stem and leaf. This model was developed by David Tilman to investigate how morphology (and to some extent physiology) can affect species' fitness and competitive ability (Tilman 1988). The vertical distribution of light and the net availability of a single soil nutrient (Tilman does not explicitly identify this resource) are included; the distribution being affected by the total biomass present in each vertical class or layer. The soil resource availability is determined by supply rate and the net uptake rate of all individuals. Each species is not comprised of individuals *per se*, but cohorts of individuals which germinate at the same time. Each cohort has various descriptive variables associated with it (root, leaf and stem biomass per individual; number of individuals within the cohort; height of all individuals within cohort; death rate). Species specific per-unit biomass characteristics are included for photosynthesis, soil resource uptake characteristics, and respiration (further differentiated into rates for root, stem and leaf).

The main emphasis of this model is the species specific allocation patterns of new biomass (growth) between root, stem and leaf, and the effect of competition on growth. Tilman's model demonstrates that sufficiently different allocation patterns can produce species differentiation along a light/soil resource gradient (given the restrictions of his assumptions). All individuals experience identical soil resource availability (assuming homogenous soil resource distribution) but taller individuals *always* shade smaller individuals: the model assumes that all leaves are formed in a single layer at the maximum height of the plant (see section 1.3 for summary of Tilman's concepts and theory).

2.1.3 Individual-based versus species-based community models

There has been relatively little work relating the community to its component individuals compared to the substantial literature relating the community to component species (see section 1.2 above). These species-based models invariably describe the species as a population composed entirely of identical individuals experiencing identical environmental conditions with little or no concession for variation (phenotypic or genetic) between individuals. In effect this is a phenomenological versus mechanistic argument: a model is either phenomenological or mechanistic depending on the level of complexity simulated. By ignoring the core mechanisms operating at the individual level species-based models may be fundamentally flawed. The theories of Grime and Tilman both function mainly at the species level, and potentially neglect processes operating upon individuals that could prove critical at community level. Consolidation of the individual with the species and the resulting community may be vital for theory maturation and development.

2.1.4 Modelling competition processes and associated complications

The predominant problem of developing a resource competition model is to realistically simulate competition for the resources between *individuals*. The conceptual definition of competition presented in section 1.5.2 is equally applicable to both nutrient and light competition, and demands a mechanistic approach to competition. Using coefficients to summarize the competitive effect of one species on another (the Lotka-Volterra equations, for example) does not describe this process, and by treating the competitive result from a particular suite of abiotic and biotic conditions as a potentially unique phenomena, has no predictive capacity.

The real world is extremely heterogenous and this is bound to have important consequences for competitive interactions at the individual scale as well as at the species scale. The only way to realistically model an individual-based competition process is to model individuals and their interactions, be they direct or indirect. So rather than having a number of operations per species describing competition, as most competition models operate, a series of operations are performed for each of the individuals present, and the performance of the species is a consequence of its component individuals. Neighbourhood models developed from a need to model sessile organisms *as* sessile organisms rather than the generalised organisms described by the Lotka-Volterra equations and variants. Czárán and Bartha (1992) classified neighbourhood models into three groups:

(a) *Discrete-space models* (also known as *cellular automata*)

These models divide the domain into discrete *cells* usually as a simple square grid, although a hexagonal grid may be used which eliminates the problems associated with unequal distance between neighbouring cells in a regular square grid. Almost all of these models limit the size of the cells to the size of one individual (for an exception see van Tongeren & Prentice 1986) and the status of the cell (occupancy, local resource levels, etc.) is determined by rules of cell interaction (see Czárán & Bartha 1992 for review; see Colasanti & Grime 1993, Silvertown *et al.* 1992 for examples). No cell is in isolation and the status of a cell depends on the status of neighbouring cells as well as its own. Certain competition processes may be modelled, soil nutrient competition for example, but not light competition as physical overlap between individuals (physical intermingling or overlapping areas of resource acquisition) are prohibited by the one individual per cell rule. The assumption that only one individual may occupy a cell at any one time, and consequently may only acquire resources from that cell alone, also implies that all individuals have a maximum size and a local limit to their area of resource acquisition regardless of the size and extension of the individual.

(b) *Distance models*

Distance models again describe a community over a domain using coordinates to represent the centre point of each individual plant but represent space as a continuous variable. Zones of influence or areas of resource acquisition are represented as a circles centred on individuals. If neighbouring circles overlap, these zones of resource acquisition also overlap, and the resources delineated by the overlapped area are shared by the (overlapping) individuals proportional to biomass - this is most applicable to light competition (Bella 1971, Lepš & Kindlmann 1987). There are several weaknesses within the inherent assumptions of this kind of model. Firstly is the assumption that there is a definite edge of the resource acquisition zone. Secondly, because space is considered continuously and not discretely, it would be extremely difficult to model a mobile resource (such as nitrogen) throughout the system as a continuous variable; it would be easier to handle spatially discrete variables. Thirdly, growth is assumed to be radially symmetric, which is biologically unrealistic (recently demonstrated by Mou *et al.* 1995). The competitive element of the model, sharing of resources within an overlap, satisfies the working competition definition, but does not lend itself to mechanistic expansion/detailing.

(c) *Tessellation models*

Individuals are positioned on a continuous plane and, like distance models, tessellation models calculate an area around an individual that represents the degree of influence which that individual exerts upon the environment. However the similarity ends there, as the areas is calculated in a very different way. The tessellation model uses an algorithm (Dirichlet or Voronoi algorithms are the most commonly used) to construct a polygonal area that is *not* radially symmetric around the individual's position. The size and shape of the polygon depends on the individual's characteristics and status as well as those of its immediate neighbours. It is hard to judge the accuracy or the value of tessellation models to describe the effect of competition, given that accurate measurement of competitive effects could be achieved. From a mechanistic perspective tessellation models fail to address the core processes, utilizing coefficients to emulate competitive effects of one individual upon another.

All of these models have a common thread: reducing a three-dimensional system to two-dimensions. The justification for this has principally been ease of modelling and simplicity of calculation. But this justification is not as valid as it used to be before the (continuing) proliferation of rapid computer programs as tools for simulation studies. The three-dimensional structure of plants had been considered by Ford and Diggle

(1981) but they too assumed radial symmetry. Recently, however, there have been a few attempts to simulate plants and plant growth in "real-space"; an admirable paper by Sorrensen-Cothern *et al.* (1993) describes a model of three-dimensional competition and growth including allocation plasticity and resulting asymmetric growth. Only if plants are modelled as three-dimensional forms can competition processes (in particular shading) and asymmetric growth, an important aspect when considering competition, be mechanistically represented. Asymmetric growth of resource capturing organs means that resource acquisition and depletion will also be asymmetric. Hence, resources must be modelled spatially and temporally and to at least the same spatial resolution as the plant form. If light and soil nutrients are to be modelled then their relationship, from the viewpoint of the plant, also needs to be considered. Thus, the criteria necessary for a mechanistic competition model are:

(a) inclusion of individuals,
(b) three-dimensional space to allow for mechanistic description of competition processes between individuals,
(c) plasticity and asymmetric growth,
(d) explicit description of resource distribution, acquisition and allocation.

There is a balance to be struck between mechanistic detail of a model and its general applicability: too much detail and the model is limited by the unwieldy number of environmental and physiological variables that must be enlisted even though its realism may be accurate; too little detail and the model's explanatory and descriptive power is lost. Also, there is a problem of hierarchy: "mechanism at one level is empiricism at another" (Sharpe & Rykiel 1991). In the context of modelling resource-competition the best tactic would seem to be to limit the mechanistic detail to the process of competition; that is criteria (a) to (d) above. Beyond this level any further mechanistic detail would detract from the importance of these processes and the generality of the model would be compromised.

2.1.5 The aims of proposed model

The model described below has been developed to investigate some of the discrepancies and conflicting arguments arising from the theories of Grime and Tilman (see Chapter 1). The original intention was to model plant competition for resources in a mechanistic manner at the individual scale such that the resulting community would be determined by competition-associated processes and not generalized species-based phenomena, *i.e.* the community composition is determined by interactions between individuals rather than between species.

The advantage of such a model is that any species (differing in traits or size) can be employed and the eventual outcome determined during the course of the simulation by mechanistic processes based on the characteristics of the resource(s), the individual plant characteristics *and* the interaction between resource and plant. Once constructed such a model could be used to investigate various issues concerning competition, resources, plant traits and plant 'strategies' (plant trait syndromes) of resource utilisation.

2.2 Description of the model

2.2.1 Introduction to the model

This model simulates above- and below-ground resource acquisition and growth of herbaceous individuals over a single growing season. As such the model is restricted to simulating either annuals or first-year perennials within a gap.

In this model, competition for light and a single nutrient are considered simultaneously; the soil resources modelled are nitrogen and phosphorus, although the model also includes water uptake and distribution through the soil in order to model nutrient mass flow effects. While the model does not describe simultaneous nitrogen and phosphorus competition, it could be expanded to do so. This model describes components in an abstracted manner. For example, the physical forms of the nutrients (*e.g.* nitrogen generally exists as either nitrate or ammonium) are not included within the model *per se*, only the absolute abundance of the element itself. Likewise, carbohydrates produced from photosynthesis are represented only by the mass of carbon. Once resource and carbon are assimilated into plant material, it is the biomass of the material that is described, unless the plant material begins decomposition.

The environment of the model is divided into two sections, above-ground and below-ground. Each section is spatially constructed from a three-dimensional array of cells; an individual plant is represented by the occupancy of many such cells. Each cell represents 0.000125 m^3: there are 8000 cells per cubic metre. Above-ground cells are referred to as *ABOVEcells*, below-ground cells as *SOILcells*. Each cell is located in three-dimensional space by a series of three coordinates: LAYER, x and y. LAYER represents the height (*ABOVEcells*) or the depth (*SOILcells*), while x and y describe the lateral position of a cell within that LAYER. Each occupied cell above- and below-ground contains a constant amount of plant material that cannot be exceeded. This constant is named *CELLmass* and, in conjunction with initial nutrient levels and light levels, effectively controls the spatial resolution of the model. The biomass of an individual plant is comprised of *ROOTbiomass* and *SHOOTbiomass*, the mass of the roots and shoot systems respectively.

A list of all variables used in the model appears in Table 2.1 at the end of this chapter.

2.2.2 Resource-plant overview

A simple plant growth scheme may be represented as three discrete processes:

(a) resource acquisition,
(b) resource assimilation,
(c) resource allocation to growth.

Although these processes may be discrete they are far from independent. Assimilation of resources is dependent on resource levels previously acquired. Likewise, allocation of new growth can be determined by the degree of acquisition and assimilation. Perhaps

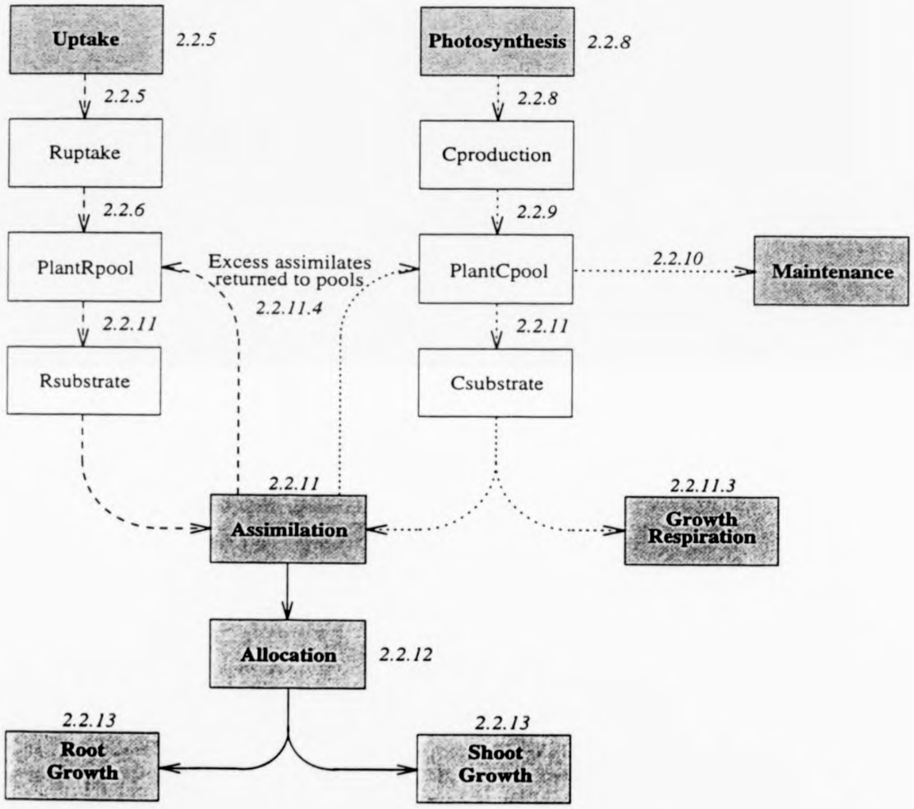


Figure 2.1

Conceptual flow diagram of the pathways of resource and carbon within an indiviual plant within the model. Executional order of processes progresses from top to bottom. The pathway of resource is represented by dashed lines; carbon by dotted lines; and assimilated resource and carbon (fresh biomass) is represented by solid lines. Filled boxes respresent plant processes; clear boxes represent plant variables. Figures in italics refer to relevent section in text.

the most important connection is the potential for positive feedback between allocation to resource acquiring organs and resource acquisition (see Chapter 3).

> **Unless otherwise stated, any further references to *resource(s)* within this chapter refer to the soil nutrient (may be either nitrogen or phosphorus), while references to *carbon* refer to the carbon products of photosynthesis.**

2.2.3 Summary of environmental and plant processes

The model comprises of any number of individual plants occupying multicellular three-dimensional space. Each individual plant begins life occupying one cell above- and below-ground at its appropriate position. Occupancy of above-ground cells enables the plant to photosynthesize carbon products (C), depending on the light status of occupied cells and the individual's species, which accumulate in the individual's internal carbon storage pool (*Cpool*). Similarly, occupied below-ground cells may acquire soil resources (R), depending on species and resource status of below-ground cells, which are stored in an internal reservoir (*Rpool*). Shading or local resource depletion act to reduce the production of carbon and acquisition of soil resource, respectively. Maintenance of occupied cells is reflected in a carbon levy (size based) on the individual's *Cpool*; if *Cpool* contains insufficient C to satisfy maintenance costs then the plant is assumed to die and relinquishes its occupation of cells. Some or all (depending on species' growth characteristics) of the plant's internal C and R are then directed towards assimilation and then growth; one unit mass of new biomass contains a constant proportion of C and R. Partitioning of growth between root and shoot depends on the species' allocation characteristics and possibly (with plastic allocation patterns) plant *Cpool* and *Rpool* status. Growth is manifested as the occupancy of currently unoccupied cells and requires the investment of a quantity of biomass per cell. As a plant grows it occupies more cells; the more cells the plant occupies the larger the surface area for *potential* resource absorption. Spatially asymmetric growth is possible within this model: the cell growth routine, described in section 2.2.13, will always promote new growth into an area of relatively high resource level. The growth routine includes a stochastic element in determining which cell(s) a plant may occupy through growth. At each time iteration, the following occurs:

(a) Resource movement in the soil,
(b) Resource uptake by roots,
(c) Light interception and photosynthesis of carbon products by shoots,
(d) Pooling of acquired soil resource and carbon into respective pools,
(e) Maintenance of existing biomass,
(f) Assimilation of R and C substrate,
(g) Partitioning of new growth between root and shoot,
(h) Root and shoot growth,
(i) Return of resource (contained in dead tissues) to the soil.

Environmental processes are (a) and (i). See Figure 2.1 for resource and carbon processing within a plant (includes plant mechanisms b,c,d,e,f,g and h).

2.2.4 Resource movement in the soil

Resource movement in the soil is determined by the movement properties of the particular resource modelled (nitrogen and phosphorus are both modelled), and the current distribution of resource throughout the soil volume (after acquisition by plants). The soil is constructed of a three-dimensional array of cells, each of which retains a value of resource (mg) contained within that cell; resource movement is determined locally (*i.e.* for a single cell and its immediate neighbours). Movement is allowed between neighbouring cells (but not diagonally adjacent cells), so with a three-dimensional arrangement a single cell in the centre of the modelled soil will have six neighbouring cells: four at the same LAYER, one immediately above and one immediately below. The cells representing the edge of modelled space (*e.g.* cells at the soil surface) have slightly different rules governing resource movement: see section 2.2.4.2. The principles of diffusion within the model for a two-dimensional plane are described first of all (section 2.2.4.1), and then the conversion to three-dimensions is demonstrated (2.2.4.3). Finally, mass flow is introduced (2.2.4.4) and included into the overall movement equation (2.2.4.5).

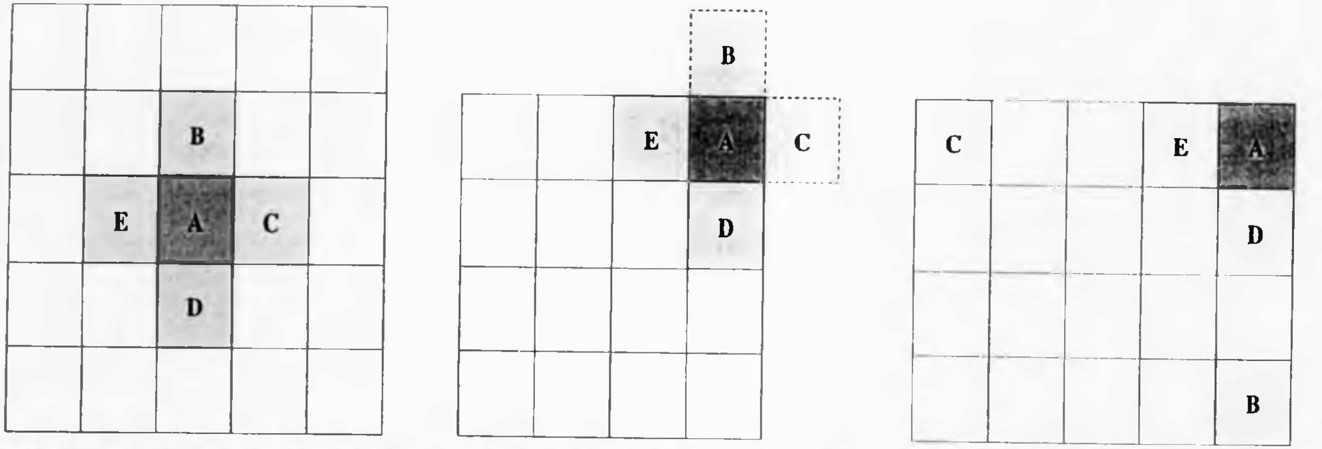
2.2.4.1 Diffusion within a two-dimensional plane

Each cell is assigned a resource value, *SoilR*, and it is a cell's own *SoilR* value and the *SoilR* values of neighbouring cells that determine the new *SoilR* value for that cell after one iteration of diffusion. Diffusion in this model is based on the principle that the resource within a cell is shared with appropriate portions of neighbouring cells' resource, thus the equations below (2.1, 2.2 and 2.3) are not true diffusion equations but approximations based on the iterative averaging of neighbouring cell portions.

In Figure 2.2a the central cell, cell X, has neighbouring cells A, B, C and D. The amount of resource in cell X, $SoilR_X$, is partitioned into n parts, where n is the number of neighbouring cells (in this case, n = 4). Each of these portions corresponds to a similar portion of each neighbour. The simplest diffusion term is given by

$$\begin{aligned} SoilR_X' &= SoilR_X + \frac{SoilR_X + SoilR_A}{2nd} + \frac{SoilR_X + SoilR_B}{2nd} + \frac{SoilR_X + SoilR_C}{2nd} + \frac{SoilR_X + SoilR_D}{2nd} \\ &= SoilR_X + \frac{n\,SoilR_X + SoilR_A + SoilR_B + SoilR_C + SoilR_D}{2nd} \end{aligned} \tag{2.1}$$

where $SoilR_X'$ is the new resource value for cell X *after* resource movement; $SoilR_A$, $SoilR_B$, $SoilR_C$ and $SoilR_D$ are the soil resource values for the neighbouring cells A, B, C and D; n is the number of neighbours (in this case four); d is a diffusion coefficient determining the speed of diffusion, where low values of d confer rapid diffusion between adjacent cells while high values confer slow diffusion. This is not a true diffusion equation, but simulates diffusion by the iterative averaging of neighbouring cell portions. Figure 2.3 shows an example of this procedure; in this example this averaging is only allowed between the central cell and immediate neighbouring cells.



(a) Neighbouring cells of cell A with which diffusion may occur. Cell A is not a border cell and therefore has a full compliment (n=4) of neighbouring cells.

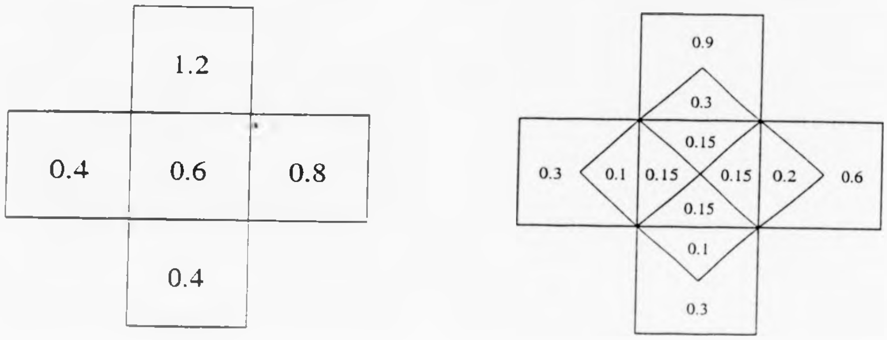
(b) Here, cell A is an edge cell within a 'pot' design. It has normal neighbours D and E, and 'ghost' cells B and C (n=4).

(c) Here, cell A is an edge cell within a 'torus' design. It has normal neighbours D and E but because edges are 'wrapped' round to opposite side, A also has cells B and C as neighbours (n=4).

Figure 2.2 The identifiation of neighbouring cells around (a) non-border cells, (b) border cells with 'pot' design, and (c) border cells with 'torus' design.

(a) SoilR values at time=T

(b) Partitioned SoilR values



(c) Redistributed partitioned values

(d) SoilR values at time=T+1

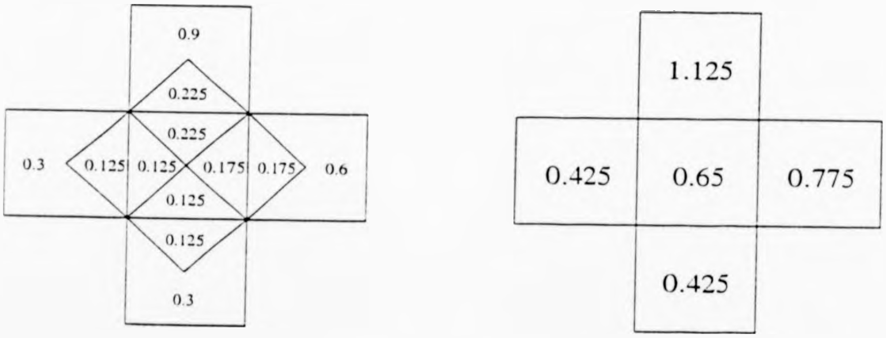


Figure 2.3

An example of diffusion of SoilR between five adjacent cells. The initial SoilR values of each cell (a) are partitioned according to the presence of neighbouring cells (b). Adjacent cells then "share" the appropriate portions of SoilR (c) and the new values of each cell are calculated (d). In this example d (diffusion coefficient) = 1.0 .

The flux of resource by this iterative averaging of resource between cell X and a neighbour, for example cell B) is therefore

$$Dflux_{X,B} = \frac{SoilR_B - SoilR_X}{2nd} \tag{2.2}$$

where $Dflux_{X,B}$ is the flux of resource into cell X from cell B. If $Dflux_{X,B} < 0$ then resource is moving out of cell X, if $Dflux_{X,B} > 0$ then resource movement is into cell X.

2.2.4.2 Border cells as special cases

Edge effects: the case for a wrap-round/torus spatial system

One of the dilemmas encountered by spatial modellers is the problem of edge effects, the term given when the outcome of spatial processes are affected by the presence of a spatial boundary. These occur when a spatial environment is modelled as a closed structure, *i.e.* the physical edges of the modelled space are defined and the volume or surface contained within these limits is finite. For example, soil resource may diffuse throughout the modelled soil, but a special case needs to be constructed for the space around an edge to avoid 'leakage' of resource from the system. With a special set of rules governing diffusion at the periphery of the spatial system, the edge would act as a barrier, and the soil system would be analogous to soil in a pot experiment. One possible edge effect with a pot design may be a feedback from the edge resulting in waves of resource running through the soil emanating from the soil boundaries. Alternatively, finite volume for the plants to occupy and grow into is likely to prejudice the growth of plants occupying sites near or at the edges. The danger is that the dynamics of the modelled system may reflect the influence of the edges present rather than the dynamics of the subject that is actually being modelled. One way to avoid this (though it does create some further problems of its own) is to model space as though the far edges of a plane are linked, just as though they are normal neighbours. This emulates an infinite 'field' of the modelled system thus eliminating edge effects, and is referred to as a 'wrap-round' or 'torus' design of modelled space.

For cells on the edge of modelled space, a modified diffusion function is required as border cells may have less than *n* neighbours (Figure 2.2b) depending upon spatial design. One must be careful, if the total soil resource level is to remain intact (*i.e.* no leakage or creation of soil resource). In the case of the '*pot*' design, border cells have their 'missing' neighbours created with identical *SoilR* values (called '*ghost*' cells) and the diffusion function is performed as equation 2.1 (Figure 2.2b). Because these ghost cells contain identical *SoilR* values to the border cell there is no net movement of resource between these cells, and the true soil resource level remains intact. For '*torus*' designs (see above), the missing neighbours of a border cell are assumed to be cells on the opposite side of the soil space (Figure 2.2c); this effectively gives a 'wrap-around' soil system and again preserves the total soil resource level.

2.2.4.3 Conversion to three-dimensions

To convert to three dimensions only requires that $n = 6$ (four neighbours on same LAYER, one immediately above, one immediately below) and the extension of equation 2.1 to

$$SoilR_X^{/} = SoilR_X + \frac{nSoilR_X + SoilR_A + SoilR_B + SoilR_C + SoilR_D + SoilR_E + SoilR_F}{2nd} \quad (2.3)$$

where $SoilR_E$ and $SoilR_F$ are the soil resource values for cells E and F, the cells immediately above and below cellX. The flux term between cell X and each neighbour retains the same formula as equation 2.2.

2.2.4.4 Mass flow

Water flow

For simplicity, the movement of water is considered in an identical manner to resource diffusion and water flux in/out of cells is governed by an equation similar to equation 2.2: water moves down a gradient generated by water uptake from a cell with high water content to a cell with lower water content (Darcy's Law, Nye & Tinker 1977). For simplicitiy, gravity is assumed not to affect the movement of water, and this may have important consequences for nutrient distribution and consequently, uptake by model plants (see section 5.1). The net flux of water from cell X into a neighbouring cell, for example cell B, is

$$Wflux_{X,B} = \frac{SoilW_B - SoilW_X}{2nWd} \tag{2.4}$$

where $Wflux_{X,B}$ is the flux of water into cell X from cell B, $SoilW_B$ and $SoilW_X$ are the amount (mg) of water present in cells B and X respectively, and Wd is a water movement coefficient equivalent to d in equation 2.2.

Mass flow movement of resource

Movement of resource by mass flow between adjacent cells is determined only by the direction of water movement between the same cells: the model does not include a link between rate of water flow and mass flow of soil nutrients. The algorithm below governs the mass flow of resource; this is an example between cell X and cell B.

$$\begin{array}{llll} \text{if} & Wflux_{X,B} > 0 & \text{then} & MFflux_{X,B} = SoilR_B / n \\ \text{if} & Wflux_{X,B} < 0 & \text{then} & MFflux_{X,B} = -SoilR_X / n \\ \text{if} & Wflux_{X,B} = 0 & \text{then} & MFflux_{X,B} = 0 \end{array} \tag{2.5}$$

where $MFflux_{X,B}$ is the potential flux of resource by mass flow into cell X from cell B (mg R), if all resource present moves by mass flow.

2.2.4.5 Incorporating diffusion and mass flow

The resource within a cell is partitioned between the proportion of resource which moves via diffusion (a) and the proportion which moves via mass flow (b) (Barber 1962, Marschner 1986). The values of these proportions contribute to the supply properties of the resource, as they determine whether the majority of movement is by diffusion (either within the soil solution or on the surface of soil particles) or mass flow (see Table 3.1 in chapter 3, and Appendix for values assigned for nitrogen and phosphorus simulations). Thus, the net movement of resource between two cells, for example into cell X from cell B, is given by

$$NETflux_{X,B} = (a \times Dflux_{X,B}) + (b \times MFflux_{X,B}) \qquad (2.6)$$

Finally, the new value for cell X the sum of all fluxes into X, given by

$$SoilR_X' = NETflux_{X,A} + NETflux_{X,B} + NETflux_{X,C} + NETflux_{X,D} + NETflux_{X,E} + NETflux_{X,F} \qquad (2.7)$$

where $SoilR_X'$ is the new value of resource in cell X after one time unit of diffusion and mass flow; $NETflux_{X,A}$, $NETflux_{X,B}$, $NETflux_{X,C}$, $NETflux_{X,D}$, $NETflux_{X,E}$ and $NETflux_{X,F}$ are the net movement fluxes from cells A, B, C, D, E and F respectively into cell X.

2.2.5 Resource uptake by plant roots

Uptake of resource only occurs at the root surface (*ie.* only in *SOILcells* occupied by healthy plants) and influx to the root is dependent upon the concentration of the soil immediately in contact with the root surface (the SoilR value of the *SOILcell*) as well as the specific plant uptake characteristics (per-unit biomass properties). The influx of resource into the root has been modelled using the Michaelis-Menten equation (Barley 1970, Novoa & Loomis 1981, Marschner 1986); no toxic effect of very high availability of soil resource are included in this model, and uptake is assumed to occur even at very low resource concentrations. The sequence of calculations for each occupied *SOILcell* is as follows:

$$celluptake = ROOTmass_X \times \frac{Imax \times SoilR_X}{Km + SoilR_X} \qquad (2.8)$$

where $SoilR_X$ is the *SoilR* level of the relevant *SOILcell*, in this case cell X; *celluptake* is the uptake rate for cell X (mg R d^{-1}); $ROOTmass_X$ is the amount of biomass present in cell X (mg root biomass; see below); *Imax* is the maximum rate of influx per-unit mass of root biomass (mg R mg^{-1} root biomass d^{-1}); and *Km* is the concentration at which *celluptake* = *Imax*/2 (mg R per *SOILcell*).

Imax and *Km* are assumed to be species specific and constant throughout the plant's life, although evidence exists that *Imax* may vary with plant age (Youngdahl *et al.* 1982) and nutrient availability (Chapin 1980). If the total root biomass of the plant is less than *CELLmass*, then *ROOTmass* is set to the *ROOTbiomass* of the occupying plant and the *celluptake* value is reduced proportionally; else *ROOTmass* = *CELLmass*. $ROOTbiomass_i$ is the total biomass of the root system of plant i.

The cumulative soil resource absorbed by the root cells of an individual plant in one day (mg R d^{-1}) is given by $Ruptake_i$.

2.2.5.1 Water uptake

Daily transpiration rate is assumed to be equal throughout the plant's shoot system and, for simplicity, independent of irradiance received or photosynthetic activety, hence

$$transpiration_i = SHOOTbiomass_i \times TranspirationRATE \qquad (2.9)$$

where $transpiration_i$ is the total mass of water transpired by plant i in one day (mg water d^{-1}), $SHOOTbiomass_i$ is the total mass of the shoot system of plant i (mg biomass), and *TranspirationRATE* is the daily per-unit shoot mass rate of transpiration (mg water mg^{-1} biomass d^{-1}). Water supply is assumed to be non-limiting to plant health and growth, therefore the total daily water uptake approximates the total water transpirated daily (Slatyer 1967, Habib & Lafolie 1991):

$$WaterUptake_i = \frac{transpiration_i}{ROOTbiomass_i} \qquad (2.10)$$

where $WaterUptake_i$ is the per-unit root biomass rate of water uptake by plant i in one day (mg water mg^{-1} root biomass d^{-1}). This provides sufficient detail of water uptake for water gradients to be generated in the soil system for mass flow calculation (see section 2.2.4.4).

2.2.6 Resource pooling

Following Baldwin (1976), all resource absorbed by individual roots cells is pooled into an internal plant resource storage pool, *Rpool*, which acts as a reservoir supplying resource substrate for assimilation:

$$Rpool_i = Rpool_i' + Ruptake_i \qquad (2.11)$$

where $Rpool_i'$ is the *Rpool* of plant i from the previous day.

2.2.7 Shading and calculation of light level of *ABOVEcells*

Light is assumed to be direct beam; diffuse beam light is not considered in this model. The direction of light is vertical (azimuth angle of 0°) and is constant. Each occupied *ABOVEcell* intercepts a fraction of the light available at that position. The light level reaching a cell, $Light_X$, is calculated from initial light level, *sunLIGHT*, and decreases according to the Beer-Lambert Law (Thornley & Johnson 1990, Sorrensen-Cothern *et al.* 1993) with interception by vertically aligned occupied *ABOVEcells*:

$$P_{transmittance} = e^{(-f \times LAD_p)} \qquad (2.12)$$

where $P_{transmittance}$ is the probability or rate of transmittance of light through an *ABOVEcell*, f is the fraction of leaf area projected on a plane normal to the beam (unitless), LAD_p is the Leaf Area Density ($m^2\ m^{-3}$) of the occupying plant p. f may be species-specific and may also vary with foliage height but is assumed to be constant (f=1) for all occupied *ABOVEcells* and plants in this model. If an *ABOVEcell* is unoccupied then for that cell LAD = 0. LAD is species-specific, and assumed to be constant through the canopy of a plant.

It follows from equation 2.12 that the amount of light reaching $ABOVEcell_X$ is determined by calculating the reduction in the light level caused by each occupied cell (above the cell) in turn:

$$Light_X = sunLIGHT - \sum_{l=LAYER_X+1}^{MAXheight} P_{transmittance}[l] \qquad (2.13)$$

where *sunLIGHT* is the level of irradiance entering the system from above (constant; unitless); l denotes the cell height; *MAXheight* is the number of vertical cell layers constructing *ABOVEcell* (integer; unitless); *LAYER* is the vertical level of cell X (integer; unitless); and $P_{transmittance}[l]$ is the probability or rate of transmittance of light through $ABOVEcell_l$.

2.2.8 Photosynthesis

At each iteration, each occupied *ABOVEcell* intercepts light and fixes carbon by photosynthesis. Light is assumed to be the only limiting factor for photosynthesis (water, CO_2 and nutrient availability are considered not to affect photosynthesis). The amount of light reaching an *ABOVEcell* is given by the variable *Light* (see section 2.2.7 above), and the amount intercepted depends on the area of leaf within that *ABOVEcell*, as determined by the leaf area density (LAD, cm^2 leaf cm^{-3} space). Following Thornley and Johnson (1990), the relationship between irradiance and photosynthetic rate is assumed to be a rectangular hyperbola. The following equations occur for each *ABOVEcell* occupied by plant i; in this example cell X is occupied by plant i:

$$LIGHTintercepted_X = light_X \times LAD_i \qquad (2.14)$$

$$PhotosyntheticRATE_X = \frac{LIGHTintercepted_X \times Kb_i}{LIGHTintercepted_X + Ka_i} \qquad (2.15)$$

$$Photosynthate_X = SHOOTmass_X \times PhotosytheticRATE_X \qquad (2.16)$$

where $LIGHTintercepted_X$ is the amount of light intercepted by the occupying plant tissue in cell X (unitless); *PhotosyntheticRATE* is the per-unit size rate of photosynthesis for cell X (mg C mg^{-1} shoot biomass d^{-1}); Ka_i (unitless) and Kb_i (mg C mg^{-1} shoot d^{-1}) are photosynthetic constants which determine the shape of the relationship curve for plant i; $\mathit{Photosynthate}_X$ is the absolute amount of carbon fixed for cell X (mg C); and $\mathit{SHOOTmass}_X$ is the amount of shoot biomass present in cell X (mg biomass).

The *PhotosyntheticRATE* equation (equation 2.15) describes a Michaelis-Menten type relationship, determined by the constants, *Ka* and *Kb*, where *Ka* is the light level at which $\mathit{PhotosyntheticRATE} = Kb/2$. At extremely high light levels, *PhotosyntheticRATE* will approximate *Kb*.

As in section 2.2.5, if the total shoot biomass of the plant is less than *CELLmass*, then $\mathit{SHOOTmass}_X$ is set to the *SHOOTbiomass* of the occupying plant and the *Photosynthate* amount is reduced proportionally; else $\mathit{SHOOTmass}_X = \mathit{CELLmass}$. $\mathit{SHOOTbiomass}_i$ is the total biomass of the shoot system of plant i.

The cumulative amount of carbon fixed by a plant i each day is called $\mathit{Cproduction}_i$.

2.2.9 Carbon pooling

Following Baldwin (1976), there is a general plant carbon storage pool *Cpool*, acting parallel to *Rpool*, which contains the carbon products of *ABOVEcell* photosynthesis, and supplies carbon for immediate assimilation into biomass (section 2.2.11) and for maintenance costs of the plant (section 2.2.10). Once $\mathit{Cproduction}_i$ has been determined, the following occurs:

$$\mathit{Cpool}_i = \mathit{Cpool}_i' + \mathit{Cproduction}_i \tag{2.17}$$

where Cpool_i' is the value of *Cpool* from the previous day.

2.2.10 Maintenance respiration

Total plant respiration is deconstructed into two components: costs associated with biosynthetic processes (growth respiration; see section 2.2.11.3); and costs concerned with the maintenance of tissues and replacement of lost biomass (maintenance respiration) (Ryle 1984, Thornley 1970, 1976). Maintenance respiration is calculated on a biomass basis: all biomass belonging to an individual plant makes a demand on that plant's carbon pool: the per-unit biomass cost of maintenance is assumed to be constant and equal for both roots and shoots.

$$MaintenanceCOST_i = maintenanceRATE(ROOTbiomass_i + SHOOTbiomass_i) \qquad (2.18)$$

MaintenanceCOST$_i$ is the absolute cost of carbon (mg C), while *maintenanceRATE* is the daily per-unit biomass carbon cost of maintenance (mg C mg^{-1} biomass d^{-1}) and is assumed to be identical for all plants. This carbon cost is deducted from the plants carbon pool, before any carbon is assimilated that day, such that:

$$Cpool_i = Cpool_i - MaintenanceCOST_i \qquad (2.19)$$

If *Cpool*$_i$ is insufficient to support the demands made upon it, then plant death occurs (see section 2.2.14).

2.2.11 Carbon and resource assimilation

The quantity of carbon and resource put forward from their respective pools for assimilation into new biomass can have a great effect on the overall growth characteristics of the plant. Growth may either be coupled to resource capture or uncoupled to resource capture (see sections 1.2.6 and 1.4.3). To simulate this difference, carbon and resource for assimilation into new biomass are submitted from the internal plant pools into substrate pools, *Csubstrate* and *Rsubstrate*, at rates determined by the plant's growth syndrome. Only the contents of these two pools can be assimilated each day. With coupled growth, fractions (or all) of the R and C pool are put forward for assimilation. With uncoupled growth, a constant absolute amount of R and C are put forward for assimilation each day. The significance of this is that 'luxury consumption' of resources (see Chapin, 1980) will occur if resource supply is greater than the rate of assimilation of resources. Both forms are included in the model; the plant-specific variable *CaptGroCOUPLED* records whether plant i has coupled growth

($CaptGroCOUPLED_i$=1) or uncoupled growth ($CaptGroCOUPLED_i$=0).

2.2.11.1 Growth coupled to resource capture

If plant i has growth coupled to resource capture then

$$Rsubstrate_i = Rpool_i \times gcR_i \tag{2.20}$$

$$Rpool_i = Rpool_i - Rsubstrate_i \tag{2.21}$$

$$Csubstrate_i = Cpool_i \times gcC_i \tag{2.22}$$

$$Cpool_i = Cpool_i - Csubstrate_i \tag{2.23}$$

where gcR_i is the fraction of $Rpool_i$ submitted for assimilation into $Rsubstrate_i$ each day (unitless); gcC_i is the fraction of $Cpool_i$ submitted for assimilation into $Csubstrate_i$ each day (unitless).

2.2.11.2 Growth uncoupled to resource capture

If plant i has uncoupled growth then the amount of R and C forwarded for assimilation as substrate is determined by the amount of R and C available in the respective plant pools. $RsubRATE_i$ is the rate of transfer of resource from $Rpool_i$ to $Rsubstrate_i$ (mg R d^{-1}) and $CsubRATE_i$ is the rate of transfer of carbon from $Cpool_i$ to $Csubstrate_i$ (mg C d^{-1}). *RsubRATE* and *CsubRATE* determine the maximum daily growth rate of plants with uncoupled growth. If there is insufficient *Rpool* to maintain the assimilation rate of *RsubRATE*, then,

$$Rsubstrate_i = Rpool_i \tag{2.24}$$

otherwise

$$Rsubstrate_i = RsubRATE_i \tag{2.25}$$

Likewise, if there is insufficient carbon in $Cpool_i$ then

$$Csubstrate_i = Cpool_i \tag{2.26}$$

otherwise

$$Csubstrate_i = CsubRATE_i \tag{2.27}$$

Finally,

$$Rpool_i = Rpool_i - Rsubstrate_i \tag{2.28}$$

$$Cpool_i = Cpool_i - Csubstrate_i \tag{2.29}$$

2.2.11.3 Growth respiration

Respiratory cost of growth covers the metabolic costs involved with the assimilation of carbon and resource into new biomass; here the costs are in units of carbon and are subsequently deducted, from the plant's Csubstrate pool.

$$respiratoryCOST_i = Csubstrate_i \times respirationRATE \tag{2.30}$$

$$Csubstrate_i = Csubstrate_i - respiratoryCOST_i \tag{2.31}$$

where $respiratoryCOST_i$ is the assimilation costs of growth (mg C) and $respirationRATE$ is the per-unit carbon cost of assimilation (mg C mg^{-1} C assimilated; assumed to be constant for all species).

2.2.11.4 Determination of excess substrate

Resource and the carbon products are assumed to be assimilated at a constant ratio (after Reynolds & Thornley 1982) given by *CRratio* (mg C mg^{-1} R). Thus, unless $Csubstrate = CRratio \times Rsubstrate$ there will be an quantity of unassimilated substrate after assimilation. As with the model of Baldwin (1976), this excess is returned to the relevant storage pool during the same time iteration to prevent waste, and the substrates are assimilated according to the following algorithms:

$$\begin{aligned} &if \quad \left(\frac{Csubstrate_i}{Rsubstrate_i}\right) \le CRratio \quad then : \\ &Cassimilate_i = Rsubstrate_i \times CRratio \ , \\ &Rassimilate_i = Rsubstrate_i \ , \\ &Cpool_i = Cpool_i + (Csubstrate_i - Cassimilate_i) \ . \end{aligned} \tag{2.32}$$

$$\begin{aligned} &if \quad \left(\frac{Csubstrate_i}{Rsubstrate_i}\right) > CRratio \quad then : \\ &Cassimilate_i = Csubstrate_i \ , \\ &Rassimilate_i = \frac{Csubstrate_i}{CRratio} \ , \\ &Rpool_i = Rpool_i + (Rsubstrate_i - Rassimilate_i) \ . \end{aligned} \tag{2.33}$$

Finally, the assimilates are converted into biomass:

$$\begin{aligned} &NewBiomass_i = \frac{Cassimilate_i}{Ccontent} \\ &or \\ &NewBiomass_i = \frac{Rassimilate_i}{Rcontent} \end{aligned} \tag{2.34}$$

where *CRratio* is the ratio at which C and R are incorporated into biomass (mg C mg^{-1} R); $Cassimilate_i$ and $Rassimilate_i$ are the final amounts of carbon and resource respectively that are assimilated; $NewBiomass_i$ is the amount of biomass constructed from *Cassimilate* and *Rassimilate* (mg biomass); *Ccontent* is the per-unit biomass content of C (mg C mg^{-1} biomass), and *Rcontent* is the per-unit biomass content of R (mg C mg^{-1} biomass).

2.2.12 Partitioning of new biomass between root and shoot

Once assimilation has occurred *NewBiomass* is allocated to *ROOTbiomass* and *SHOOTbiomass* by the partitioning coefficients, *ROOTallocate* and *SHOOTallocate*. These coefficients are determined using the relative levels of remaining resource and carbon in *Rpool* and *Cpool* such that

$$ROOTallocate_i = \frac{Cpool_i + (CRratio \times PartR_i \times Rpool_i) - (PartC_i \times Cpool_i)}{(CRratio \times Rpool_i) + Cpool_i} \quad (2.35)$$

$$SHOOTallocate_i = \frac{Rpool_i - (CRratio \times PartR_i \times Rpool_i) + (PartC_i \times Cpool_i)}{(CRratio \times Rpool_i) + Cpool_i} \quad (2.36)$$

where $PartR_i$ and $PartC_i$ are constants that influence the pattern of allocation at different R and C substrate levels; $ROOTallocate_i$ and $SHOOTallocate_i$ are the fractions of new biomass directed to root and shoot respectively such that

$$ROOTallocate_i + SHOOTallocate_i = 1.0 \quad (2.37)$$

The allocation patterns that are characterized by *PartR* and *PartC* are a crucial link between above- and below- ground competition. These equations were derived from the ratio of R and C within the plant, in terms of potential biomass (hence *PartR* is scaled to *PartC* by *CRratio*), and *PartR* and *PartC* are introduced to control the response of root/shoot allocation to the relative sizes of Rpool and Cpool. This is similar to the partitioning model presented by Reynolds and Thornley (1982).

This approach to root/shoot allocation is supported by evidence suggesting that communication of some sort (mediated by nutrients or, more likely, hormones) exists between the root and shoot systems of a plant, such that growth may be allocated with respect to the relative activity of the structures (Jackson 1993), and there is evidence that the allocation of biomass to root and shoot is determined by the internal unassimilated nitrogen content of the plant, in just such a way as described by the equations above (McDonald & Davies 1996).

The allocation patterns that may be produced by this model range from constant allocation between root and shoot irrespective of resource and light levels, to dynamic allocation patterns with variable degrees of plasticity (see section 3.3.3). If $PartR+PartC=1.0$ then allocation is constant, while if $PartR+PartC<1.0$ then the resulting allocation pattern is plastic; if $PartR>PartC$ then the allocation pattern will be biased towards roots, *i.e.* more biomass will be allocated to roots than shoots in general. Optimal plastic allocation between root and shoot only occurs if both *PartC* and *PartR* are set to zero. Growth is distributed between root and shoot:

$$ROOTincrease_i = ROOTallocate_i \times NewBiomass_i \tag{2.38}$$

$$SHOOTincrease_i = SHOOTallocate_i \times NewBiomass_i \tag{2.39}$$

where $ROOTincrease_i$ and $SHOOTincrease_i$ represent the amount of growth available to root and shoot respectively (mg biomass).

2.2.13 Root and shoot growth

Growth of both root and shoot (the additional occupancy of unoccupied *SOILcells* or *ABOVEcells* by an individual) are treated in an identical manner. The growth routine of this model has two stages: firstly, the difference between previous biomass and post-growth biomass is calculated and converted into the number of extra cells required for the individual to achieve the new biomass value (section 2.2.13.1); secondly, a location for each of these cells is found that satisfies some simple rules (section 2.2.13.2).

2.2.13.1 Calculation of cell number

Root and shoot biomass (*ROOTbiomass* and *SHOOTbiomass* respectively) values are real numbers but the occupied cells that represent the root or shoot cannot reflect the true biomass value (being integer based). Thus, a function translating biomass into a number of cells with equivalent mass is needed:

$$cellnumber = f_r\left(\frac{biomass}{CELLmass}\right) \tag{2.40}$$

where *cellnumber* is the number of cells that are represented biomass, and f_r denotes a function rounding down a real number to an integer. With such a relationship converting real numbers to integers, there will be times when the number of cells constituting a plant is less then the actual biomass of the plant; the value of *CELLmass* determines the resolution of this relationship. The number of cells to be grown is given by

$$CELLgrowthnumber = f_r\left(\frac{biomass'}{CELLmass}\right) - f_r\left(\frac{biomass}{CELLmass}\right) \tag{2.41}$$

where *CELLgrowthnumber* is the number of new cells the plant has capacity to grow; *biomass′* is the total mass of the organ (root or shoot) including the additional biomass expected from growth; and *biomass* is the mass of the organ the previous day (*i.e.* before this day's growth). Thus for root growth:

$$CELLgrowthnumber_{root} = f_r\left(\frac{ROOTincrease_i + ROOTbiomass_i}{CELLmass}\right) - f_r\left(\frac{ROOTbiomass_i}{CELLmass}\right) \tag{2.42}$$

while for shoot growth:

$$CELLgrowthnumber_{shoot} = f_r\left(\frac{SHOOTincrease_i + SHOOTbiomass_i}{CELLmass}\right) - f_r\left(\frac{SHOOTbiomass_i}{CELLmass}\right) \tag{2.43}$$

2.2.13.2 Location of growth

Using an algorithm, described below, a suitable location for each cell to be 'grown' is found which satisfies all the following rules:

(1) cell must be previously unoccupied,

(2) cell must be adjacent to a occupied cell belonging to the same individual plant,

(3) if several immediately adjacent cells satisfy (1) and (2) then the cell with highest resource level is the location for growth.

If there are no available cells present at that depth/height the subsequent LAYER is considered (*i.e.* deeper/higher).

Identification of a suitable cell is achieved through a search of cells by a template from the original initial cell of an individual plant (PlantX, PlantY, LAYER=1; see appendix program), extending outwards from this cell until either a suitable cell is found or a certain number of template movements (*TimeOut*) occur, in which case the growth search template is promoted to the subsequent LAYER. The rules governing the growth of a cell by plant i are as follows:

(s1) *TimeOutCOUNT*=0. Set template position to $PlantX_i$, $PlantY_i$, LAYER (LAYER=1 initially).
(s2) establish occupancy status and resource (light or SoilR) quantity of each cell neighbouring template position.
(s3) if an unoccupied cell exists, identify the one with greatest resource quantity, then go to s7.
(s4) if no unoccupied cell exists move template (using random lateral direction) into neighbouring cell only if cell is occupied by plant i. *TimeOutCOUNT*=*TimeOutCOUNT*+1.
(s5) if *TimeOutCOUNT* ≤ *TimeOut* then go to s2.
(s6) if *TimeOutCOUNT* > *TimeOut* then increase template LAYER by one. Go to s1.
(s7) Grow into cell.

The loops within these rules are performed until the criteria are satisfied and growth may occur. This is repeated for each cell to be grown, as determined above (see Appendix Program for further details).

2.2.13.3 Increase of root and shoot mass

Once all cell growth has been completed, root and shoot mass are increased as follows

$$ROOTbiomass_i = ROOTbiomass_i^{\prime} + ROOTincrease_i \qquad (2.44)$$

$$SHOOTbiomass_i = SHOOTbiomass_i^{\prime} + SHOOTincrease_i \qquad (2.45)$$

where $ROOTbiomass_i^{\prime}$ and $SHOOTbiomass_i^{\prime}$ are the values of $ROOTbiomass_i$ and $SHOOTbiomass_i$ prior to growth (*i.e.* from the previous day).

2.2.14 Plant death and the return of resources to the environment

Plant death can occur at several stages of the plant processes that are performed during each iteration. The significance of death in this model is the potential for the return of nutrients to the soil and the prospect of gaps below-ground and especially above-ground, where previously shaded *ABOVEcells* receive an increase in light following the death of an individual. The location and quantity of dead organic material in the soil is retained in *SoilOrgMat*, an array parallel to *SoilR*. Following the death of a plant its presence is removed from the physical space that it previously occupied: the relevant *SOILcells* and *ABOVEcells* become unoccupied. As each *SOILcell* that the plant occupied is removed, the organic material that constructed the occupied *SOILcell* (*CELLmass*) accumulates as *SoilOrgMat* in the corresponding *SOILcell*. Shoot biomass accumulates at the surface of *SOILcells* (*LAYER*=1).

2.2.14.1 Decomposition

Decomposition occurs each time iteration on all dead organic material in the soil, and any resource that may be released appears as an increase in *SoilR* level at the same location (cell).

$$SoilR_X = SoilR_X + (decayRATE \times Rcontent \times SoilOrgMat_X) \qquad (2.46)$$

$$SoilOrgMat_X = (1 - decayRATE) \times SoilOrgMat_X \qquad (2.47)$$

where *decayRATE* is the rate of decay of the resource component of organic material (mg R mg^{-1} R d^{-1}).

2.2.15 Programming of the model

The model was implemented as a PASCAL computer program running on a UNIX system (see Appendix Program). Each section of the model was written as a separate procedure and tested to satisfactory working order before incorporation into the main program; this was in an effort to decrease the number of 'bugs' and to produce a program based on accessible individual components that can be modified easily.

Table 2.1. A list of all variables used in the model.

Variable	units	type	description
a	none	*SoilR* variable, real	proportion of R movement by diffusion
ABOVEcell	none	spatial array	cells above-ground
b	none	*SoilR* variable, real	proportion of R movement by mass flow
CaptGroCOUPLED	none	plant variable, boolean	recorded whether a plant has growth coupled or uncoupled to R and C acquisition
Cassimilate	mg C	plant variable, real	amount of C assimilated after growth respiration
CELLgrowthnumber	number of cells	plant variable, integer	number of cells to be grown
CELLmass	mg biomass per cell	constant, real	relates biomass to space for both *ABOVEcells* and *SOILcells*
cellnumber	number of cells	plant variable, integer	number of cells representing biomass
celluptake	mg R	*SOILcell* variable, real	uptake rate for each occupied *SOILcell*
Ccontent	mg C mg^{-1} biomass	constant, real	C content per-unit biomass
Cpool	mg C	plant variable, real	unassimilated C within plant
Cproduction	mg C d^{-1}	plant variable, real	total amount of C fixed by a plant in one day
CRratio	mg assim. C mg^{-1} assim. R	constant, real	ratio linking R and C contents in biomass
CsubRATE	mg C d^{-1}	plant variable, real	maximum daily rate of C submission for assimilation
Csubstrate	mg C	plant variable, real	amount of C submitted from *Cpool* for assimilation
d	none	resource variable, real	diffusion coefficient
decayRATE	mg R mg^{-1} R d^{-1}	*SoilR* variable, real	daily rate of decomposition of R present in organic material within *SOILcells*
Dflux	mg R	*SoilR* variable, real	flux of R by diffusion between two neighbouring *SOILcells*
f	none	plant variable, real	fraction of leaf area projected on a plane normal to light beam
gcR	none	plant variable, real	fraction of *Rpool* submitted for assimilation (coupled growth)
gcC	none	plant variable, real	fraction of *Rpool* submitted for assimilation (coupled growth)
i	none	integer	denotes individual plant
Imax	mg R mg^{-1} root biomass d^{-1}	plant constant, real	maximum per-unit mass R uptake rate
Ka	none	constant, real	photosynthetic rate coefficient
Kb	mg C mg^{-1} shoot biomass d^{-1}	constant, real	photosynthetic rate coefficient
Km	mg R per *SOILcell*	plant constant, real	affinity of R uptake: external concentration at which *celluptake* = *Imax*/2
LAD	m^{2} m^{-3}	plant constant, real	Leaf Area Density
LAYER	cell height	integer	denotes the height (*ABOVEcells*) or depth (*SOILcells*) of a cell
LIGHTintercepted	none	*ABOVEcell*/plant variable, real	light intercepted by the occupying plant tissue in an *ABOVEcell*
MaintenanceCOST	mg C	plant variable, real	total cost of maintenance respiration of a plant each day
MaintenanceRATE	mg C mg^{-1} biomass d^{-1}	constant, real	daily per-unit mass maintenance cost
MAXheight	cell height	*ABOVEcell* variable, integer	number of cell layers in *ABOVEcell* array
MFflux	mg R	*SoilR* variable, real	flux of R by mass flow between two neighbouring *SOILcells*
n	none	integer	number of neighbours of each *SOILcell*
NETflux	mg R	*SoilR* variable, real	Overall flux of R by diffusion and mass flow between two neighbouring *SOILcells*
NewBiomass	mg biomass	plant variable, real	amount of biomass to be grown by a plant each day
PartR	none	plant constant, real	allocation coefficient
PartC	none	plant constant, real	allocation coefficient
Photosynthate	mg C	*ABOVEcell*/plant variable, real	amount of C fixed during one day in an *ABOVEcell*
PhotosytheticRATE	mg C mg^{-1} shoot biomass d^{-1}	*ABOVEcell*/plant variable, real	rate of C fixation by occupying plant tissue in an *ABOVEcell*
$P_{transmittance}$	none	*Light* variable, real	probability of transmittance of light through an *ABOVEcell*

Table 2.1 (continued)

Variable	units	type	description
Rcontent	mg R mg^{-1} biomass	constant, real	R content per-unit biomass
respiratoryCOST	mg C	plant variable, real	total costs of growth respiration
respirationRATE	mg C mg^{-1} C d^{-1}	constant, real	per-unit carbon cost of assimilation
ROOTallocate	none	plant variable, real	fraction of *NewBiomass* allocated to *ROOTbiomass*
ROOTbiomass	mg biomass	plant variable, real	total mass of a plant's root system
ROOTincrease	mg biomass	plant variable, real	amount of *NewBiomass* allocated to *ROOTbiomass*
ROOTmass	mg biomass	*SOILcell* variable, real	biomass present in an occupied *SOILcell*
Rpool	mg R	plant variable, real	unassimilated R within plant
RsubRATE	mg R d^{-1}	plant variable, real	maximum daily rate of R submission for assimilation
Rsubstrate	mg R	plant variable, real	amount of R submitted from *Rpool* for assimilation
Ruptake	mg R	plant variable, real	total R acquired by a plant in one day
SHOOTallocate	none	plant variable, real	fraction of *NewBiomass* allocated to *SHOOTbiomass*
SHOOTbiomass	mg biomass	plant variable, real	total mass of a plant's shoot system
SHOOTincrease	mg biomass	plant variable, real	amount of *NewBiomass* allocated to *SHOOTbiomass*
SHOOTmass	mg biomass	*ABOVEcell* variable, real	biomass present in an occupied *ABOVEcell*
sunLIGHT	none	constant, real	amount of light input to *ABOVEcell* system each day
SOILcell	none	spatial array	cells below-ground
SoilOrgMat	mg biomass per *SOILcell*	spatial array of real	the amount of (dead) organic material present in each *SOILcell*
SoilR	mg R per *SOILcell*	spatial array of real	the amount R present in each *SOILcell*
SoilW	mg water per *SOILcell*	spatial array of real	the amount water present in each *SOILcell*
TranspirationRATE	mg water mg^{-1} biomass d^{-1}	constant, real	the daily per-unit shoot mass rate of transpiration
Wflux	mg water	*SoilW* variable, real	flux of water between two neighbouring *SOILcells*
Wd	none	water variable, real	water movement coefficient
x	cell width	integer	denotes the position of a cell along x-axis
X	none	none	denotes a particular cell (either *ABOVEcell* or *SOILcell*, depending on context)
y	cell width	integer	denotes the position of a cell along y-axis

Chapter 3

Simulation Runs

3.1 Introduction

3.1.1 General description of simulation runs

The model described in the previous chapter was implemented as a PASCAL computer program (presented in the Appendix). Due to the different specifications of the simulation runs (*e.g.* replication numbers, spatial dimensions, number of individuals and spatial positions) several programs were used though all were derived from a common source, and mainly differed in parameter settings and not program structure.

The simulation runs fall into three categories: those that focus specifically on R supply characteristics, those concerned with plant traits, and selected plant trait simulation runs with no above- or no below-ground interspecific competition. These categories are referred to as R supply, plant trait, and split competition, respectively.

Table 3.2 contains a full list and description of runs; runs are referred to by a number followed by 'n' or 'p' representing a nitrogen or phosphorus simulation. Different species of plants were constructed for use in the plant trait, split competition and random position runs; each species has a unique set of characteristics (see Table 3.3 for a list of species and associated traits). A full list of the parameter values governing R supply for both nitrogen and phosphorus, and other constant values are included in Table 3.1.

3.1.2 Spatial parameters

For all the simulation runs, the volume simulated is: above-ground: 10 × 10 cells horizontally (0.25 m^2), 20 cells vertically (1 m); below-ground: 10 × 10 cells horizontally (0.25 m^2), 20 cells vertically (1 m).

Table 3.1. General parameter values used in N and P simulations.

Parameter	**Nitrogen**	**Phosphorus**	**Units**
Soil parameters			
a	0.21	0.98	unitless
b	0.79	0.02	unitless
d	10	1000	unitless
SoilR level	*InitialSoilR*		mg Nutrient per *SOILcell*
11	1.01	0.06733	
10	0.82	0.05467	
9	0.65	0.04333	
8	0.50	0.03333	
7	0.37	0.02467	
6	0.26	0.01733	
5	0.17	0.01133	
4	0.10	0.00667	
3	0.05	0.00333	
2	0.02	0.00133	
1	0.01	0.00067	
Other environmental parameters			
decayRATE	0.0	*	mg R mg^{-1} R d^{-1}
Wd	1.0	*	unitless
sunLIGHT	1.0	*	unitless
Plant parameters			
Ka	0.5	*	unitless
Kb	0.1312	*	mg C mg^{-1} shoot biomass d^{-1}
respirationRATE	0.25	*	mg C mg^{-1} C d^{-1}
maintenanceRATE	0.015	*	mg C mg^{-1} biomass d^{-1}
CELLmass	20	*	mg biomass per cell
TranspirationRATE	10.0	*	mg water
CRratio	15	225	mg C mg^{-1} R
Ccontent	0.45	0.45	mg C mg^{-1} biomass
Rcontent	0.03	0.002	mg R mg^{-1} biomass

* denotes parameter value is identical to that assigned in nitrogen simulation

Table 3.2. List of Simulation runs. The subscript n or p denotes a nitrogen or phosphorus simulation; all simulations were performed for nitrogen and phosphorus competition.

Species	**Run Number**
Reference Species	
a	1 (n,p)
a × a	2 (n,p)
Constant Allocation traits	
a × b1	3 (n,p)
a × b2	4 (n,p)
a × b3	5 (n,p)
a × b4	6 (n,p)
a × b5	7 (n,p)
a × b6	8 (n,p)
a × b7	9 (n,p)
b2 × b6	10 (n,p)
b2	11 (n,p)
b6	12 (n,p)
a × b4 × b5 × b6 × b7	m1 (n,p)
Plastic allocation traits	
a × c1	13 (n,p)
a × c2	14 (n,p)
c1	15 (n,p)
c2	16 (n,p)
a × d1	17 (n,p)
a × d2	18 (n,p)
d1 × d2	19 (n,p)
d1	20 (n,p)
d2	21 (n,p)
Coupled vs. uncoupled growth	
a × e	22 (n,p)
a × f	23 (n,p)
e × f	24 (n,p)
e	25 (n,p)
f	26 (n,p)
Combined traits	
a × g	27 (n,p)
a × h	28 (n,p)
g × h	29 (n,p)
g	30 (n,p)
h	31 (n,p)
Above-ground competition only	
a × a	32A (n,p)
a × a (lower P values)	—
a × b6	33A (n,p)
a × c2	34A (n,p)
e × f	35A (n,p)
g × h	36A (n,p)
Below-ground competition only	
a × a	32B (n,p)
a × a (lower P values)	—
a × b6	33B (n,p)
a × c2	34B (n,p)
e × f	35B (n,p)
g × h	36B (n,p)

Table 3.3. List of variables assigned to all model species.

	Root			Shoot		Growth					Allocation	
Species	*TimeOut*	*Km*	I_{max}	*TimeOut*	LAD	*CaptGroCOUPLED*	*cgR*	*cgC*	*RsubRATE*	*CsubRATE*	*PartR*	*PartC*
Reference Species												
a	10	0.001 (N) 6.67×10^{-5} (P)	0.04 (N) 2.67×10^{-3} (P)	10	0.3	TRUE	0.5	0.5	-	-	0.5	0.5
Constant Allocation												
b1	*	*	*	*	*	*	*	*	*	*	0.8	0.2
b2	*	*	*	*	*	*	*	*	*	*	0.7	0.3
b3	*	*	*	*	*	*	*	*	*	*	0.6	0.4
b4	*	*	*	*	*	*	*	*	*	*	0.4	0.6
b5	*	*	*	*	*	*	*	*	*	*	0.3	0.7
b6	*	*	*	*	*	*	*	*	*	*	0.2	0.8
b7	*	*	*	*	*	*	*	*	*	*	0.1	0.9
Plastic Allocation												
c1	*	*	*	*	*	*	*	*	*	*	0.3	0.3
c2	*	*	*	*	*	*	*	*	*	*	0.1	0.1
d1	*	*	*	*	*	*	*	*	*	*	0.5	0.2
d2	*	*	*	*	*	*	*	*	*	*	0.2	0.5
Growth												
e	*	*	*	*	*	TRUE	1.0	1.0	-	-	*	*
f	*	*	*	*	*	FALSE	-	-	0.03 (N) 0.002 (P)	0.45 (N) 0.45 (P)	*	*
Combined Traits												
g	*	*	*	*	*	FALSE	-	-	0.03 (N) 0.002 (P)	0.45 (N) 0.45 (P)	0.6	0.4
h	*	*	*	*	*	TRUE	1.0	1.0	-	-	0.2	0.5

* denotes that the values assigned is the same as for species *a*. - denotes variable is not applicable to species: used for coupled/uncoupled growth variables. (N) or (P) next to a value refers to the values used in Nitrogen or Phosphorus simulation.

3.1.3 Temporal parameters

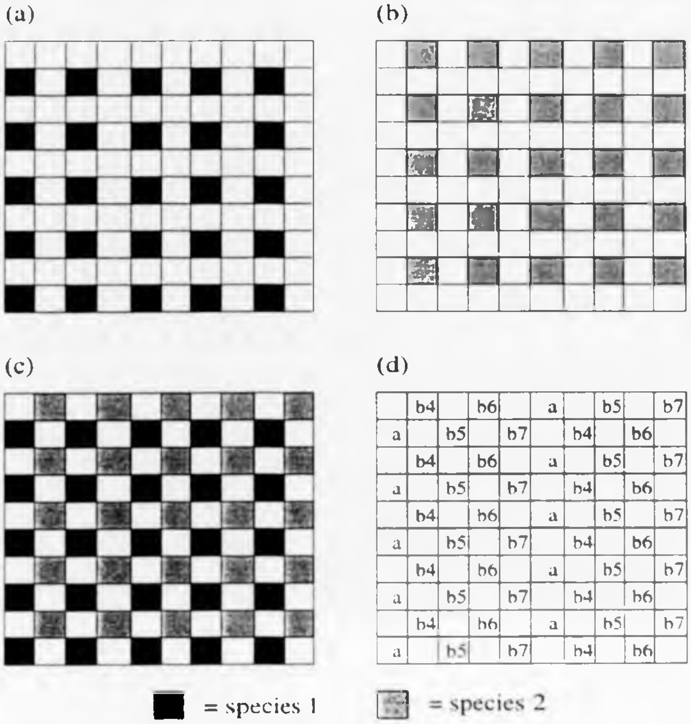
The period of time simulated is 60 days for each replication. No longer time period than this could be justified as per-unit mass maintenance costs are assumed to be independent of age and plant size and also no allocation to reproductive tissues were included in the model. Each iterative step of the model is a single day.

3.1.4 Soil Resource parameters

Soil nutrients nitrogen and phosphorus were chosen because both are major limiting resources in natural vegetation and yet have very different movement and supply properties (Marschner 1986). As described in the previous chapter, only the processes of mass flow and diffusion are assumed to occur. Soil nutrient levels are set to *InitialSoilR* (mg R per cell) at *TIME*=0. No other input (to the soil or the system) of either resource was assumed to occur (*i.e.* no decomposition: *decayRATE*=0).

Though soil water and its movement are included in the model, it is not simulated with a high degree of accuracy (no evaporation, rainfall, effect of gravity, response of plant to water supply) but is included to generate gradients between cells for mass flow calculations. The quantity of soil resource moving by mass flow is assumed to be independent of the water gradient's magnitude (movement relies on the direction of water flow), thereby avoiding explicit consideration of water.

To simulate a soil resource gradient, there are 11 different values assigned to *InitialSoilR* for both nitrogen and phosphorus. The range for nitrogen is from 0.01 mg N per cell (80 mg N m^{-3} soil) to 1.01 mg N per cell (8080 mg N m^{-3} soil), while for phosphorus the range is from 0.00067 mg P per cell (5.333 mg P m^{-3} soil) to 0.06733 mg P per cell (538.667 mg P m^{-3} soil). Note that the values for phosphorus are 15 times smaller than nitrogen: this is to scale soil phosphorus to soil nitrogen in the same proportion as the organic P:N ratio (*i.e.* 1:15, derived from *CRratio*[N simulations]=15 and *CRratio*[P simulations]=225). The values for each R level are shown in Table 3.1.



(d)

	b4		b6		a		b5		b7
a		b5		b7		b4		b6	
	b4		b6		a		b5		b7
a		b5		b7		b4		b6	
	b4		b6		a		b5		b7
a		b5		b7		b4		b6	
	b4		b6		a		b5		b7
a		b5		b7		b4		b6	
	b4		b6		a		b5		b7
a		b5		b7		b4		b6	

Figure 3.1
Positions of individuals in plant traits runs for (a) monoculture of species 1, (b) monoculture of species 2, (c) mixture of species 1 and 2, and (d) the positions of species in runs 40n and 40p.

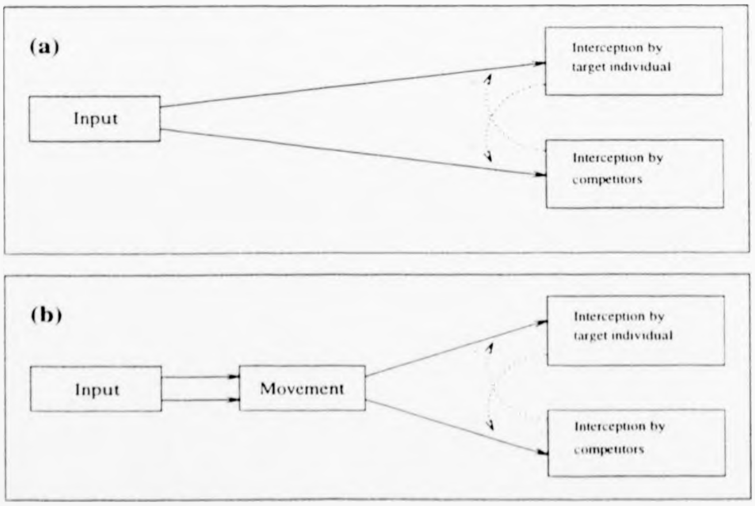


Figure 3.2
Conceptual supply properties of light (a) and soil nutrients (b). Solid lines represent resource, dotted lines respresent the effect of competition.

3.1.5 Spatial arrangement of individuals

The plant trait runs utilize an additive design such that either 50 individuals (mixture: 25 individuals of each species) or 25 individuals (monoculture: 25 individuals of one species) are used. These are arranged as in Figure 3.1(a)-(c). The use of an additive design follows from the competition definition in section 1.5. The positions of individuals in the multi-species runs (40n and 40p) are shown in Figure 3.1(d).

3.1.6 Replication details

It is necessary to include replications because of the stochastic element of the growth routine (see section 2.2.13.2 and Appendix program); these are referred to as *GROWTHreplicates*. In the plant trait and split competition runs, there are 20 *GROWTHreplicates* for each R level (20 × 11 = 220).

3.1.7 The use of a reference species, species *a*

A reference species is used against which all model species may be compared both in terms of performance and in competitive ability. This model species type is referred to as species *a*, the morphological and physiological traits of which are listed in Table 3.3. The properties assigned to species *a* are intended to be competitively neutral (*e.g.* root/shoot allocation is constant and unbiased, *i.e.* root:shoot ratio=1) so that the competitive ability of species *a* should be 'moderate' relative to the other model species and can be used for comparative purposes. See section 3.3.2 for description of the performance of species *a* along the soil resource gradients.

3.2 R supply

3.2.1 Introduction

Though it has been known for some time that different soil nutrients exhibit different movement characteristics within the soil (Nye & Tinker 1977), the major theories attempting to describe competition for light and nutrients within an ecological context have so far ignored any possible effect that the supply characteristics of a resource may have on the outcome of competition for that resource (Huisman 1994, though see Huston & DeAngelis 1994 for consideration of resource supply). Plants may affect the supply of resources to acquisition sites in both positive and negative ways other than by direct resource competition (Goldberg 1990), yet few studies have determined the influence of such interactions on plant performance relative to competition. Attention has shifted recently to consider supply properties of resources in the context of competition.

As mentioned previously (section 2.1.2) Tilman's ALLOCATE model assumes soil resources are spatially homogeneous (all individuals have equal access to *all* the resource available) and exhibit instantaneous transport to roots.

Conceptually, there are two processes affecting the acquisition of a unit of resource by an individual: supply and interception. This is helpful for contrasting the unique characteristics of different resources, and the possible implications for competition. Conceptually, supply of a resource refers to the rate at which a unit of resource moves to a specific site of resource acquisition of an individual plant. Supply is therefore a function of the environmental availability (input) and the transport properties (movement to acquisition site) of the resource (see below for special consideration of light); see Figure 3.2. Interception is the rate of removal of a unit of resource by an acquisition site from the resource supplied to that acquisition site. Although supply and interception rates may be independent, the interception rate obviously cannot exceed the supply rate.

Input of resource to the system

This is the addition of a unit of resource to the system's available resource pool from external abiotic sources (*e.g.* fertilization, rainfall) or from internal biotic sources (*e.g.* mineralization, loss from plant tissues).

Movement of resource to the site of acquisition

This is the transfer of units of resource from the available resource pool direct to a zone of resource acquisition per unit of time. This action depends on the interaction between the resource and the media through which it moves. For example, nitrogen movement through the soil to the root surface will depend on the form of nitrogen, specific solubility and diffusion characteristics, soil properties, and plant properties such as transpiration rate, uptake rate (causing diffusion gradient) and proliferation of root system (distance from root surface to resource). When the movement of a resource to an acquisition site and subsequent interception is essentially instantaneous (*e.g.* direct input of nitrogen to root surface from local decomposition) this is termed direct interception.

This concept of movement of nutrients through the soil medium, assume no effect of mycorrhiza, which may significantly affect the pathway from source to acquisition site, described above. For example, phosphorus and nitrogen acquired from the soil by mycorrhiza may move through the mycorrhizal network to the root surface of a plant (Newman 1988). Resources from other neighbouring plants may also move through the mycorrhizal network, if a source-sink relationship develops (Newman 1988, Eissenstat 1990, Newman & Eason 1993).

Light as a special case

All light arrives at the surface of the leaf by direct interception; thus there is no equivalent of a resource supply pool for light, only input to the system and direct interception. Within this conceptual framework where does light competition occur? Shading of the surface of a leaf reduces the absolute quantity of light available for direct interception, reducing the total energy acquired by that leaf and consequently the rate of photosynthesis: this is conceptually equivalent to reduction of resource quantity supplied to a root surface due to the presence of competing root systems. Thus, light competition acts to reduce the supply of light to photosynthetic tissue and can only be accomplished by direct interception (see Figure 3.2).

Depletion zones

The extent to which a depletion zone of a soil nutrient extends from an acquisition site depends on the supply properties of the nutrient into the depletion zone.

As an example, phosphorus depletion zones rarely exceed a distance of 1 cm (usually only 2 or 3 mm) from the root surface (Bhat & Nye 1974*a*, 1974*b*) as the majority of phosphorus movement is by diffusion. In contrast nitrogen, moving mainly by mass flow, is expected to travel a much greater distance to the root surface, though if supply exceeds acquisition there will be an accumulation of nitrogen at the root surface. Thus, for a given density of acquisition zones (cm^2 root surface cm^{-3} soil volume), competition for nitrogen is more likely to occur than competition for phosphorus (Harper 1977).

3.2.2 R parameters used in simulations for N and P

Values for R supply parameters used for nitrogen and phosphorus are listed in Table 3.1.

3.2.3 Use of the model to contrast the supply properties of N and P

Simulations

The simulations performed in this section use a modified version of the model used in the rest of this chapter. In these simulations, only one individual plant is modelled, and this comprises of a 'block' of occupied *SOILcells* in the top-centre of modelled space – no growth is permitted to occur such that the resulting distribution of soil R was an accurate reflection of the supply properties of the soil resource. The root system acquires soil R at the per-unit biomass rates of species *a* (see section 3.3.2) and the length of simulation was 60 days. This was performed with both N and P as the soil resource, and at high (level 9) and low (level 3) soil R levels.

Results

The spatial distribution of soil R, relative to the value of *InitialSoilR* (*i.e.* for each *SOILcell*, relative Soil R = *SoilR* / *InitialSoilR*), is shown in Figure 3.3; the relative soil R values for both high and low soil P levels were identical, therefore only the results from the low P level are included. The position of the root system is most apparent in the P results (Figure 3.3c), where the absence of Soil P from the centre part

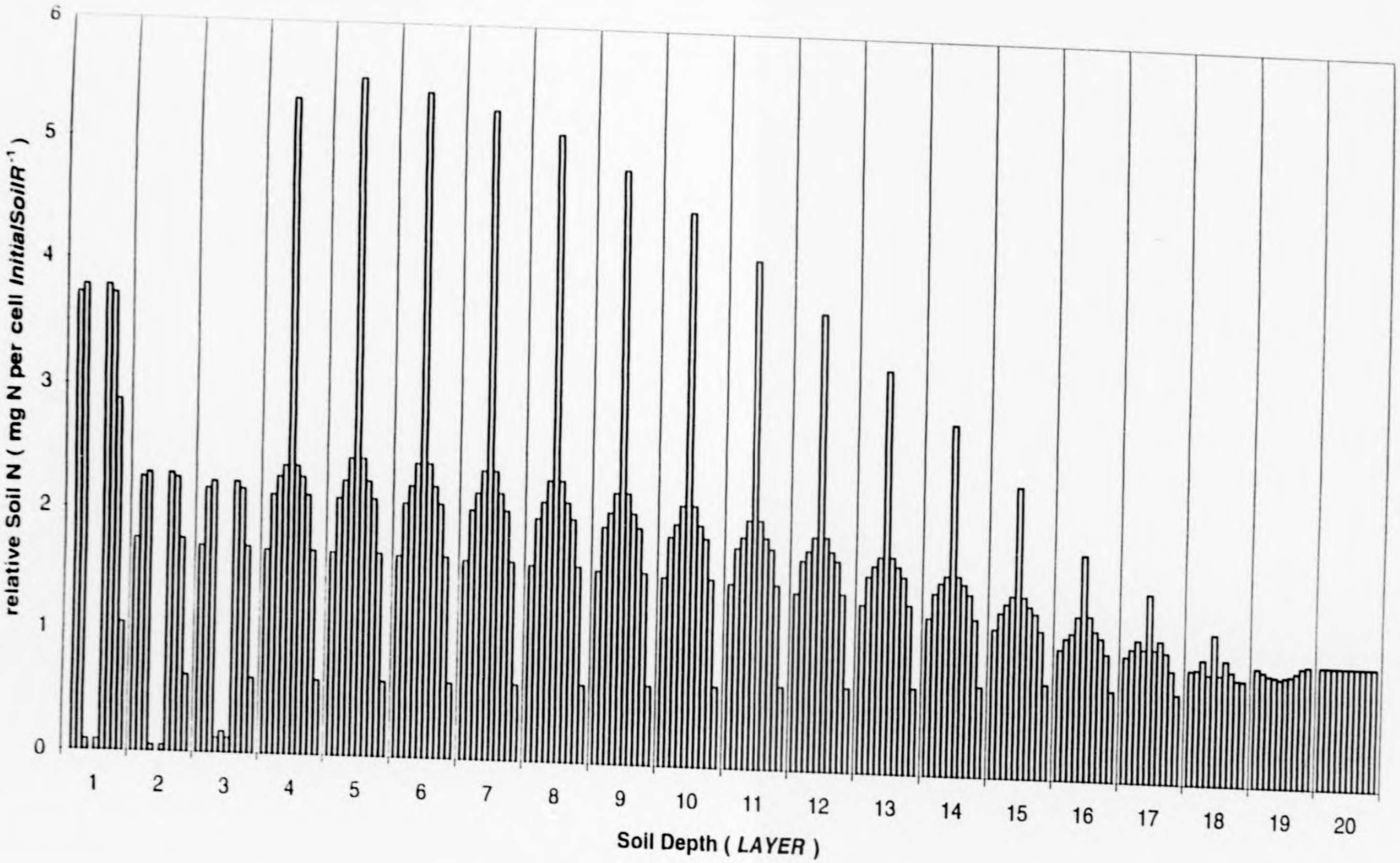


Figure 3.3 (a) Distribution of Soil R though soil profile: low N level.
Bars within each LAYER represent Soil N values in the x plane.

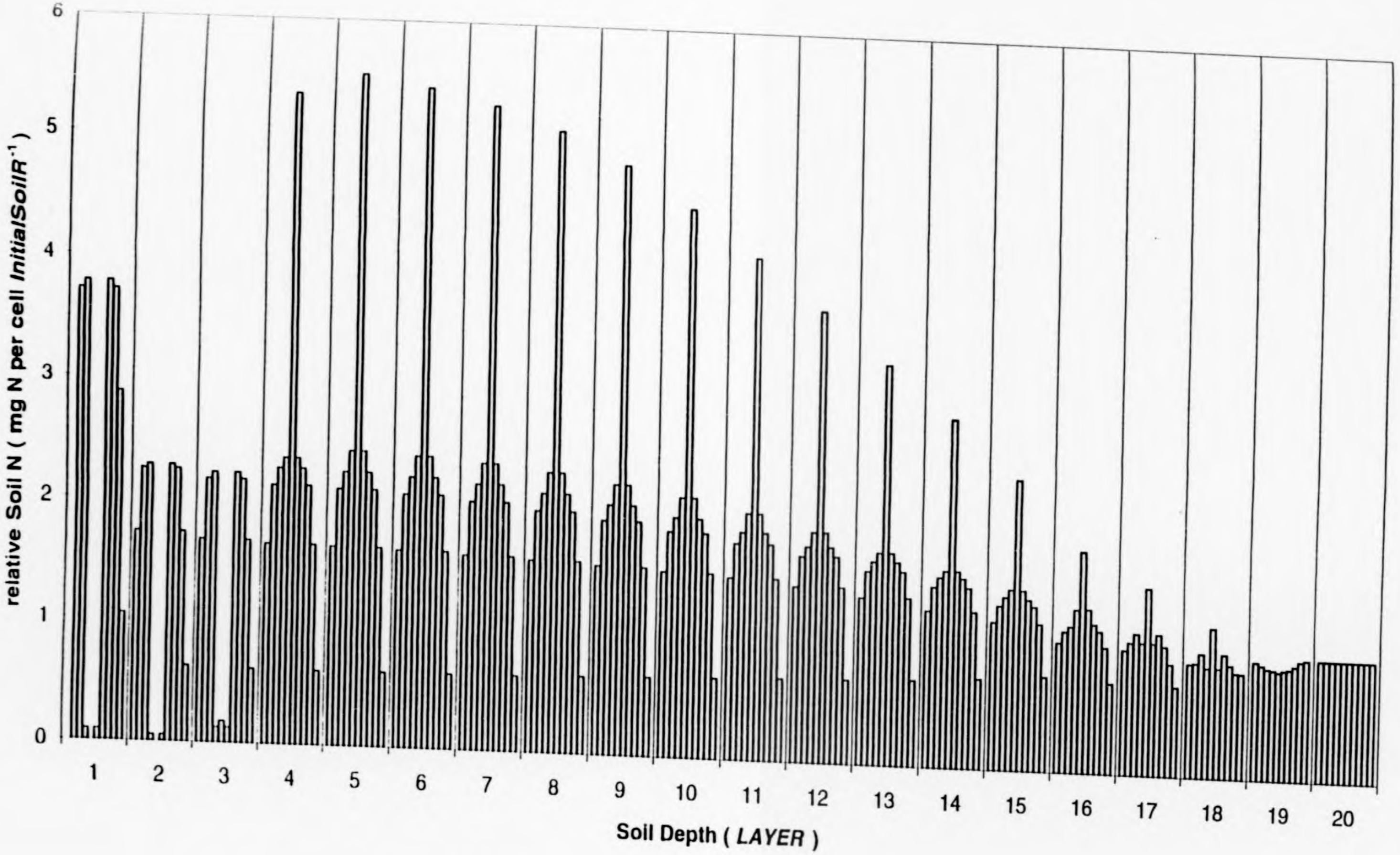


Figure 3.3 (a) Distribution of Soil R though soil profile: low N level.
Bars within each LAYER represent Soil N values in the x plane.

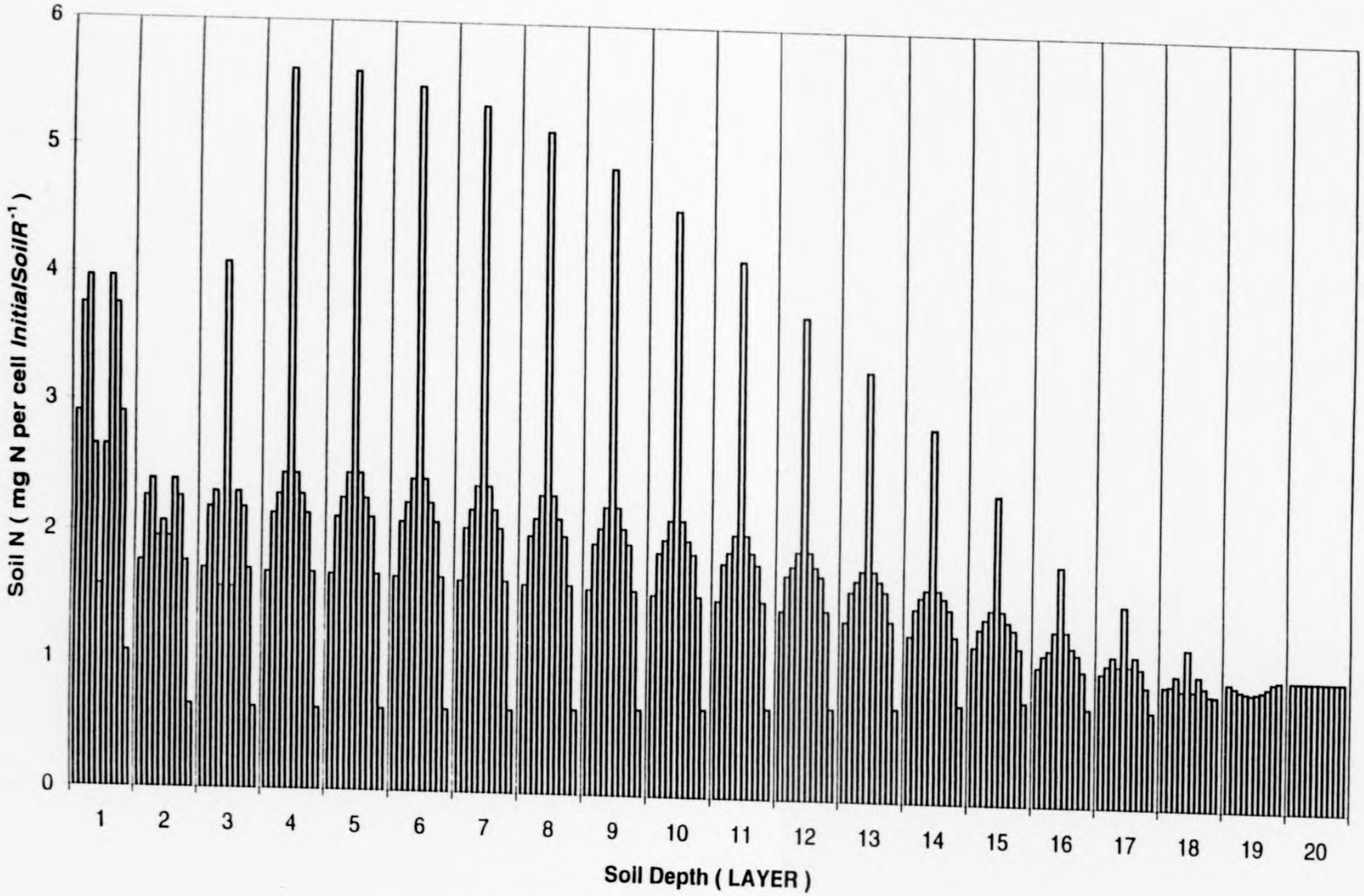


Figure 3.3 (b) Distribution of Soil R through soil profile: high N level.
Bars within each LAYER represent Soil N values in the x plane.

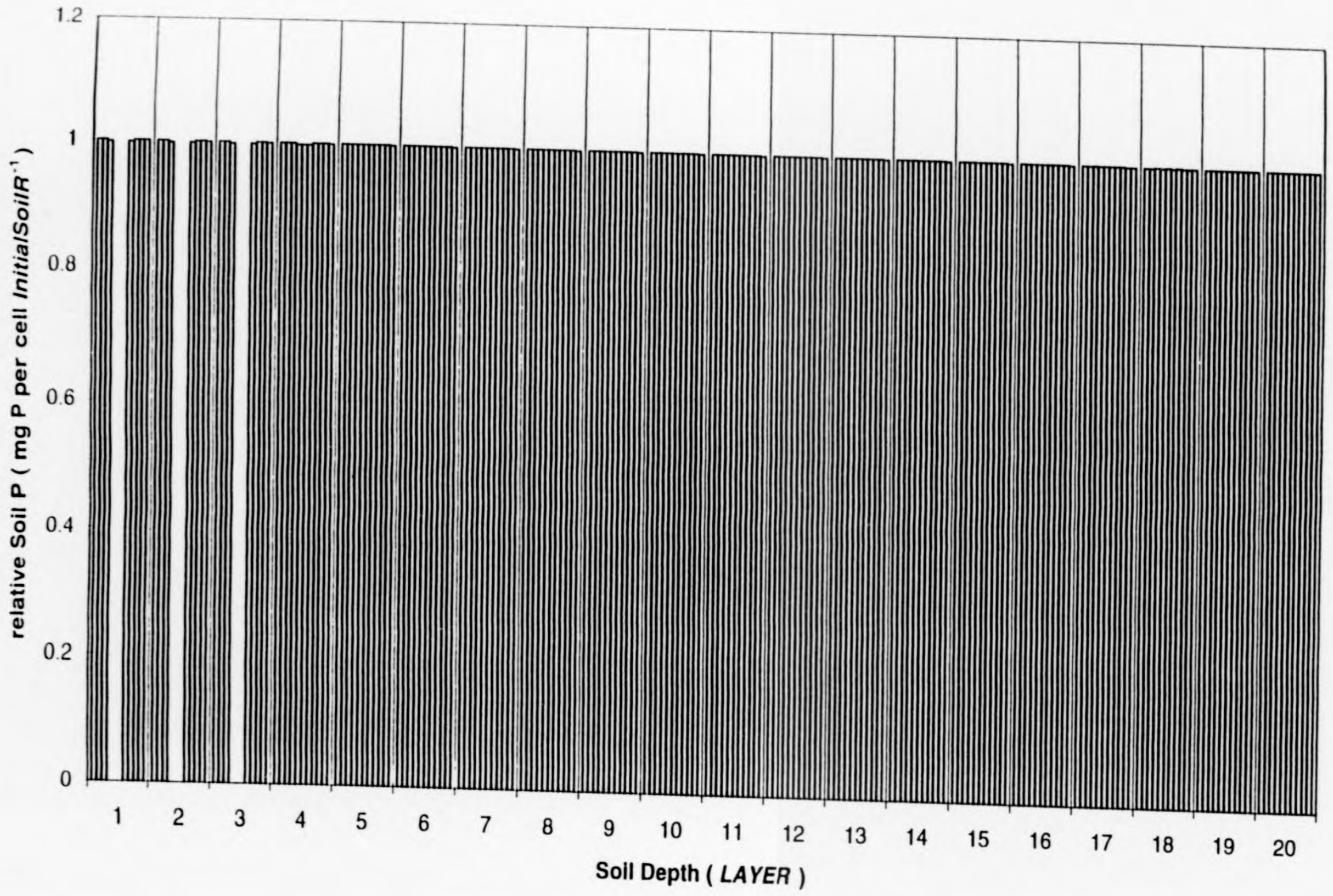


Figure 3.3 (c) Distribution of P through soil profile.
Bars within each LAYER represent Soil N values in the x plane.

of LAYERs 1, 2 and 3 corresponds exactly to the position of the block root system. This absence of nutrient is where uptake at the root surface is greater than the supply to the root surface via diffusion and mass flow. There is an accumulation around the root system in the N simulations (relative Soil R > 1) caused by mass flow to the root. Conversely, in the phosphorus simulation there is only depletion of soil P and no accumulation at the root surface. A small zone of depletion exists for phosphorus irrespective of input level, yet in the nitrogen simulation while depletion zones exist in both high and low simulations, the degree of depletion relative to input level is greatest in the low input level. This suggests that at high N input levels, individuals may not influence each other via depletion zones as such, but via the re-distribution of N by mass flow *and* depletion.

3.2.4 The effect of competition on R supply to a subject individual

With various assumptions (*e.g.* no positive effects of competition on performance, sensu Goldberg 1990) competition acts to reduce resource interception by the resource acquisition sites of a subject individual. In this respect, the effect of competition on R supply is quantitatively identical to physical impedance of resource movement from source to site of acquisition (see McConnaughay & Bazzaz 1992*a*, 1992*b*), or a lower overall availability of resource (with no competition). If competition reduces R supply then the subject individual should respond as it would in a monoculture with an equivalent R supply level and a light level equivalent to the levels experienced by an individual in mixture. **In this context, a plant does not actively compete for resources but merely experiences a reduction in resource availability due to competition: thus, plant resource competition can only be a *passive* process.**

It is the temporal and spatial lag between input and supply that permits nutrient competition. All light competition is by *direct* interception. Competition for N and P is predicted to differ, in that the intensity of P competition should be less than the intensity of N competition for a given time period at an equivalent input level (unit biomass produced per unit mass of element). This prediction is based on the different movement properties of N and P, and the subsequent difference in size of depletion zones. Harper

(1977:337) suggests that for phosphate ions the "extreme localization of depletion zones minimizes the chance that a rootlet of one plant will interfere with the availability of phosphate to another", though competition for P has been shown to occur (Caldwell *et al.* 1985, 1987; Krannitz *et al.* 1991). However, this difference in competition intensity may only be present at low soil nutrient levels, where depletion zones are most apparent for nitrogen (see above). Where possible this prediction is tested for all simulations by comparing the CIr which competing individuals and species experience, though the results may be confounded by the additional occurrence of light competition and the competitive abilities of the competing species. Hence, the results from intra-specific competition in monoculture of species *a* with below-ground competition only, should present the most representative results for comparison (see section 3.4.3).

3.3 Plant traits

3.3.1 Introduction

A great deal of research has investigated the physiological basis of competitive ability in an attempt to understand the mechanisms governing a species' success or failure in certain habitats and conditions. Many of these studies have focused on specific plant traits which relate directly to the environment of the plant such as root:shoot ratio, leaf area index and ratio, and specific tissue activity rates (for examples see Aerts *et al.* 1992, Olff *et al.* 1990). Prompted by the observation that species from productive habitats have significantly higher RGR_{max} values than species from unproductive habitats, various studies have sought to describe physiological differences between such species types, focusing on growth rate with respect to nutrient availability (for examples see Boot & Mensink 1991, Kachi & Rorison 1991, Rorison *et al.* 1981) and the ecological significance of growth rate (van Andel & Biere 1990, Chapin 1980, Grime & Hunt 1975, Poorter 1990). Architectural differences between the herbaceous species in habitats of differing productivity have also received widespread attention (see Caldwell & Richards 1986, Fitter 1987). Invariably, such studies are comparative, contrasting species adapted to unproductive habitats with species adapted to productive habitats.

The simulations performed here attempt to investigate the link between simple plant traits (biomass allocation and growth rate) and the competitive ability these traits confer, and also the relationship between the CIr experienced by competitors and the CA of the subject species.

3.3.2 Species *a* — the reference species

Introduction

As stated in section 3.1.7, species *a* is the reference species by which the competitive ability of all other model species may be determined. The traits assigned to species *a* are presumed to be competitively neutral, *i.e.* species *a* is intended to be a non-specialist with regards to competitive ability above- and below-ground and over a gradient of soil resource availability. Subsequently, the allocation pattern of species *a* is unbiased and constant with a root:shoot ratio of 1 (*PartR*=0.5 and *PartC*=0.5; see section 2.2.12). Growth characteristics of *a* feature a 'moderate' assimilation rate with growth coupled to resource acquisition: *gcR*=0.5 and *gcC*=0.5 (see section 2.2.11). The plant variables assigned to species *a* are listed in Table 3.3.

Simulations

Species *a* is simulated in monoculture at two densities: 'mono' monoculture density, *i.e.* 25 individuals within modelled space; and 'mixture' density, *i.e.* 50 individuals within modelled space (see section 3.1.5). These simulations are performed along an N and P gradient (runs 1n, 1p, 2n, and 2p: see Table 3.2). This enables the intra-specific competition intensity which *a* experiences to be calculated.

Results

The results from these simulations are presented in Figures 3.4n and 3.4p. The information used from the 'mixture' density is not from all individuals of *a* in the simulation, but 25 individuals in the same initial positions as in the 'mono' density monoculture; this follows an identical format to the species pair mixture simulations and in effect treats species *a* at the 'mixture' density as two separate competing populations.

Yields, mortality and plant size

Species *a* achieves a yield at all points along the R gradients at standard monoculture density (*i.e.* species *a* is viable); this is important considering the role of

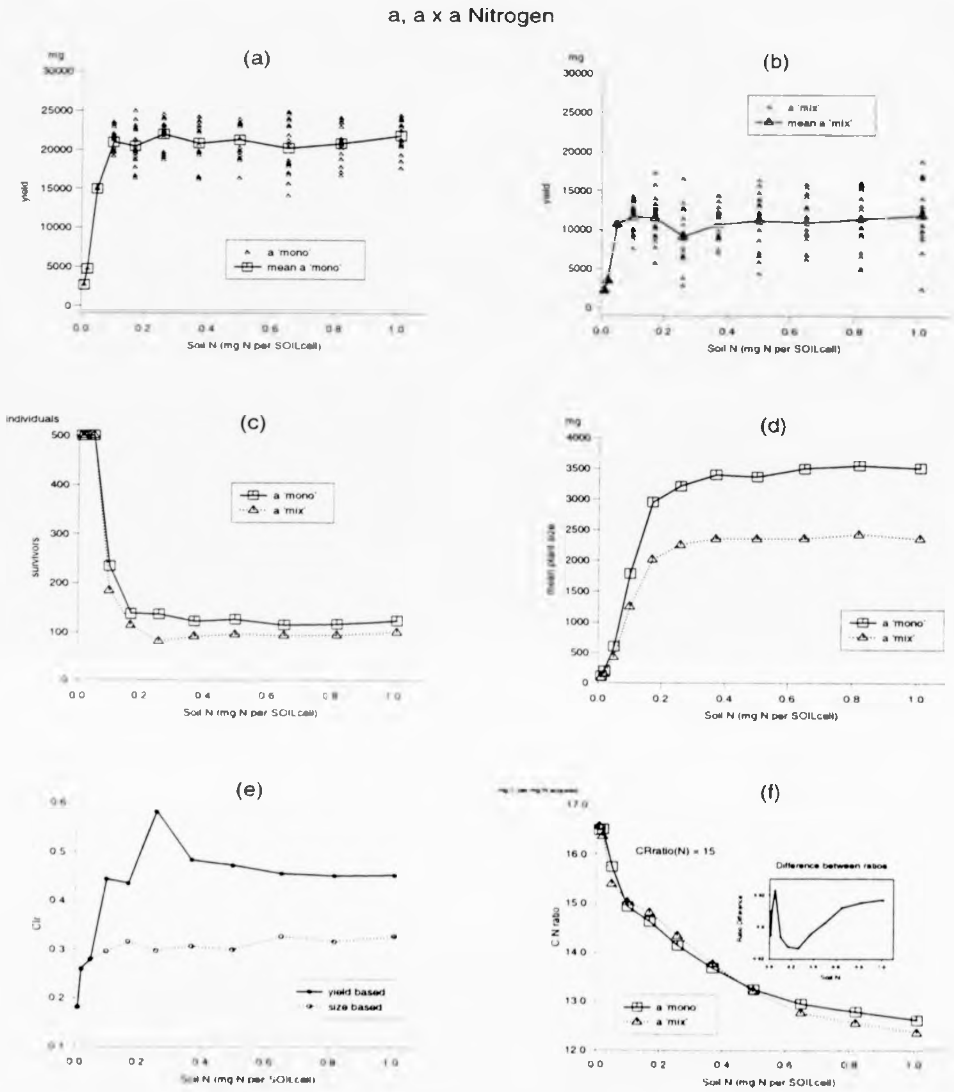


Figure 3.4n. Results of reference species *a* at low ('mono') and high ('mix') densities across Soil N gradient: (a) yield at low density; (b) yield at high density; (c) number of surviving individuals; (d) mean size of surviving individuals; (e) relative Competition Intensity (CIr); (f) ratio of acquired resources.

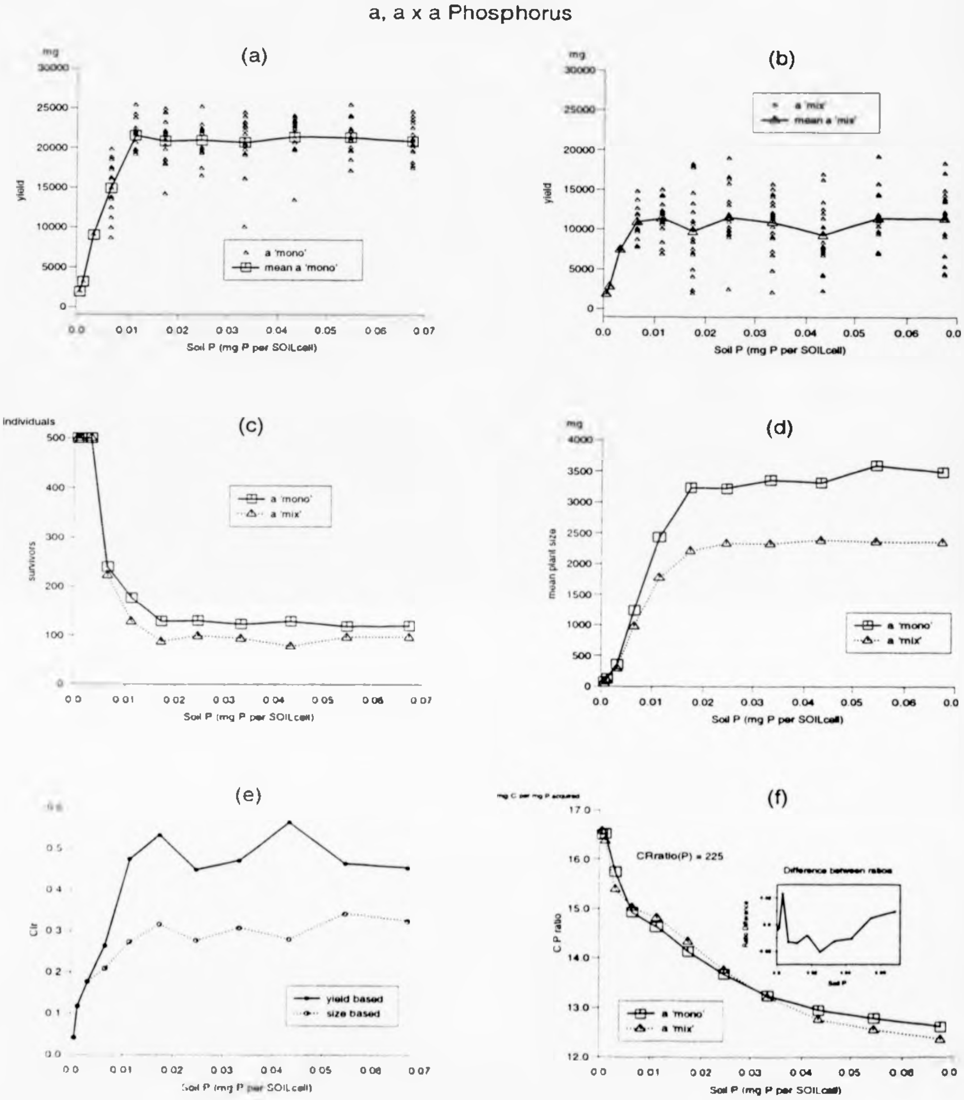


Figure 3.4p. Results of reference species *a* at low ('mono') and high ('mix') densities across Soil P gradient: (a) yield at low density; (b) yield at high density; (c) number of surviving individuals; (d) mean size of surviving individuals; (e) relative Competition Intensity (CIr); (f) ratio of acquired resources.

species *a* as a reference species. The mean yield and mean plant size of *a* decreases with an increase in density between 'mono' and 'mixture' densities (the mean yield refers to the yield of the population of 25 individuals; total yield of *all* 50 individuals of *a* was about the same as for 25 individuals; see above).

At Soil R levels 1,2 and 3 there is no plant death; above this total mortality increases with increasing yield (*i.e.* reaches maximum). The spatial resolution of the model limits the level of accuracy in determining competition processes: this is likely to affect the results most at low R levels where individuals consist of few cells, in contrast to high R levels where individuals are comprised of many cells. Self-thinning occurs: mortality increases both along the R gradient (with increasing productivity) and with an increase in density. Mean plant size (*i.e.* mean size of surviving plants), while increasing with Soil R to a maximum size set by plant traits and environment, also decreases with an increase in density. All individual plant sizes are identical at the lowest R level (both N and P simulations), while self-thinning is apparent at the highest R levels: this suggests that the selected gradient range encompasses the full range of plant yield response to R level.

Ratio of acquired resources (C:R acquired ratio)

A trade-off between ability to compete above- and below-ground should be exhibited in the ratio between total C and total Soil R acquired; the total includes C and R incorporated into biomass in addition to the amount of C and R stored within *Cpool* and *Rpool* respectively. Where *C:R acquired ratio* > *CRratio* (as defined in the model, section 2.2.11.4) R limits growth; conversely, where *C:R acquired ratio* < *CRratio*, C limits growth. Thus, as soil R increases, growth becomes less limited by R and increasingly limited by light.

The effect of competition on total acquisition of resources may be seen by the difference between the C:R ratios of *species a* at low (mono) and high (mix) densities, scaled by *CRratio*:

$$RatioDifference = \frac{(C{:}R\ acquired\ ratio_{mono}) - (C{:}R\ acquired\ ratio_{mix})}{CRratio} \quad (3.1)$$

where $C{:}R\ acquired\ ratio_{mono}$ and $C{:}R\ acquired\ ratio_{mix}$ refer to the ratios at low (mono) and high (mix) densities, and *CRratio* is the ratio of C and R incorporated into biomass (as defined in section 2.2.11.4). The results are shown on the inset plots of Figures 3.4n(f) and 3.4p(f).

If competition is predominantly for soil R, $C{:}R\ acquired\ ratio_{mono} < C{:}R\ acquired\ ratio_{mix}$, and $RatioDifference < 0$; if competition is predominantly for light, $C{:}R\ acquired\ ratio_{mono} > C{:}R\ acquired\ ratio_{mix}$, and $RatioDifference > 0$. The results of this method of competition analysis are expected to differ considerably between species, as different resource utilization and maintenance rates will affect the ratio (*e.g.* plastic allocation, section 3.3.3.2, acts to maintain a relatively constant acquisition ratio), hence this analysis is only performed for species *a*.

The results from this ratio analysis suggest that competition derived from an increase in density shifts the ratio in a general way along the soil R gradient: at very low R levels, C is more limiting than R; at intermediate R levels, R becomes more limiting than C; and at high R levels, C becomes limiting again. There are quantitative differences between the *RatioDifference* for N and P, though both follow this general pattern. However, as *a* has constant, unbiased allocation of growth to root and shoot, regardless of environment, and given that the net carbon expenditure for a root cell is potentially greater than that of a shoot cell (shoot cells produce C), the *C:R acquired ratio* is likely to shift according to plant size, and environmental R:C supply level ratio, therefore confounding these results.

Competition Intensity

The relative competition intensity that species *a* experiences is calculated using two measures of performance: by the relative reduction in yield (yield based CIr), and by the relative reduction in mean plant size (size based CIr). The resulting intensities are shown in Figures 3.4n(e) and 3.4p(e) across nitrogen and phosphorus gradients respectively. In general terms, competition intensity appears to be greater at higher nutrient supply levels than at lower levels in both cases.

It must be remembered that this cannot be a definitive test of theoretical predictions concerning overall competition intensity over environmental gradients for the following reasons: this is not a natural plant community and the intensity measured here is the net effect of component above- and below-ground competition intensities. The relative contribution to net CIr of above- and below-ground CIr is expected to be sensitive to the parameter settings of the model, particularly those determining relative acquisition rates of above- and below-ground resources.

Effect of R supply properties on yield, plant size and competition

The different movement properties of N and P are apparent in the differences between the yields and mean plant size at both densities, though there was only a significant difference at low R levels (levels 1 to 3).

3.3.3 Allocation

Introduction

The presumption that co-existing species utilize resources in different ways has been long been invoked as an explanation of species differentiation along resource gradients (*e.g.* Chapin 1980, Grime 1979, Tilman 1982): differential allocation of new biomass between above- and below-ground plant parts, or more specifically between nutrient and light intercepting tissues, is one possible way in which this difference between species may be manifested (Tilman 1988).

The general axiom that species from unproductive habitats have greater root:shoot ratios than species from productive habitats is well established in plant ecology (see Chapin 1980). The reasoning behind this is that a high root:shoot ratio is advantageous in nutrient-poor conditions (unproductive habitats) as it confers a greater surface area for nutrient absorption, all else being equal (*e.g.* respiration and 'tolerance' traits). The trade-off between rate of nutrient acquisition and photosynthetic rate (allocation to root vs. allocation to leaf) is presumed to cause differentiation of species abundance along a productivity gradient and forms the basis for Tilman's ALLOCATE model (see sections 1.3.5 and 2.1.2) as different ratios confer different competitive abilities above- and below-ground (Tilman 1988).

While there is evidence that species of unproductive habitats do tend to exhibit greater root:shoot ratios (Chapin 1980, Tilman 1988), the supposed generality of this axiom is questioned by several studies (see Arts *et al.* 1992; Berendse & Elberse 1990, Elberse & Berendse 1993), though it appears in these cases that potentially reduced nutrient acquisition is compensated for by other traits (*i.e.* reduced loss of resources from individuals, greater efficiency of use, increased absorptive area per-unit mass of root). Thus, these results do not necessarily contradict the Resource Ratio hypothesis (Tilman 1982) as they may be considered 'special cases' of the theory (*e.g.* Huisman 1994). Many of the recent studies investigating root:shoot ratio and species habitat type have included plastic allocation between root and shoot (see section 3.3.3.2), as well as within root and shoot systems (Grime *et al.* 1986, 1989; Jackson *et al.* 1990), though the implications of plasticity for competition at the species and community level remain largely unknown.

3.3.3.1 Constant allocation

Introduction

Like the species modelled in Tilman's ALLOCATE model, species *b1* through to *b7* (see Table 3.3) possess constant allocation between root and shoot, though the root:shoot ratio differs between these species ranging from 4 (species *b1*) to 0.11 (species *b7*). These species only differ from species *a* in allocation pattern.

While allocation between root and shoot undoubtably affects the ability of a species to acquire nutrient and light resources, a particular allocation pattern does not necessarily confer the same acquisition ability for different soil nutrients: P uptake is expected to be closely correlated to root mass because the root must intercept to reach the (relatively) immobile P (see section 3.2); N uptake may be significantly influenced by water uptake rates which, in turn, are affected by transpiration rates and the root:shoot ratio of the individual.

Simulations

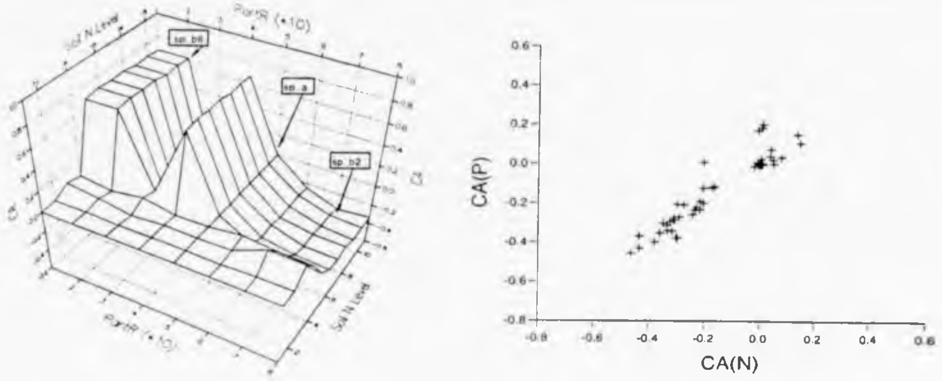
Species *b1* to *b7* are all simulated in competition with species *a* (runs 3 - 9) to determine the competitive ability of each allocation pattern across both nitrogen and phosphorus gradients. In addition, monoculture simulations of species *b2* (high allocation to root) and species *b6* (high allocation to shoot) and a mixture simulation of *b2* with *b6* are performed (runs 11, 12 and 10 respectively). This enables the relative intensity of competition (CIr) to be determined for all competing species in runs 4, 8 and 10. Finally species *a*, *b4*, *b5*, *b6* and *b7* are simulated in a multi-species simulation across both soil N and P gradients (run m1).

Results

The CA results of runs 3 - 9 are shown in Figure 3.5. More detailed results for runs 8, 10, 11 and 12 are shown in Figures 3.6n, 3.6p, 3.7n and 3.7p. The multi-species run m1 results are shown in Figure 3.22.

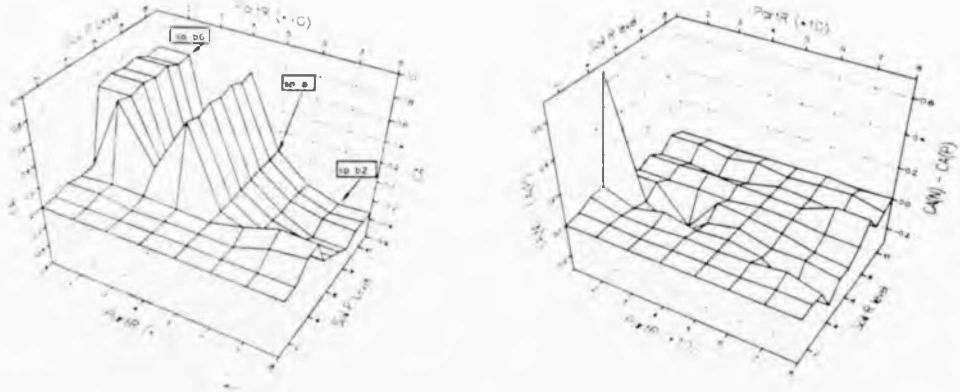
Viability of allocation pattern

Some allocation patterns are not viable, even under monoculture conditions: too much allocation to roots produces a daily maintenance demand that cannot be met by photosynthesis. For example, species *b2* only survives at the lowest soil R supply level of the P gradient (Fig. 3.7p).



(e) Size based CA, Nitrogen

(g) Size based CA(N) vs. size based CA(P)



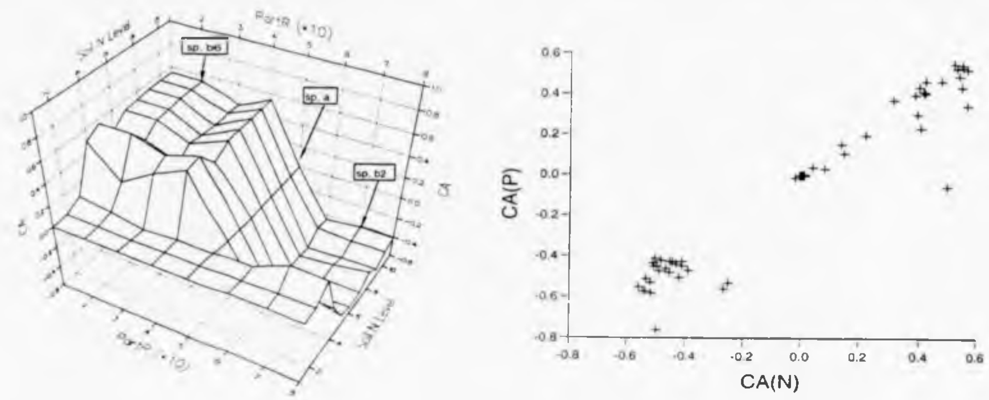
(f) Size based CA, Phosphorus

(h) Difference between size based CA(N) and CA(P)

Figure 3.5. Competitive Abilities of species *b1* through to *b7* across both N and P gradients, where species *b1* has highest allocation to root, and species *b7* has highest allocation to shoot: (a) yield based CA across N gradient; (b) yield based CA across P gradient; (c) and (d) comparison between yield based CA across N and P gradients. See over for (e) to (h).

(a) Yield based CA, Nitrogen

(c) CA for Nitrogen vs. CA for Phosphorus



(b) Yield based CA, Phosphorus

(d) Difference between CA(N) and CA(P)

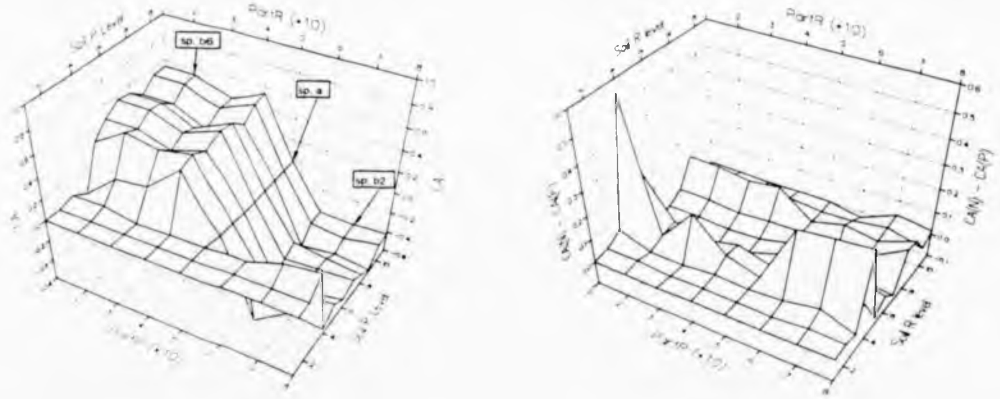


Figure 3.5 (continued) Competitive Abilities of species *b1* through to *b7* across both N and P gradients, where species *b1* has highest allocation to root, and species *b7* has highest allocation to shoot: (e) size based CA across N gradient; (f) size based CA across P gradient; (g) and (h) comparison between size based CA across N and P gradients.

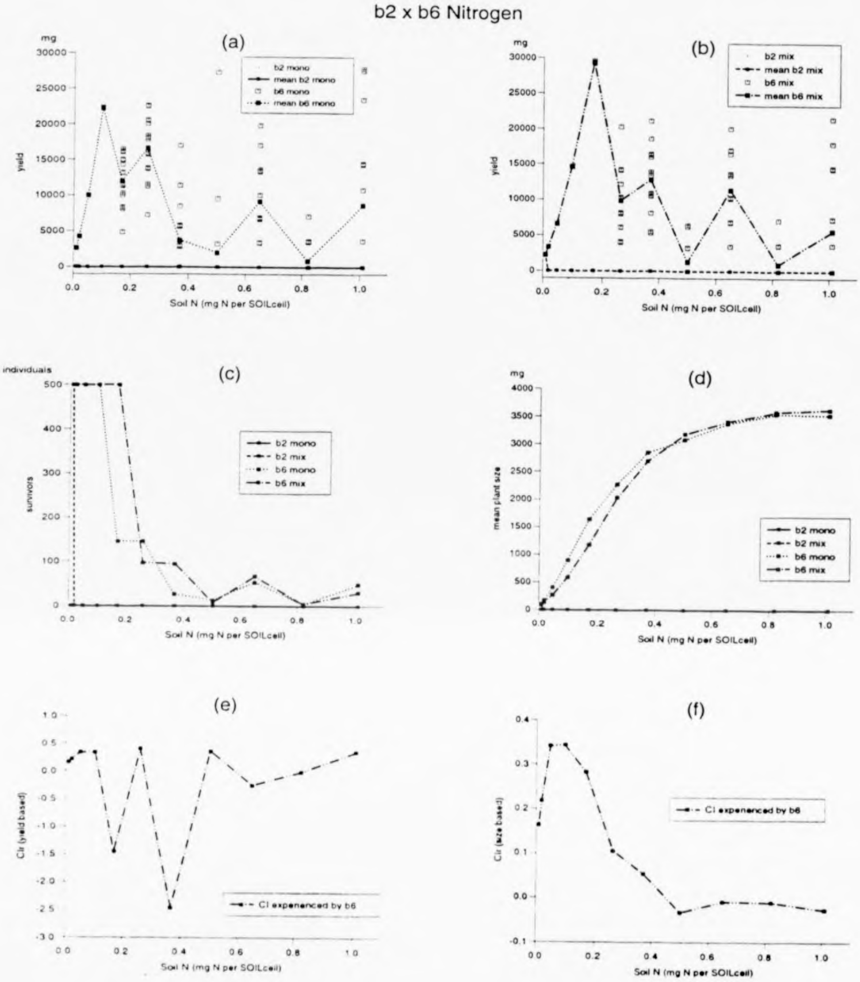


Figure 3.6n. Results of competition between species *b2* (high root allocation) and *b6* (high shoot allocation) across Soil N gradient: (a) yields in monoculture; (b) yields in mixture; (c) number of surviving individuals; (d) mean size of surviving individuals; (e) yield based CIr; (f) size based CIr.

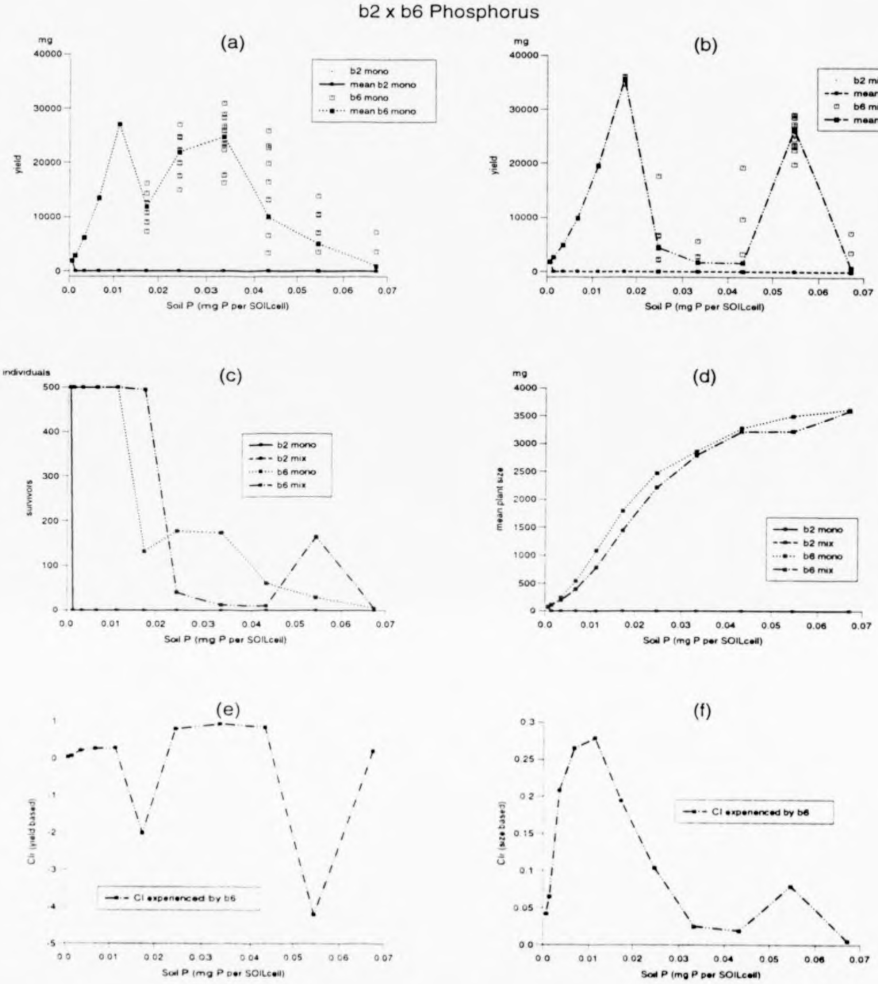


Figure 3.6p. Results of competition between species *b2* (high root allocation) and *b6* (high shoot allocation) across Soil P gradient: (a) yields in monoculture; (b) yields in mixture; (c) number of surviving individuals; (d) mean size of surviving individuals; (e) yield based CIr; (f) size based CIr.

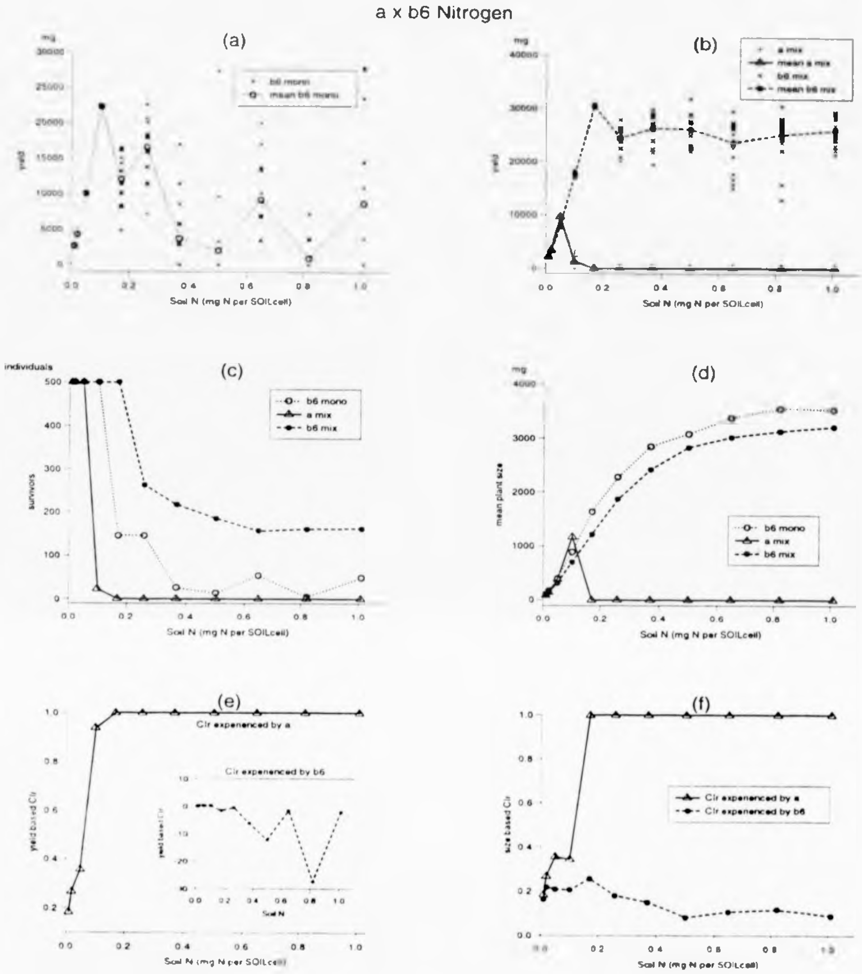


Figure 3.7n. Results of competition between species *a* (moderate root allocation) and *b6* (high shoot allocation) across Soil N gradient: (a) yields in monoculture; (b) yields in mixture; (c) number of surviving individuals; (d) mean size of surviving individuals; (e) yield based CIr; (f) size based CIr.

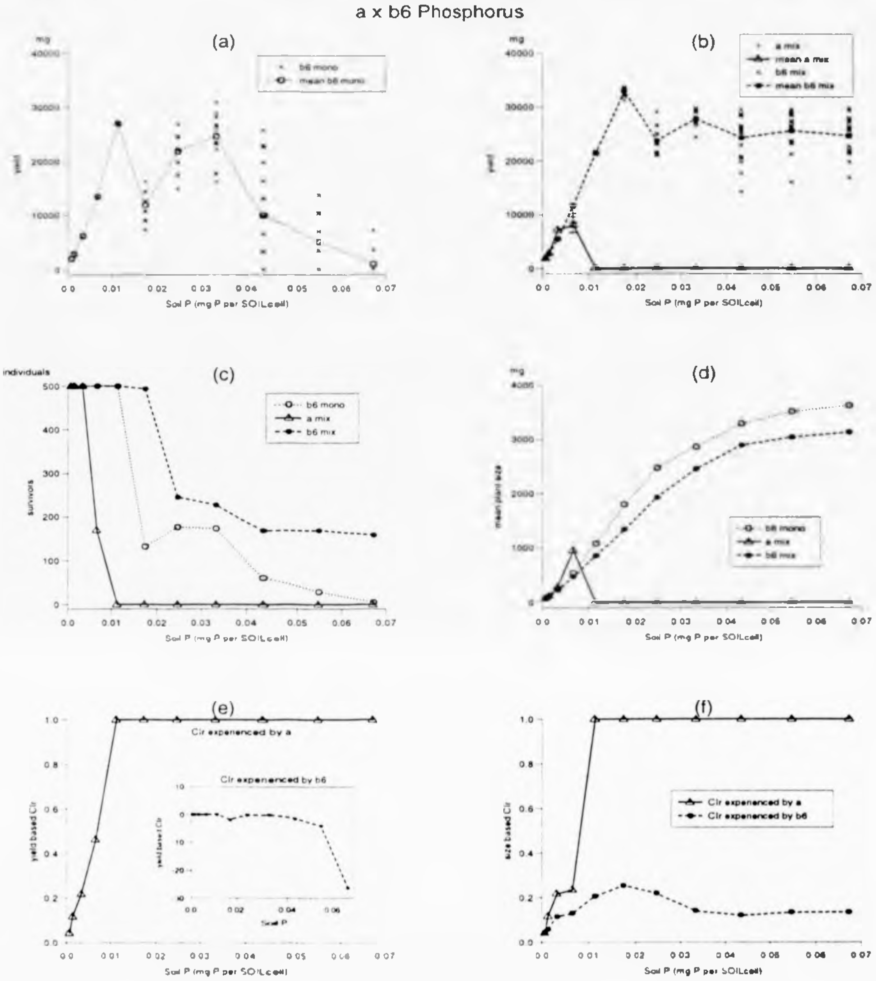


Figure 3.7p. Results of competition between species *a* (moderate root allocation) and *b6* (high shoot allocation) across Soil P gradient: (a) yields in monoculture; (b) yields in mixture; (c) number of surviving individuals; (d) mean size of surviving individuals; (e) yield based CIr; (f) size based CIr.

Competitive Ability of species b1 to b7 over R gradient

The yield based Competitive Abilities (as defined in section 1.5.4) of species *b1* to *b7* are shown in Figure 3.5: these are the CA of the species at the population level. There is little difference between species CA at very low Soil R levels (levels 1 and 2) though high allocation to roots (species *b1* and b2) does confer a slight competitive advantage (CA>0). At higher Soil R levels (levels>2), higher allocation to shoot confers a greater competitive ability, where competition is predominantly for light (see section 3.4). The final yields of species *b2* and *b6* in run 10 cannot be predicted from the respective competitive abilities of the species, as CA is based on reduction in the performance of species *a* regardless of the viability of a species, though the qualitative outcome can. Allocation to shoot would seem to be much more competitively advantageous than allocation to root. This is most likely due to the assumptions of the model, mainly that plant death may occur from insufficient C, but not from insufficient R, hence the model system is likely to favour plants with a high ability to compete for light. In addition, light is the limiting resource at the majority of Soil R levels (see Figures 3.4n(f) and 3.4p(f), and also section 3.4).

Comparison between CA with N and P competition, Figure 3.5(c), is not the same as competitive ability for N or P as resources, as CA here also includes ability to compete for light, and this will affect the performance of reference species *a* as well as its own performance. Thus, this cannot be a test of the correlation between competitive abilities for different resources (see section 1.4.3). However, the most striking difference between the competitive abilities across N and P gradients, is the CA under N simulation of species *b7* (very high shoot allocation) is much greater than the CA under P simulation at R level 4.

Competition intensity

b2 × *b6* (run 10): CIr across the R gradient can only be calculated for *b6* as *b2* suffer total mortality in monoculture (and mixture) at all but one R level. At the population scale (yield based CIr), *b6* experiences variable CIr, even performing better in mixture than in monoculture (overyield, *sensu* Wilson 1988). At the individual scale (size based CIr), *b6* experiences maximal CIr at low soil R levels; the intensity decreases with increasing soil R. This suggests that the greatest impact of *b2* on *b6* occurs at low soil R levels where *b2* exerts greatest CA; see Figure 3.5(e) and (f).

Multi-species simulation

In runs 40n and 40p, species *a*, *b4*, *b5*, *b6* and *b7* are simulated in competition with each other across N and P gradients respectively. As the competitive abilities for these species show little differentiation in relation to their allocation characters, direct multi-species competition is performed in an attempt at clarification. The density of each species is 10 individuals within the normal volume of space (see section 3.1.5); no monoculture runs at this density are performed so the CIr experienced by each species can not be determined. The results are presented in Figure 3.22.

As Soil R increases, there is a qualitative change in the relative abundance of the species. The mean yields of the species over the soil P gradient, follow the RWR of the species, *i.e.* as soil P increases the dominant (*i.e.* greatest biomass) species are *a*, *b4*, *b5* and *b6*. Along the soil N gradient, the order of dominants is slightly different; this is due to the confounding effect of root:shoot ratio and consequent transpiration rate on N acquisition (due to the mass flow properties of N; see above).

3.3.3.2 Plastic allocation

Introduction

The inclusion to the simulations of a plastic allocation response to the environment is more realistic than assuming a constant allocation pattern as many studies investigating root:shoot ratio across a resource gradient have revealed a plastic response (Robinson & Rorison 1988, Berendse & Elberse 1989, 1990; Kachi & Rorison 1989, Boot 1990, Olff *et al.* 1990, Boot & Mensink 1991, Aerts *et al.* 1992, Kasperbauer & Hunt 1992). This response is presumed to be ecologically advantageous by attempting to maintain an optimal balance between light and soil resources which limit growth (Reynolds & Thornley 1982, Chapin *et al.* 1987), and therefore reduce the effect of competitive processes on these resources. Allocation plasticity also has major implications for the Resource Ratio theory: if all plants may adjust their allocation pattern in response to environmental changes induced by other plants (resource competition, sensu Tilman 1988; *e.g.* reduced light due to shading) then the concept of competitive superiority resulting from possession of the most 'suitable' (constant) allocation pattern must be questioned. Tilman suggests that allocational plasticity may only be advantageous in habitats that the individual finds 'sub-optimal' (Tilman 1988:309-310).

Species

Species *c1* and *c2* represent moderate and high degrees of unbiased plasticity in allocation of biomass to root and shoot (see Table 3.3). Unbiased in this context means that the allocation pattern does not 'favour' either root or shoot, the root weight ratio (RWR) of *c1* may vary between 0.7 and 0.3 depending on environmental conditions; RWR of *c2* may vary between 0.9 and 0.1 . By comparison, species *d1* and *d2* feature 'biased' plastic allocation: RWR of *d1* may vary between 0.8 and 0.5, while the RWR of *d2* may vary between 0.5 and 0.2. These species only differ from species *a* in allocation pattern.

Simulations

Species *c1*, *c1*, *d1* and *d2* are all simulated in monoculture (runs 15, 16, 20 & 21 respectively) and in competition with species *a* (runs 13, 14, 17 and 18 respectively); species *d1* and *d2* are simulated in competition with each other (run 19).

Results

The results for *c1* (mono) and *a* × *c1* (mix) are shown in Figures 3.8n and 3.8p. The results for *c2* (mono) and *a* × *c2* (mix) are shown in Figures 3.9n and 3.9p. The results for *d1* and *d2* (monocultures) and *d1* × *d2* (mixtures) are shown in Figures 3.10n and 3.10p. The competitive abilities of species *c1*, *c1*, *d1* and *d2* are shown in Figure 8.

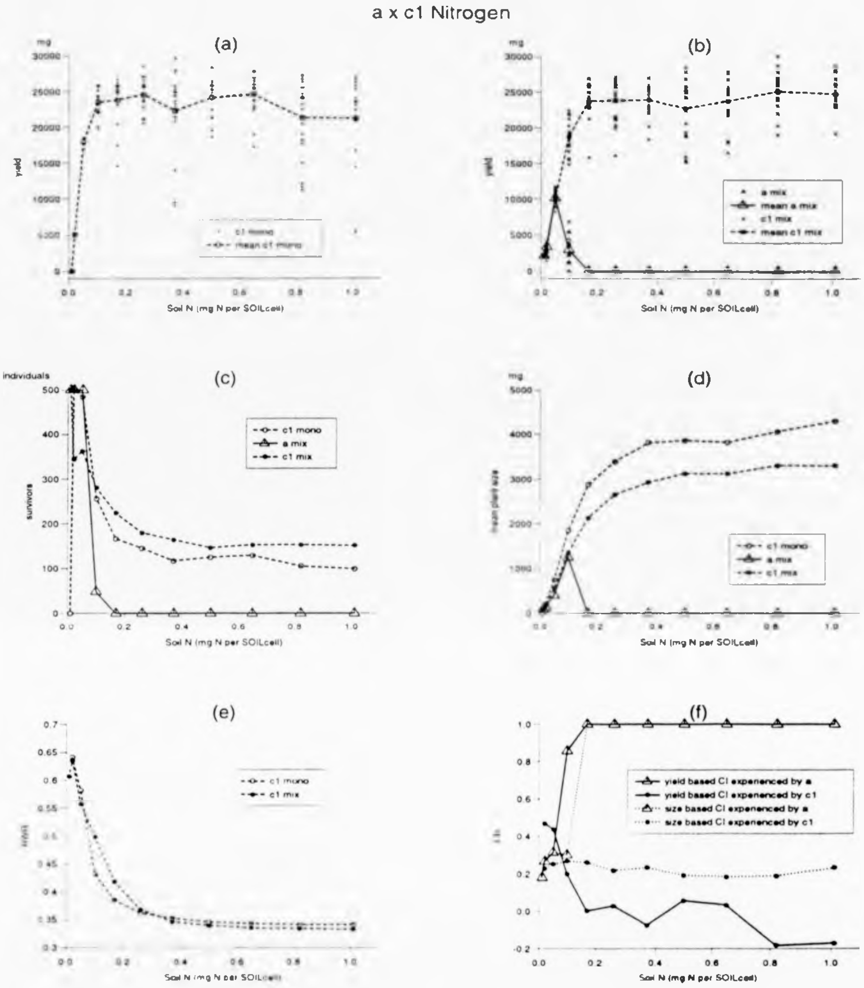


Figure 3.8n. Results of competition between species *a* (constant allocation) and *c1* (plastic allocation) across Soil N gradient: (a) yields in monoculture; (b) yields in mixture; (c) number of surviving individuals; (d) mean size of surviving individuals; (e) root weight ratio (RWR, mg root mg^{-1} total biomass); (f) yield and size based CIr.

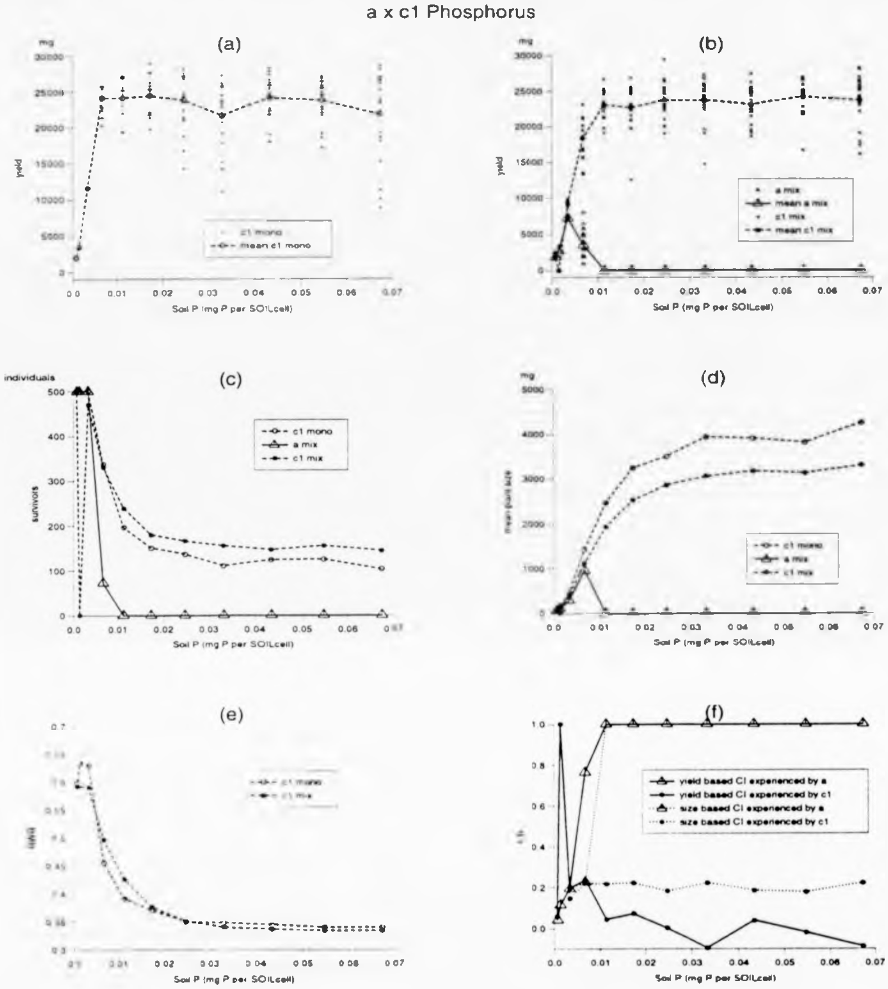


Figure 3.8p. Results of competition between species *a* (constant allocation) and *c1* (plastic allocation) across Soil P gradient: (a) yields in monoculture; (b) yields in mixture; (c) number of surviving individuals; (d) mean size of surviving individuals; (e) root weight ratio (RWR, mg root mg^{-1} total biomass); (f) yield and size based CIr.

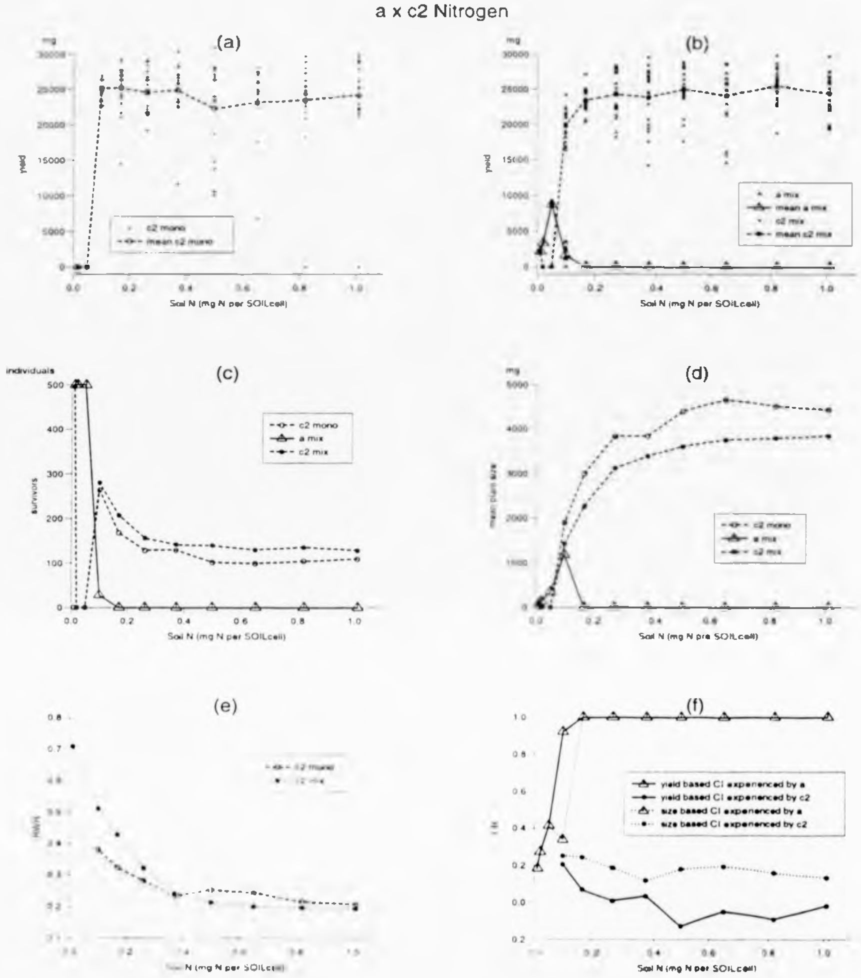


Figure 3.9n. Results of competition between species *a* (constant allocation) and *c2* (highly plastic allocation) across Soil N gradient: (a) yields in monoculture; (b) yields in mixture; (c) number of surviving individuals; (d) mean size of surviving individuals; (e) root weight ratio (RWR, mg root mg^{-1} total biomass); (f) yield and size based CIr.

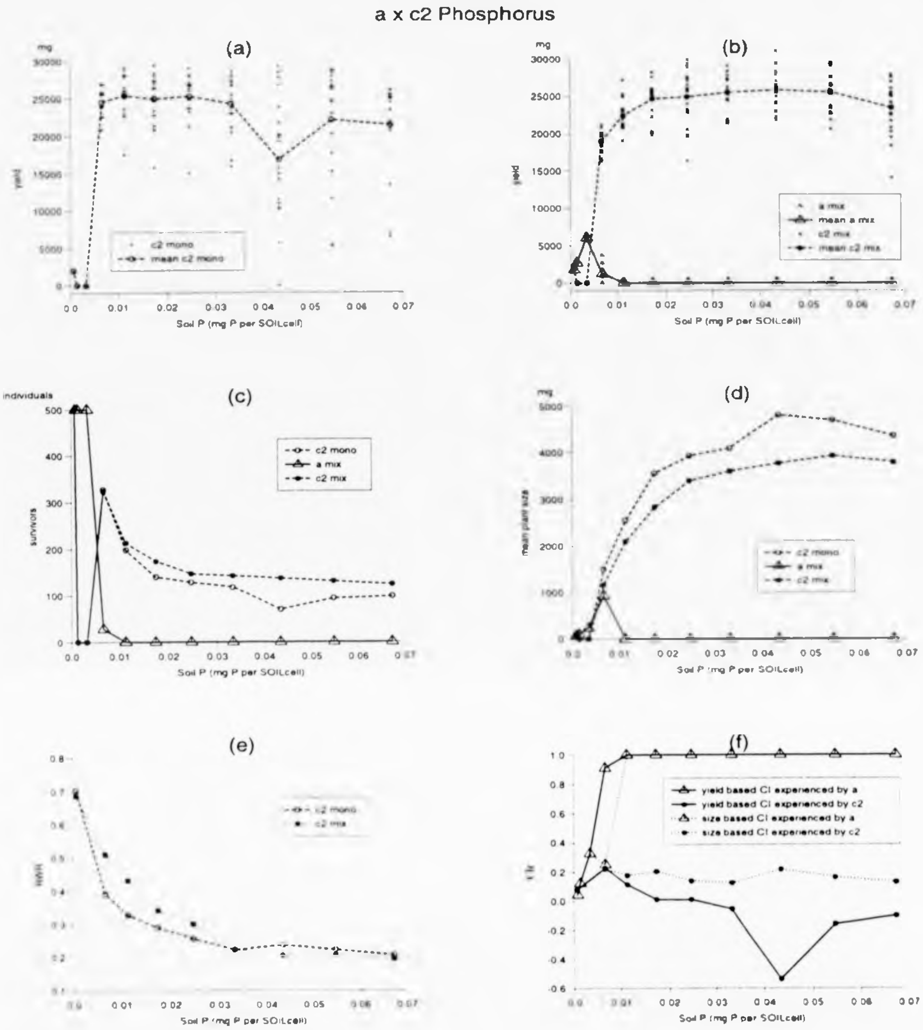


Figure 3.9p. Results of competition between species *a* (constant allocation) and *c2* (highly plastic allocation) across Soil P gradient: (a) yields in monoculture; (b) yields in mixture; (c) number of surviving individuals; (d) mean size of surviving individuals; (e) root weight ratio (RWR, mg root mg^{-1} total biomass); (f) yield and size based CIr.

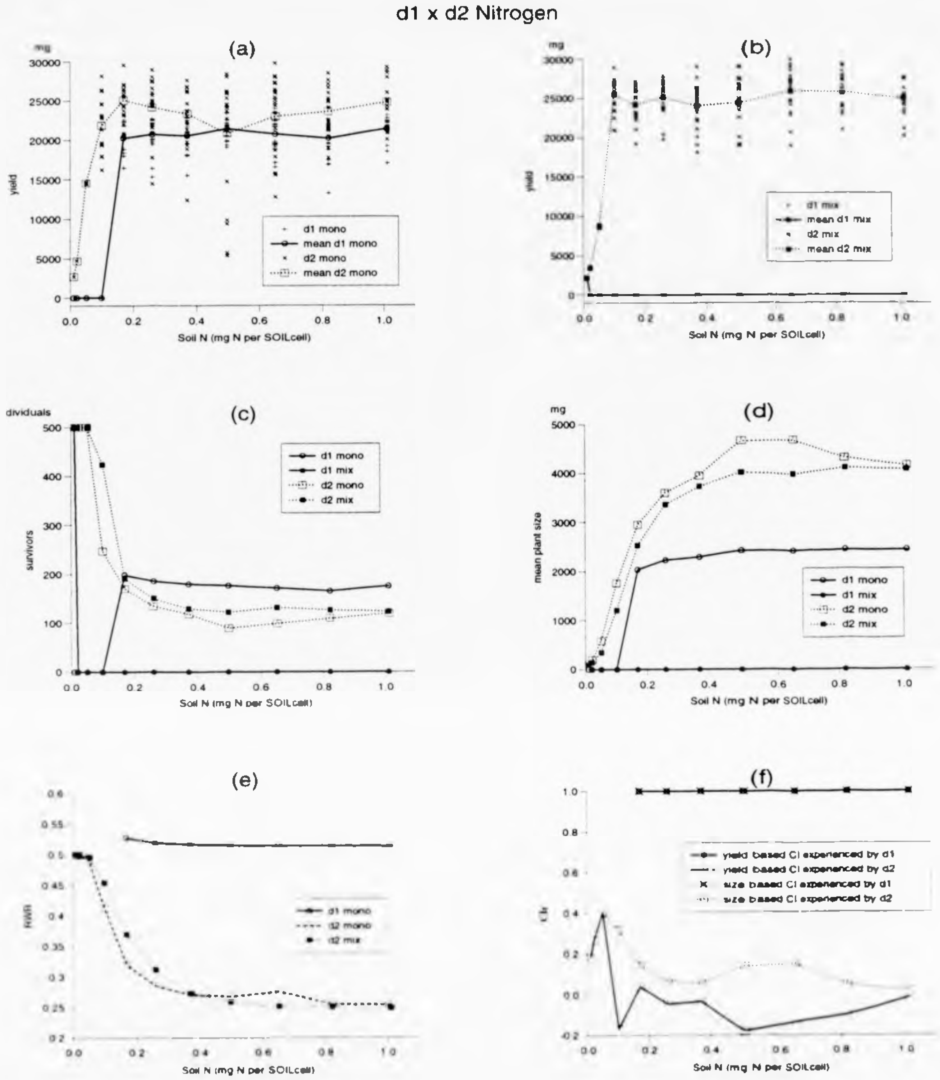


Figure 3.10n. Results of competition between species *d1* (plastic root-biased allocation) and *d2* (plastic shoot-biased allocation) across Soil N gradient: (a) yields in monoculture; (b) yields in mixture; (c) number of surviving individuals; (d) mean size of surviving individuals; (e) root weight ratio (RWR, mg root mg^{-1} total biomass); (f) yield and size based CIr.

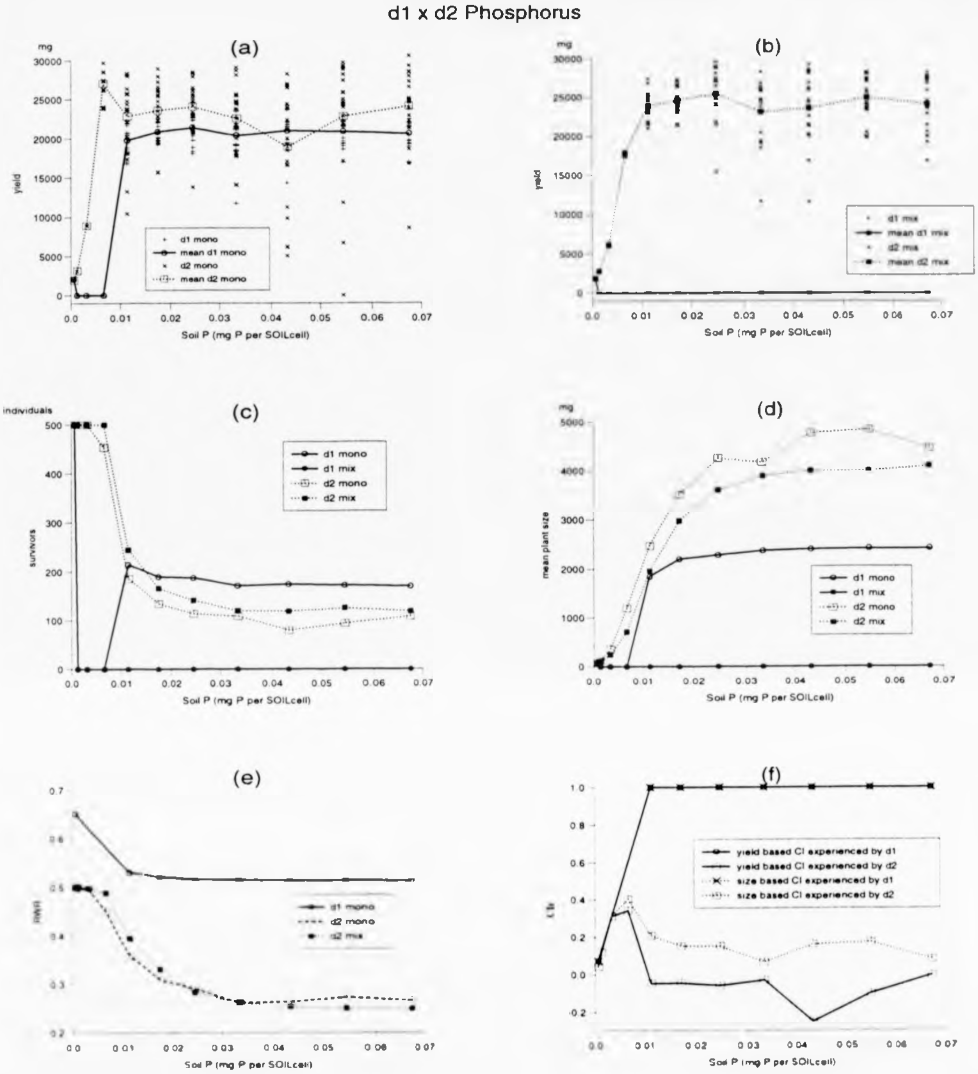


Figure 3.10p. Results of competition between species *d1* (plastic root-biased allocation) and *d2* (plastic shoot-biased allocation) across Soil P gradient: (a) yields in monoculture; (b) yields in mixture; (c) number of surviving individuals; (d) mean size of surviving individuals; (e) root weight ratio (RWR, mg root mg^{-1} total biomass); (f) yield and size based CIr.

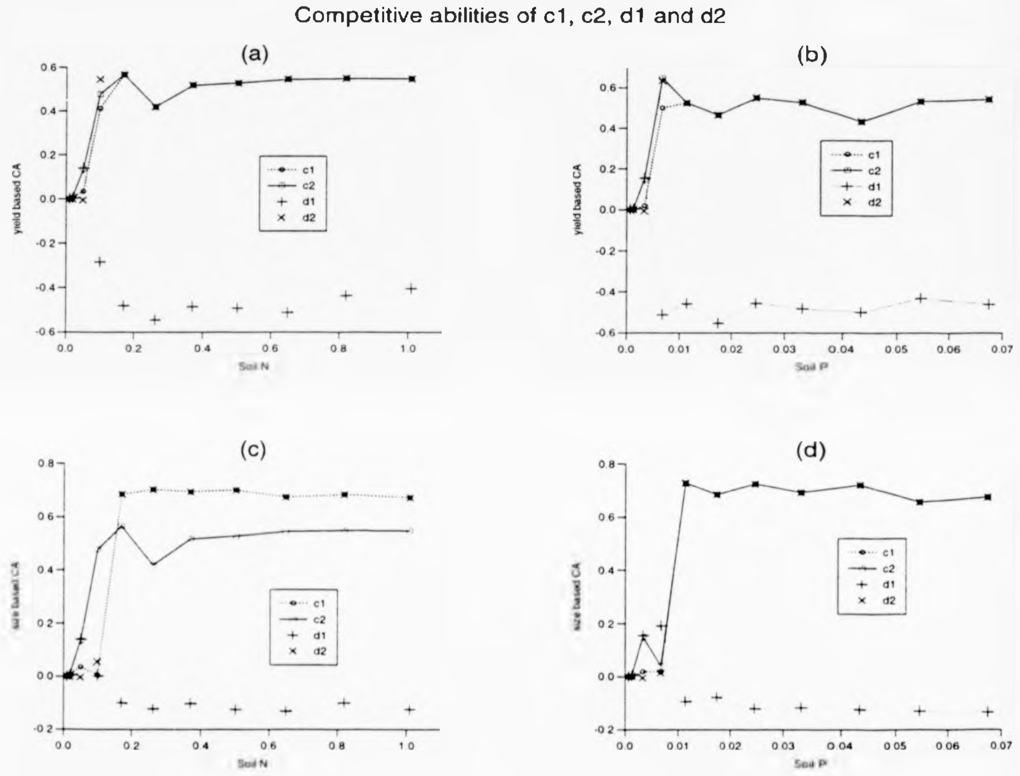


Figure 3.11. Competitive Abilities of species *c1*, *c2*, *d1* and *d2* across both N and P gradients: (a) yield based CA across N gradient; (b) yield based CA across P gradient; (c) size based CA across N gradient; (d) size based CA across P gradient.

Yields, mortality and plant size

A plastic allocation response does not necessarily confer a viable plant at all Soil R levels. For example, an individual with an extremely plastic allocation response will not survive at low R levels if the growth allocated to shoot is insufficient to provide the carbon based maintenance costs of the whole plant. This occurs at low soil N levels for species *c1* and at several Soil N levels for species *c2* in the nitrogen monoculture runs. Mean plant size of *c1* and *c2* in monocultures are consistently greater than for *a*, and both *c1* and *c2* outcompete species *a* in runs 13 and 14 in both N and P simulations.

Root weight ratios

The root weight ratios (RWR) of species *c1*, *c2*, *d1* and *d2* decrease as Soil R level increase. As Soil R increases, the ratio of C:R of the internal *Rpool* and *Cpool* (see section 2.2.12) increases, prompting the change in allocation. The effect of competition switching from predominantly below-ground to predominantly above-ground as Soil R increases (see section 3.4) is manifested in the difference between the RWR from monoculture and mixture (competition) runs (see Figures 3.8n(e), 3.8p(e), 3.9n(e) and 3.9p(e)). Where R most limits growth, RWR from mixture is greater than RWR from monoculture, signifying a compensatory increase in allocation to root; where C is most limiting, RWR from mixture is lower than RWR from monoculture as the plants exhibit a compensatory increase in shoot allocation. The RWR values of *c2* (the most plastic species) explain why species *b1* to *b3* (RWR more than 0.5) perform so badly at almost all Soil R levels: a RWR of more than 0.5 is best suited to R levels less than 4.

Competition Intensity

The CIr that the populations of *c1* and *c2* experience (yield based CIr) in competition with *a* generally decreases as Soil R increases, while the individuals of *c1* and *c2* (size based) experience little change in CIr along the nutrient gradients: this is because the plastic response that *c1* and *c2* possess decrease the competitive effect that species *a* exerts. The population and the individuals of species *a* experience increasing competition intensity with increasing soil R, until shading by *c1* and *c2* provokes full mortality in mixture.

In runs 19n and 19p (plastic, root biased allocation vs. plastic, shoot biased allocation), the population and individuals of species *d1* experience maximal competition intensity. The individuals of *d2* experience greater intensity than the population of *d2*.

Competitive Abilities

The competitive abilities of species *c1*, *c2*, *d1* and *d2* are shown in Figure 3.11, for the population (yield based CA) and the individual (size based CA). Unbiased plastic allocation (species *c1* and *c2*) conveys a competitive advantage, as does plastic response biased towards shoot (*d2*), in comparison with species *a*. However *d1*, with plastic response biased to root, has a lower CA than species *a* except at the lowest R levels, but here *d1* is unviable (in monoculture) where high allocation to root is predicted to be an advantage. Thus, although plasticity generally confers a competitive advantage (compared to a non-plastic response), the advantage is dependent on the bias of allocation. There appears to be differential ability between N and P simulations for individuals of *c2* to compete: *c2* exhibits a greater individual CA across a P gradient than a N gradient. This is another example of the effect of allocation pattern on transpiration rate and uptake rate of N (see section 3.3.3.1). The root:shoot ratio generated by extreme plasticity is not the optimum ratio required for N uptake; a less extreme allocation pattern (*c1*) performs better, though there is no difference in CA across a P gradient.

Effect of R supply properties on yields and competition

Other than the effect of root/shoot allocation on CA (described above) there is little qualitative difference between these N and P simulations. Any significant difference between mixture yields for N and P simulations occurs only at low soil R levels (levels 1 to 4). At low R levels where below-ground competition is maximal (see section 3.4) individuals experience generally greater CIr (size based) in the N simulations than in the P simulations, supporting the prediction made in section 3.2.

3.3.4 Coupled vs. uncoupled growth

Introduction

Growth characteristics are predicted to have profound implications for the competitive ability of a species (see sections 1.2.6 and 1.4.3) and the outcome of competition (Firbank & Watkinson 1990). It is not clear whether the growth rate of a species has been selected *per se*, or an inevitable consequence of selection acting on components of growth (*e.g.* resource use efficiency or factors reducing loss rates; see Garnier 1991, Poorter 1990). Two contrasting types of growth have been suggested for species adapted to productive habitats and unproductive habitats, the difference being the way in which the plant relates growth rate with resource acquisition rate: growth may either be coupled or uncoupled to resource acquisition (Grime 1988, Koide 1991).

Growth that is coupled to resource acquisition (*i.e.* growth rate is dependent on acquisition rate) is predicted to be of competitive advantage in habitats with abundant resources where survival stems from the rapid acquisition of resources. The positive feedback generated between resource acquisition and growth by such a growth regime serves to maximize resource acquisition rate.

Growth that is uncoupled to resource acquisition (*i.e.* growth rate is independent of acquisition rate), also termed 'luxury consumption' (Chapin 1980), enables internal 'storage' of acquired resources, thereby ensuring survival in conditions where such resources are essential and supply is periodic (Chapin 1980, Grime 1988).

Species

Species *e* has fully coupled growth (gcR=1.0, gcC=1.0; see Table 3.3), *i.e.* all resources acquired each day are submitted for assimilation into biomass (no storage as such, though see section 2.2.11). Species *f* has growth uncoupled from resource acquisition with a maximum growth rate of 1 mg biomass d^{-1} (see Table 3.3). Both species only differ from species *a* in growth characteristics.

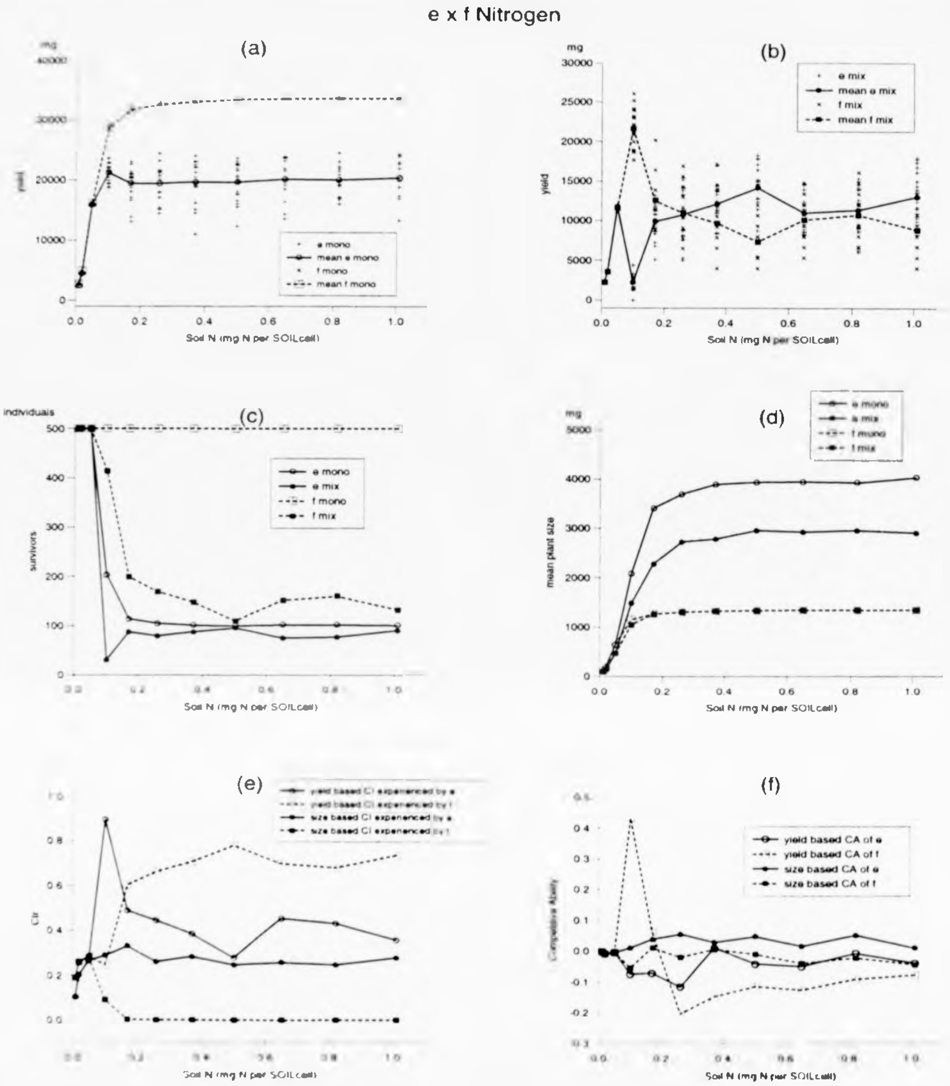


Figure 3.12n. Results of competition between species *e* (coupled growth) and *f* (uncoupled growth) across Soil N gradient: (a) yields in monoculture; (b) yields in mixture; (c) number of surviving individuals; (d) mean size of surviving individuals; (e) yield and size based CIr; (f) yield and size based CA.

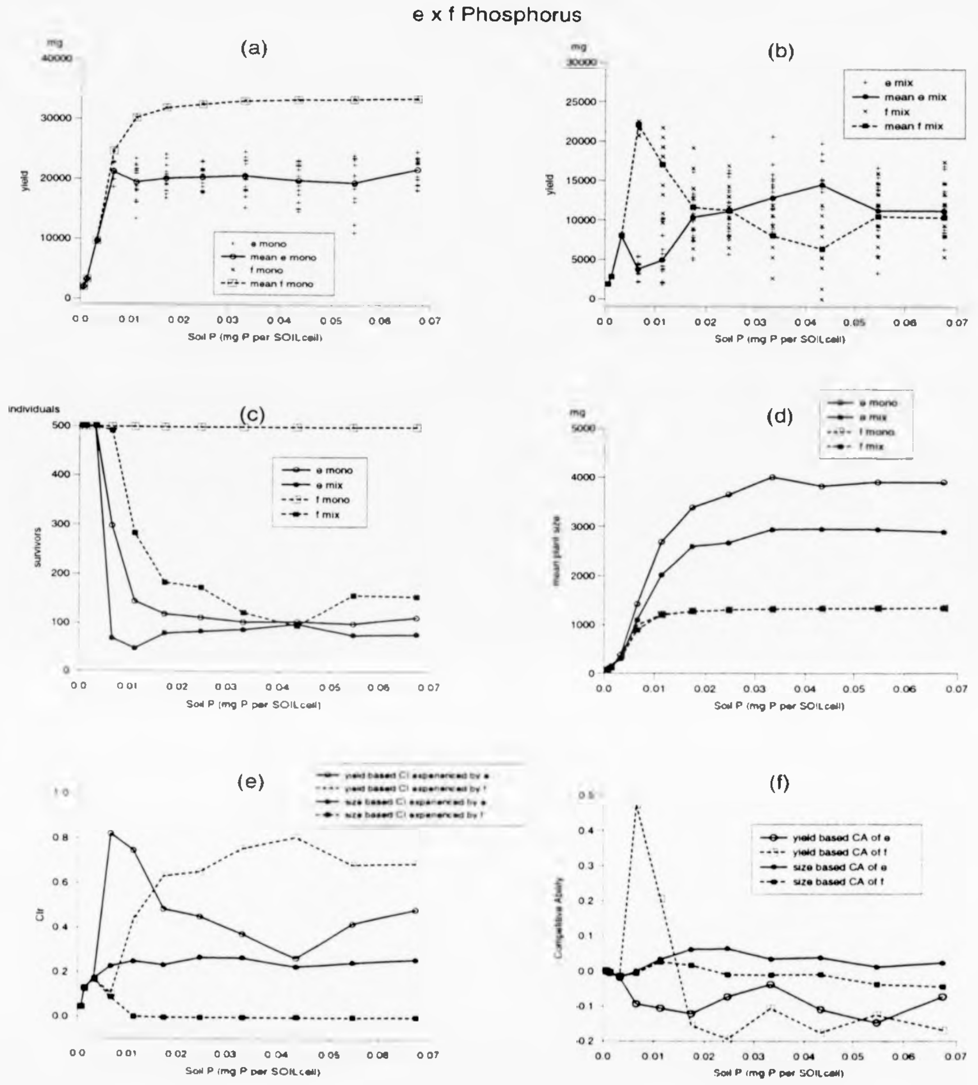


Figure 3.12p. Results of competition between species *e* (coupled growth) and *f* (uncoupled growth) across Soil P gradient: (a) yields in monoculture; (b) yields in mixture; (c) number of surviving individuals; (d) mean size of surviving individuals; (e) yield and size based CIr; (f) yield and size based CA.

Simulations

Species *e* and *f* are simulated in mixture (run 24), in monoculture (runs 25 and 26 respectively), and in mixture with species *a* (runs 22 and 23 respectively). This allows the calculation of CIr which *e* and *f* experience in mixture, and the CA of both *e* and *f*.

Results

The results for this section are shown in Figures 3.12n and 3.12p.

Yield, mortality and plant size

In monoculture *f* produces a greater mean yield than *e* at all Soil R levels in both N and P simulations; all individuals of *f* survive in monoculture at all Soil R levels in both the N and P simulations, where as *e* suffers slightly greater mortality than species *a* in monoculture (Fig. 3.12n(a,c) and 3.12p(a,c)). This difference in mortality is because *f* does not commit all acquired resources to growth but maintains a large internal 'store' of resources, which help buffer individuals against temporary resource supply reduction. This will be most beneficial to individuals experiencing shading by taller competing individuals and consequent reduction in C fixation: a large *Cpool* enables the individual to accommodate maintenance costs and survive. Thus *f* experiences no self-thinning, while *e* does. However, the distribution of yields achieved by *e* and *f* are variable and at some R levels there was considerable overlap of yields between the species.

In competition (mixture *e* × *f*, run 24) there is a 'switch' in competitive outcome: *f* produces a greater mean yield at low Soil R levels, while *e* produces a greater mean yield at higher Soil R levels under both N and P competition simulations (Fig. 3.12n(b) and 3.12p(b)).

Competition Intensity

At the population level, CIr that the two species experience in mixture corresponds well to the competitive outcome across the soil R gradient. The CIr that *e* experiences peaks at R level 4 (where *f* is dominant) and decreases at higher R levels, while *f* experiences increasing CIr

The individuals of both species experience different CIr than the populations: *e* experiences minimal CIr at R levels > 4, while *f* experiences a general increase with increasing soil R level (this occurs for both N and P gradients). At this same scale, competition is more intense for nitrogen than phosphorus at low soil R levels, for both *e* and *f*; this supports the prediction made in section 3.2 .

Competitive Ability

The competitive abilities of *e* and *f* also correspond well to the outcome of competition: the population of *f* (yield based CA) has the greater CA at low R levels, while at higher R levels the population of *e* has the greater CA. Thus, the 'switch' from *f* to *e* can be predicted from yield based CA.

The CA of the individuals of *e* was less than then CA of individuals of *f* at all R levels, except at R levels 1 to 3 (Fig. 3.12n(f) and 3.12p(f)). This suggests that uncoupled growth confers a competitive advantage only at low soil resource availability, at higher levels of R input coupled growth is of greater advantage.

Effect of R supply properties on yield and competition

There is a significant difference between the yields achieved by each species in mixture only at low R levels, and at these levels the individuals of both species experience greater CIr in the N simulation than the P simulation.

3.3.5 Combined Traits

Introduction

While the aim of the above sections is to investigate single plant traits and competitive outcome, this section attempts to bring together allocation and growth traits into more realistic plant species representative of plants adapted to unproductive and productive habitats. Note that the species constructed here only possess differences in allocation and growth 'regimes'.

Species

Species *g* is presumed to be representative of species adapted to unproductive habitats and the assigned traits attempt to reflect this (see Table 3.3). Species *g* has a constant allocation pattern biased to roots (*PartR*=0.6, *PartC*=0.4) – Tilman (1988) predicts that high investment in root mass is advantageous in an unproductive habitat, while the CSR model predicts no or low plasticity in allocation of plants adapted to unproductive habitats (see sections 1.2.6 and 1.4.3). *g* possesses uncoupled growth, as this too is predicted to be an adapted plant trait in unproductive habitats (see section 3.3.4): thus *g* has a maximum growth rate of 1 mg biomass d^{-1} as for species *f* (see Table 3.3). Species *g* is not strictly comparable with the Stress-Tolerator syndrome of the CSR model, as the only 'tolerance' trait it possesses is the accumulation of a resource reserve when acquisition is greater than assimilation rate.

Species *h* is presumed to be representative of species adapted to productive habitats (see Table 3.3). Both Grime and Tilman predict that species adapted to such habitats will exhibit a low root:shoot ratio and the CSR model predicts a high degree of plasticity in allocation of biomass between root and shoot (see sections 1.2.6, 1.4.3 and 3.3.3). Consequently, the allocation pattern of *h* is plastic and biased to shoot as for species *d2* (*PartR*=0.2, *PartC*=0.5). Species *h* has been assigned coupled growth as for species *e* (*g*cR=1.0, *g*cC=1.0; see Table 3.3) – this trait is also predicted to be of advantage in a productive environment (see section 3.3.4).

Simulations

The simulations are: species *a* in mixture with *g* (run 27) and with *h* (run 28); *e* and *f* in mixture (run 29) and both species as monocultures (*e* mono: run 30; *f* mono: run 31). This allows the calculation of CIr that *g* and *h* experience in mixture, and also the calculation of the CA of both *g* and *h*.

Results

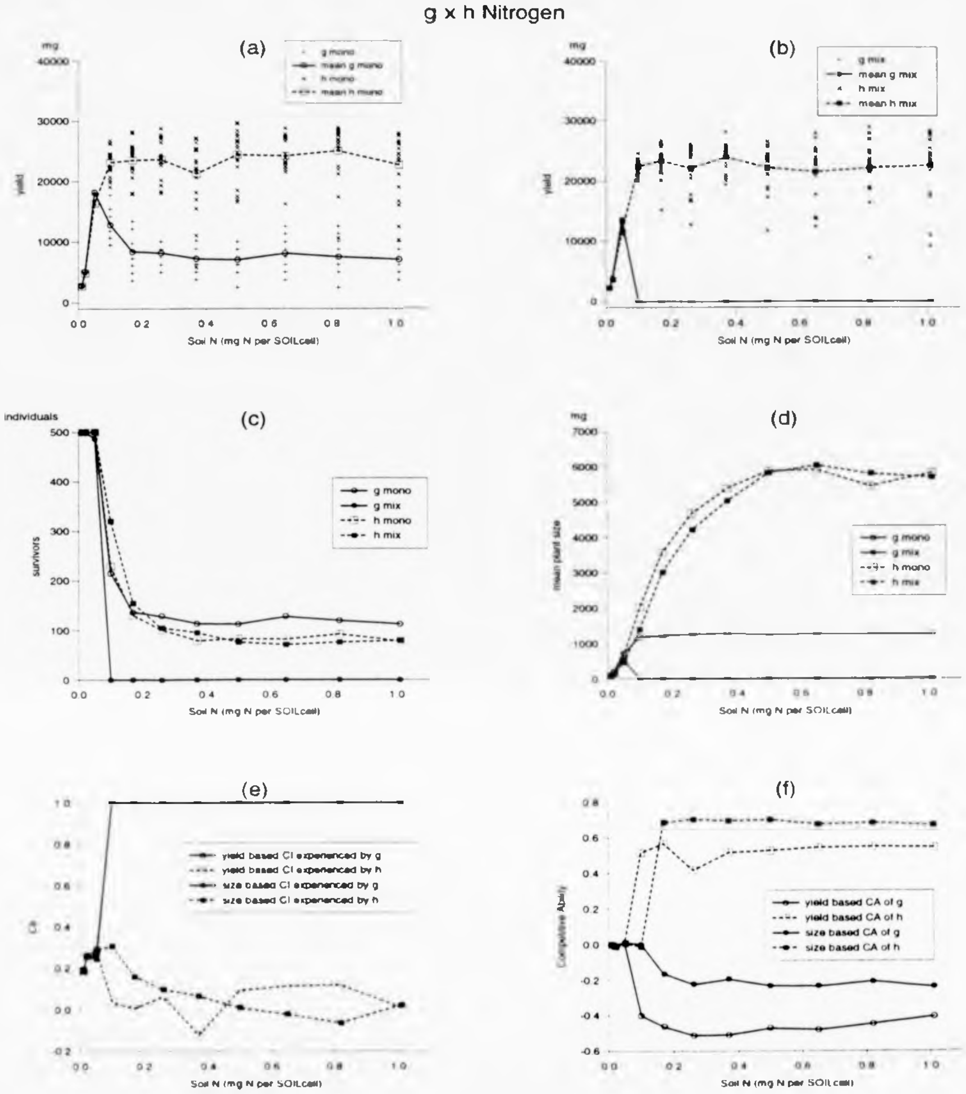


Figure 3.13n. Results of competition between species *g* (high root allocation, uncoupled growth) and *h* (high shoot allocation, coupled growth) across Soil N gradient: (a) yields in monoculture; (b) yields in mixture; (c) number of surviving individuals; (d) mean size of surviving individuals; (e) yield and size based CIr; (f) yield and size based CA.

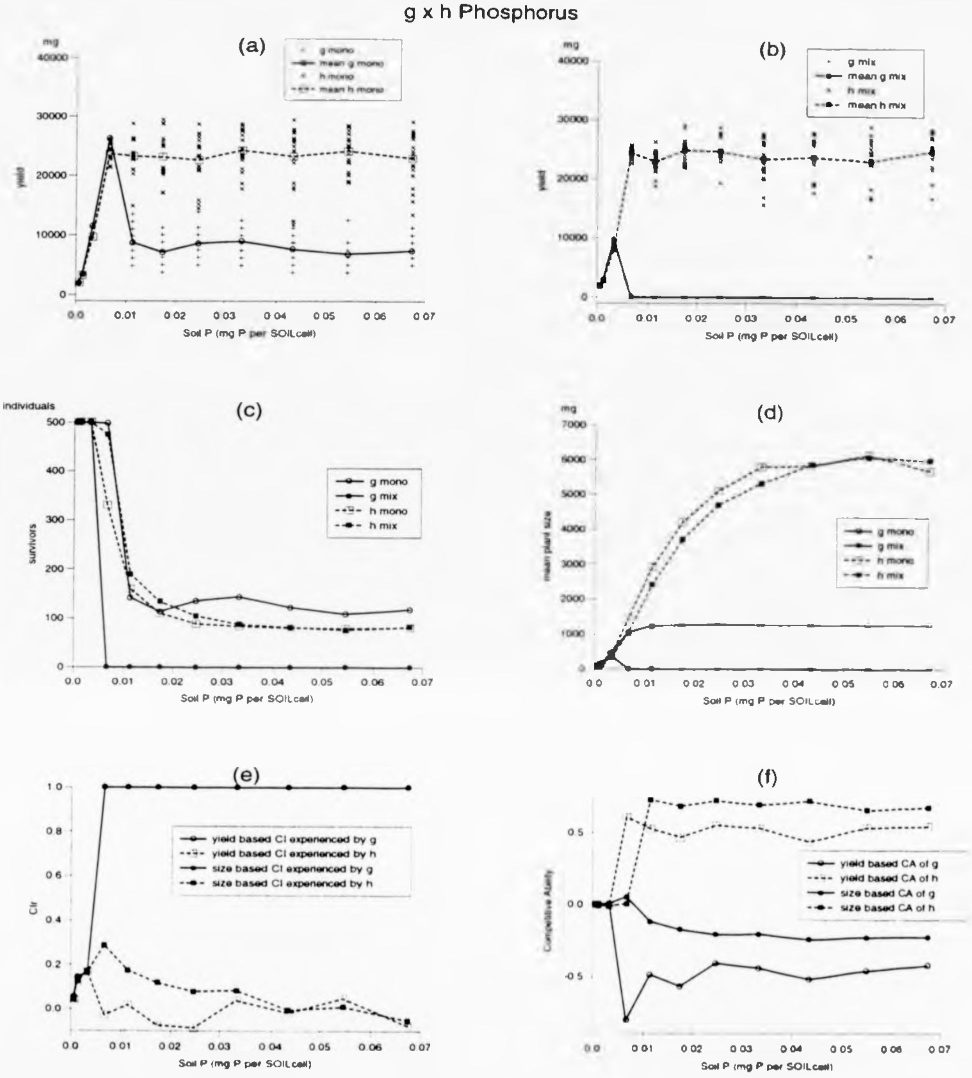


Figure 3.13p. Results of competition between species *g* (high root allocation, uncoupled growth) and *h* (high shoot allocation, coupled growth) across Soil P gradient: (a) yields in monoculture; (b) yields in mixture; (c) number of surviving individuals; (d) mean size of surviving individuals; (e) yield and size based CIr; (f) yield and size based CA.

The results for this section are shown in Figures 3.13n and 3.13p.

Yield, mortality and plant size

Both species are viable in monocultures: *h* experiences greater mortality in monoculture than *g* reflecting the effect of resource storage on self-thinning (see species *f* performance in section 3.3.4), though *h* achieves a greater average monoculture yield than *g* at soil N levels 3 and soil P levels > 4. In competition, no individuals of *g* survive in any of the replications at any R level > 3 for both N and P simulations where *h* is the outright superior competitor. However, at R level 3 species *g* achieves a greater average yield than *h* in both N and P simulations.

Competition Intensity

The CIr of the two populations matches the competition outcome: *g* experiences maximal competition intensity (CIr=1.0) for all R levels greater than 3, while *h* experiences less intense competition. Individuals of *g* experience maximal CIr, while individuals of *h* experience decreasing CIr as soil R increases, after peaking at R level 4. Competition in the N simulation is more intense than in the P simulation at low soil R levels.

Competitive Ability

At soil R levels > 3, the competitive abilities of *g* and *h* are very different: this is reflected in the yield outcome in competition. Thus, although the CA of each species could be used to predict the competitive outcome in qualitative terms, no quantitative prediction could be made.

Effect of R supply properties on yield and competition

For both species there is a significant difference between yields in mixture only at low R levels (levels 1 to 3). At these low R levels, individuals of both species experience more intense competition in the N simulation than the P simulation, though at higher R levels individuals of *h* generally experience greater CIr in the P simulation than the N simulation.

3.3.6 Discussion

Yields

Final yield appears to be extremely variable at most soil R levels for most competition simulations (the notable exception being species *f* in monoculture; see section 3.3.4 for explanation). The only stochastic element of these simulations is within the growth of individuals into unoccupied cells (Cell Growth Routine: see section 2.2.13 and Appendix Program). In some cases, even though the species have implicit differences, final yields from different replications at the same soil R level do not necessarily reflect the mean yield relationship. One of the fundamental assumptions of this model is that plants compete simultaneously for space and resources: this is a consequence of space being divided into discrete units (cells) which only one individual may occupy at any one time. It is this discrete differentiation of space and the chance occupancy of it that inevitably gives rise to spatial heterogeneity of individuals and resource distribution, and consequently the variable yields. Such heterogeneity (generated by stochasticity) may then play a crucial part in promoting the coexistence of species that otherwise, at least according to classic competition theory (*e.g.* Competitive Exclusion Principle), would tend toward monoculture.

Mortality

As the only cause of mortality in this model is insufficient unassimilated carbon for maintenance respiration, it is not surprising that unviable species are exclusively those which invest high allocation to root at the expense of increased carbon fixation through shoot allocation. All species (except species *f*) show evidence of self-thinning in monoculture. This was not explicitly described in the model but arises from the discrete occupancy of above-ground space and subsequent light competition. The relaxation of the assumption that no decompositional processes act on dead tissue and allow resources to become available for acquisition by surviving individuals (*decayRATE*=0), is likely to influence the nature of competition and spatial dynamics of the soil resources, though this is not tested here.

The effect of R supply properties on competition

The contrasting properties of N and P (discussed in section 3.2) generally only have a significant effect on competitive outcome (yields of competing species) at low soil R levels (levels 1,2 and 3): such low levels coincide with maximum intensity of below-ground competition (see section 3.4). Individuals generally experience greater CIr in the N simulation than the P simulation at low R levels, thus lending support to the prediction made in section 3.2 (though see section 3.4 and simulations with no inter-specific above-ground competition). This does not imply that competition for nitrogen is more intense than for phosphorus in natural systems, as the input levels and per-unit mass uptake rates of N and P were scaled according to *CRratio* (see section 3.1.4 and Table 3.3), and this precise balance between N and P is extremely unlikely to occur in a real field system. However, this does illustrate the need to treat resources by their properties, as competition for each resource may be unique in character. Most of the studies of competition intensity, utilizing an experimental manipulation of the availability of a resource to create a productivity gradient, have only considered different additional levels of nitrogen (Wilson & Tilman 1991, 1993, 1995) or combined nutrients (Reader 1990, Aerts *et al.* 1991, DiTommaso & Aarssen 1991, Turkington *et al.* 1993; see also Goldberg 1990); no studies have so far contrasted competition intensity over experimental gradients (with naturally occurring ranges) of different resources in turn (*i.e.* factorial), though Belcher *et al.* (1995) used soil depth to create a productivity gradient.

Competition Intensity

One surprising result is that CIr < 0 occurs quite often, and while this may be indicative of the use of mean yields in the calculation of CIr, negative CIr is only experienced by species in mixture with inferior competitors (as determined by CA). A probable explanation is that inter-specific competition depresses the growth, and therefore the intensity of intra-specific competition of the subject species, for the duration of the simulations. Thus the yield of a species in additive mixture may be greater than in monoculture.

The relationship of CIr and soil R is sensitive to the species and the competitive situation. Where species are competitively superior to competing species, such as *h* in competition with *g* at high R levels (section 3.3.5), the 'superior' species tends to experience lower intensities of competition than their competitors. The CIr results presented here cannot be used to refute Tilman's hypothesis that CIr remains constant across a productivity gradient (although productivity has not been used it can be seen that yield per-unit area increases in a curvilinear fashion with increasing soil R) as the relationship between light and nutrient competition intensity within the model is probably different to that found in nature. As the CIr an individual experiences is a result of simultaneous above- and below-ground competition, this relationship is crucial in determining CIr across a soil resource gradient (see section 3.4).

The difference between the intensity of competition which populations experience, as measured by the relative reduction in total yield, and that which individuals experience, as measured by the relative reduction in mean plant size, highlights the need for theories to distinguish between individual and species scales: no studies have yet measured CIr at both individual and population scales. The predictions made in section 3.2 concerning competition for N and P are supported by the CIr which individuals experience in N and P simulations, but this is not the case at the scale of the population. There is no clear relationship between CIr as experienced by individuals and populations: this presents a possible problem in linking the population to its component individuals.

Plant Traits and Competitive Ability

Competitive ability as defined in this thesis (section 1.5.4) is based on the reduction of a reference species' performance, in terms of yield of the population and mean plant size. The resulting CA of the model species tends not to discriminate clearly between species, *i.e.* the CA are generally grouped into 'good' and 'bad' competitors, though this may be due to the distribution of CA according to the calculation in section 1.5.4 (*i.e.* $0.0 \leq \mathrm{CA} \leq 1.0$). The use of a model 'phytometer' (*sensu* Gaudet & Keddy 1988) in these simulations is not a very good 'tool' with which to measure CA, though this is probably because species *a* possesses a root:shoot ratio for optimum performance between Soil R levels 3 and 4 (see RWR of *c2* across Soil R gradient in section 3.3.3.2). However, the use of such principles in the field has been successful (Gaudet & Keddy 1988), though the application of a phytometer is very much restricted by the performance of the phytometer across an environmental gradient.

Competitive ability depends upon the traits possessed by a species and the availability of nutrients, *i.e.* there is variation in CA for all species along the Soil R gradient and is not a fixed ability as the CSR model suggests (Grime 1979). From Figure 3.5, it can be seen that high allocation to root confers a slight advantage at low Soil R levels (where Soil R is most limiting), and high allocation to shoot confers high CA at higher Soil R levels (where light is most limiting). Uncoupled growth is advantageous at low Soil R levels, while fully coupled growth appears to be slightly disadvantageous, at the population scale, while the traits assigned to species *g* and *h* confer very different CA's. As with CIr, the CA of individuals and populations may differ considerably along the Soil R gradients.

3.4 Competition above- and below-ground

3.4.1 Introduction

In a classic experiment Donald (1958) separated the above- and below-ground components of competition, and demonstrated an interaction between root and shoot competition. This work has been extremely influential, and a host of similar experiments followed (see Wilson 1988 for review).

Snaydon has studied root and shoot competition between species mixtures using partitions to impede above- and below-ground inter-specific interactions between neighbouring individuals while intra-specific interactions are preserved (Snaydon 1979, Remison & Snaydon 1980, Martin & Snaydon 1982, Snaydon & Howe 1986, Tofinga *et al* 1993), though the design of these experiments also removes competition for space, and does not examine whether the spatial restriction caused by the partitions inhibits the performance of individuals, *e.g.* a difference in performance of a single individual grown in isolation (or in monoculture) caused by the presence partitions above- and/or below-ground.

Most recently, the application of a mechanistic approach to competition has resulted in several experiments examining root and shoot competition at two different productivity levels (Aerts *et al.* 1991, Wilson & Tilman 1991, 1993, 1995) or along a soil depth gradient (Belcher *et al.* 1995). However, methodological problems exist with the separation of shoot and root systems, due to the physical impossibility of separating above- or below-ground competition without interfering with the supply *and* acquisition of the resource by competing individuals.

For example, light competition may be removed between a subject individual and its neighbours by the tying back of the neighbours' shoots (Wilson & Tilman 1991), but there is the possibility that the action of tying back could reduce light interception by the neighbours, and therefore reduce their growth and potentially reduce the below-ground effect of the neighbours, which is precisely the factor under investigation in such an experiment. Wilson & Tilman (1991) attempted to validate their experiment against just such an event by comparing soil nutrient and light available to the subject individuals: if soil nutrient levels were not significantly different from 'full' competition treatment and light levels were not significantly different from 'no competition' treatment, then there is assumed to be no significant effect on neighbours growth by the action of tying back (Wilson & Tilman 1991: 1052). The approaches used by these recent experiments to separate out above- and below-ground competition remove all inter- and intra-specific competition for a resource and, therefore, are unable to permit an additive design by which the effect of inter-specific competition (not intra- plus inter-specific) may be measured.

The necessary criteria for the separation of light and soil resource competition may be defined, following on from the conceptual definition of competition presented in section 1.5.2 . For the removal of light competition, light supply to an individual must equal that supplied to the individual in the absence of inter-specific light and soil resource competition (*i.e.* equivalent to that in monoculture), while simultaneously the soil resource available to the same individual must equal that supplied to the individual in the presence of full intra- and inter-specific light and soil resource competition (*i.e.* equivalent to that in mixture). The reverse applies for removal of soil resource competition. Notice that it is the supply element of resource acquisition that is used here (see section 3.2.1); the actual quantity of resource acquired depends also on the size of the resource acquiring organ which, in turn, depends on the acquisition of other resources, the 'opposite' (above- or below-ground) resource being of particular importance. Thus, it is not possible to separate entirely the effect of above-and below-ground competition.

With the criteria detailed above, it is virtually impossible to conduct such an experiment on real plant populations, especially preserving intra-specific competition while removing inter-specific competition between populations, though this may be achieved at the individual scale in the absence of all intra-specific competition (*e.g.* Wilson & Tilman 1995, Belcher *et al.* 1995). This, however, is where a simulation model of plant competition can be extremely useful, as it is a relatively simple task to reorganize the rules governing the occupancy of space and resource distribution such that the criteria above may be met. Hence, the model described in chapter 2 was modified (see appendix) such that four 'treatments' are possible for two competing species populations:

monoculture	intra-specific competition above- and below-ground only
above only	intra- and inter-specific competition above ground, intra-specific competition below-ground
below only	intra-specific competition above ground, intra- and inter-specific competition below-ground

full competition	intra- and inter-specific competition above ground, intra- and inter-specific competition below-ground

Monoculture and full treatments are identical to monoculture and mixture runs as described in section 3.3; references made to **no above-** and **below-ground competition** refer only to the lack of *inter-specific* competition between competing populations.

Selected mixtures from the plant traits section are simulated with above- and below-ground competition only – these are described below.

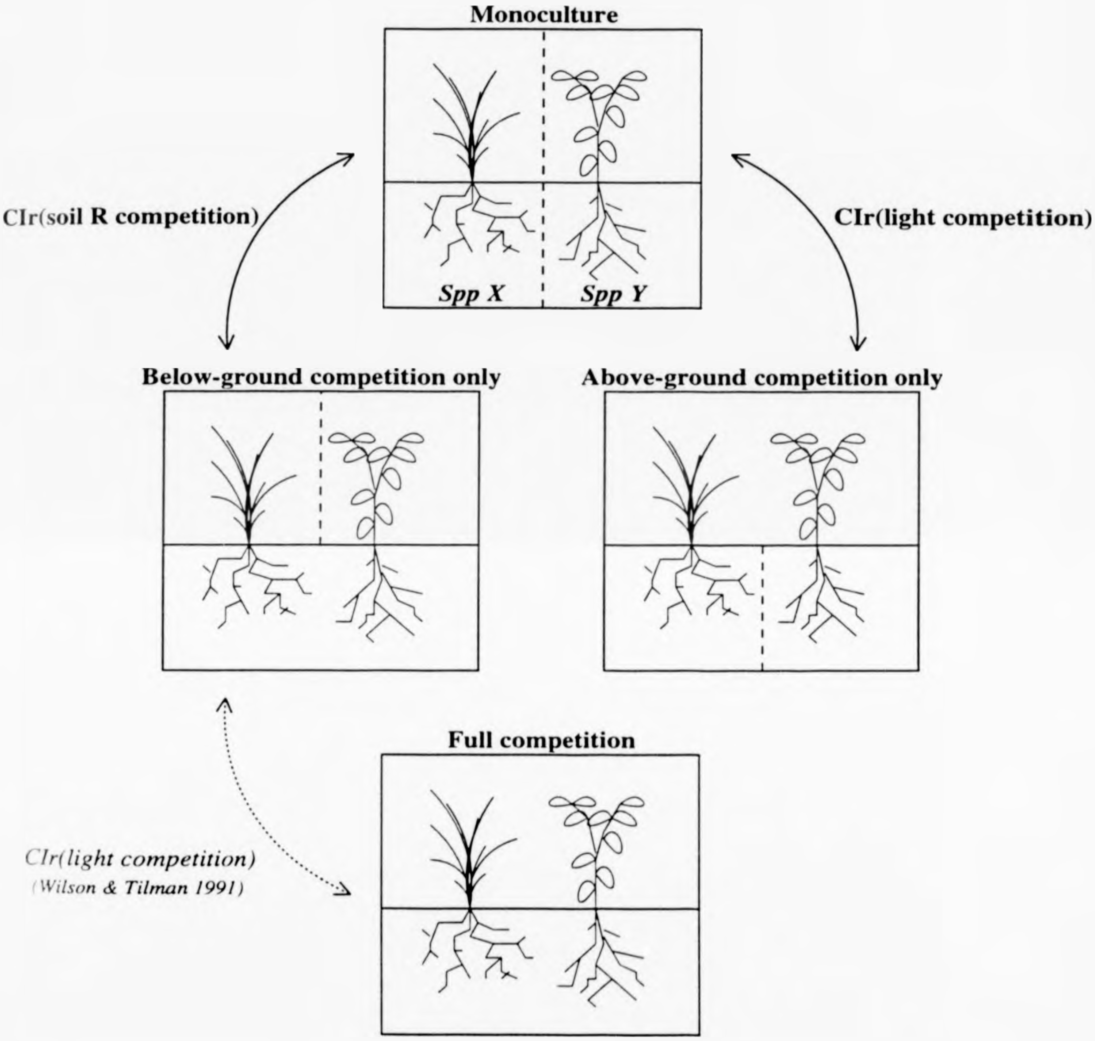


Figure 3.14 Schematic diagram showing the basis of CIr calculations for above- and below-ground competition. Dashed lines represent separation of competing tissues of species X and Y, by any method (see text). Arrowed lines represent comparisons in CIr calculations; the method used by Wilson & Tilman (1991) to calculate the intensity of light competition is represented by the dotted arrowed line.

3.4.2 Simulations

Modification to model space and resources

Inorder to satisfy the criteria stated in section 3.4.1, several changes to the principal PASCAL program were necessary concerning the occupancy of space and resource availability of two species in mixture.

The following example is for the simulation of no inter-specific root competition between two species. No changes to the program are made to the occupancy of space and access to light above-ground by the two species. However, the roots of each species inhabit separate volumes below-ground, while the shoots of each species occupy the same volume above-ground. Each species-specific space below-ground contains the same initial distribution and quantity of soil R, and all other operations within each space (occupancy, uptake, soil R and water movement, and growth) are performed as normal. Thus, while both species experience above-ground conditions in a similar fashion to full competition, each species experiences below-ground monoculture conditions (*i.e.* neither species may directly intercept units of soil R from the other). However, because of the interdependence of root and shoot functions implicit in the growth and partitioning elements of the model, below-ground growth and uptake may still be influenced by the other species via inter-specific above-ground competition.

Inter-specific light competition is removed in a similar manner: the roots of the two populations inhabit the same volume of soil, but the shoots of the populations inhabit two separate volumes, therefore only intra-specific light competition may occur.

Calculation of CIr for above- and below-ground competition

The few experiments to have measured competition intensity experienced above- and below-ground separately (Belcher *et al.* 1995, Wilson & Tilman 1991, 1993, 1995) have all followed the format of Wilson and Tilman (1993), where three competition 'treatments' are performed on *individuals*: (1) no neighbours (mono), (2) neighbours roots (NR) and (3) neighbours roots and shoots (NRS), followed by the calculations:

$$CIr_{below\text{-}ground\ competition} = \frac{P_{mono} - P_{NR}}{P_{mono}} \tag{3.2}$$

$$CIr_{above\text{-}ground\ competition} = \frac{P_{NR} - P_{NRS}}{P_{NR}} \tag{3.3}$$

$$CIr_{full\ competition} = \frac{P_{mono} - P_{NRS}}{P_{mono}} \tag{3.4}$$

where P_{mono}, P_{NR} and P_{NRS} are the performance of the subject individual with no neighbours present, only neighbours roots present, and both neighbours roots and shoots present, respectively (a neighbour may be of any species). This approach removes both inter- and intra-specific competition, and assumes that the effect of full competition is the sum of above- and below-ground competition, such that:

$$\frac{P_{mono} - P_{NS}}{P_{mono}} = \frac{P_{NR} - P_{NRS}}{P_{NR}} \tag{3.5}$$

where the left-hand term is the CIr of above-ground competition derived from the method of calculating CIr below-ground (equation 3.2; see Fig. 3.14), P_{NS} is the performance of the subject individual with only neighbour shoots present and neighbour roots absent. It follows that

$$\frac{P_{NRS}}{P_{NR}} = \frac{P_{NS}}{P_{mono}} \ . \tag{3.6}$$

Although feasible and reasonable there is no experimental evidence yet to support this assumption. Consequently, the calculation of above-ground competition intensity employed by Wilson and Tilman (1991, 1993, 1995) and Belcher *et al.* (1995) is not strictly comparable with the measurement of below-ground competition intensity, as the presence/absence of light competition occurs with root competition present, while the presence/absence of root competition occurs with shoot competition absent (see Fig. 3.14). This assumption is tested in section 3.4.3.1. The approach taken by these studies reflects the difficulty of removing below-ground competition while maintaining above-ground competition. This was achieved by Aerts *et al.* (1991) though all treatments had equal rooting volume, therefore the presence of competing roots followed a replacement design, rather than the additive design required for CIr calculation (see section 1.5).

As described above, the model was altered to systematically remove above- and below-ground competition. The calculations for CIr above- and below-ground used in the following sections are:

$$CIr_{below} = \frac{P_{mono} - P_{NR}}{P_{mono}} \qquad (3.7)$$

$$CIr_{above} = \frac{P_{mono} - P_{NS}}{P_{mono}} \qquad (3.8)$$

Calculation of above- and below-ground competitive ability

Above- and below-ground competitive ability are calculated according to the methodology presented in section 1.5.4 (*i.e.* the reduction in performance of reference species a in mixture relative to the performance of a in 'mono' and 'mixture' density monoculture), thus only the species which are simulated in above- or below-ground competition treatments with a could have such CA calculated. The calculations are as follows:

$$CA_{above}[X] = \frac{P[a_{aa,NS}] - P[a_{aX,NS}]}{P[a_a]} \tag{3.9}$$

where $CA_{above}[X]$ is the competitive ability above-ground of species X, $P[a_{aa,NS}]$ is the performance of one of the populations of a in 'mixture' density monoculture with no inter-specific below-ground competition between the two populations (run 32A), $P[a_{aX,NS}]$ is the performance of a in mixture with species X with no inter-specific below-ground competition, and $P[a_a]$ is the performance of a in 'mono' density monoculture (run 1);

$$CA_{below}[X] = \frac{P[a_{aa,NR}] - P[a_{aX,NR}]}{P[a_a]} \tag{3.10}$$

where $CA_{below}[X]$ is the competitive ability below-ground of species X, $P[a_{aa,NR}]$ is the performance of the sub-population of a in 'mixture' density monoculture with no inter-specific above-ground competition between the two sub-populations (run 32B), $P[a_{aX,NR}]$ is the performance of a in mixture with species X with no inter-specific above-ground competition.

Selected runs

The runs selected from the trait runs are $a \times a$ (a at 'mixture' density; runs 32A, 32B), $a \times b6$ (runs 33A, 33B), $a \times c2$ (runs 34A, 34B), $e \times f$ (runs 35A, 35B) and $g \times h$ (runs 36A, 36B).

All species pairs are simulated in factorial manner with above-ground competition only, below-ground competition, and N and P gradient treatments. Yields from monoculture and mixture runs, as presented in section 3.3, are used in the calculation of CIr and for comparative purposes.

For runs 32A and 32B, the simulations treat species *a* as two independent populations of 25 individuals of *a* such that in the no above-/below-ground competition treatments, there is no above- or below-ground competition *between* these two populations but competition remains *within* the population, in a similar manner to runs 2n and 2p (section 3.3.2). For the other runs in this section, inter-specific competition is removed by the method detailed above.

3.4.3 Results of split competition treatments

3.4.3.1 *a* × *a* : the reference species in low and high density monoculture

The results for *a* at 'mixture' density with only above-ground (runs 32An and 32Ap) and only below-ground (runs 32Bn and 32Bp) competition are shown in Figures 3.15n and 3.15p. As for run 2 (*a* × *a*; 'mixture' density), the results shown are for a population of 25 individuals of *a* in competition with the remaining 25 individuals of *a*, *i.e.* additive design.

Yields and mortality

The removal of above-ground competition produces a greater mean yield than that attained by the removal of below-ground competition at R levels > 3 for both N and P indicating that above-ground competition has a greater effect on yield than below-ground competition, for R levels > 3 (see also CIr results below). Above-ground competition also induces a greater level of mortality than below-ground competition (Figures 3.15n(b) and 3.15p(b)), as may be expected given that mortality in this model results only from C deficiency.

Competition Intensity above- and below-ground

CIr of above- and below-ground competition are calculated following the definitions shown in equations 3.7 and 3.8, and are shown in Figures 3.15n(c,d) and

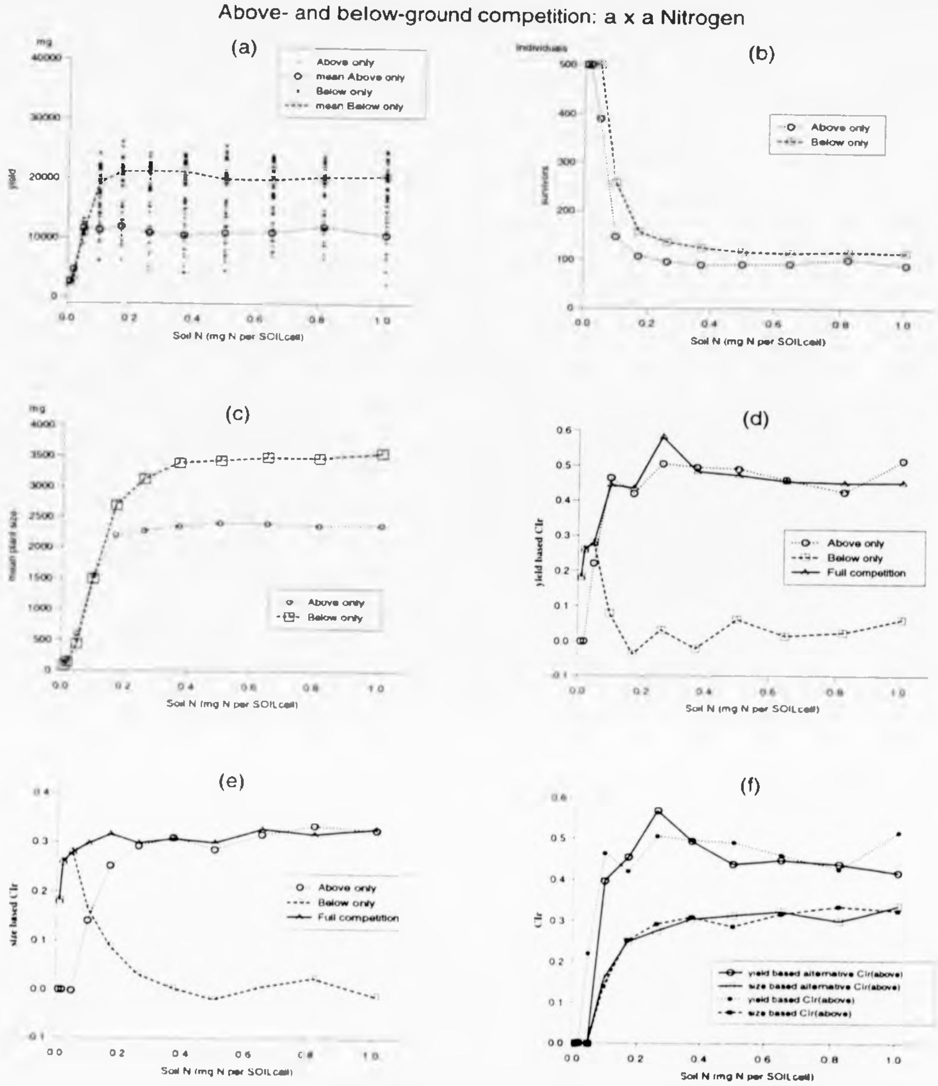
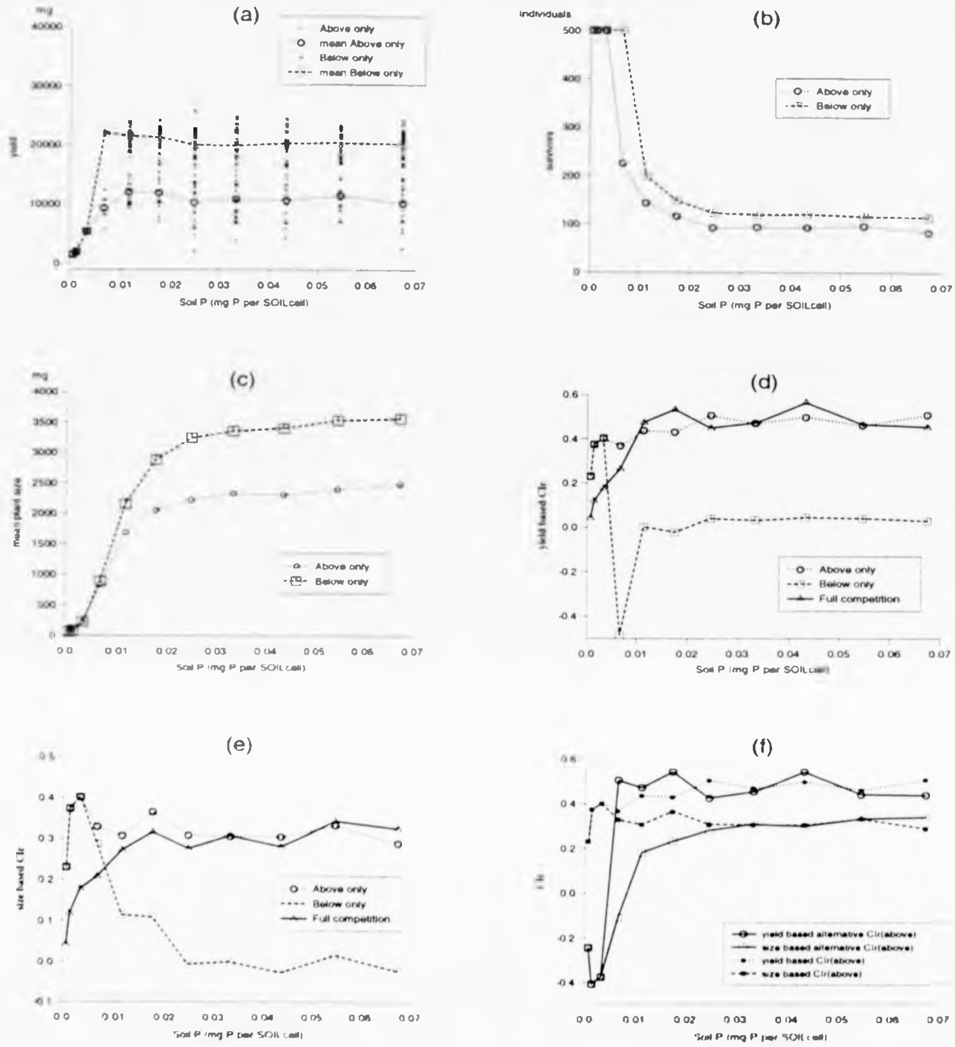


Figure 3.15n. Results of reference species *a* with above- and below-ground competition across Soil N gradient: (a) yields at low density; (b) yields at high density; (c) mean size of surviving individuals; (d) yield based CIr; (e) size based CIr; (f) comparison between different methods of measuring $\mathrm{CIr}_{\mathrm{above}}$ (see sections 3.4.2 and 3.4.3) .



Above- and below-ground competition: a x a Phosphorus

Figure 3.15p. Results of reference species *a* with above- and below-ground competition across Soil P gradient: (a) yields at low density; (b) yields at high density; (c) mean size of surviving individuals; (d) yield based CIr; (e) size based CIr; (f) comparison between different methods of measuring $\mathrm{CIr}_{\mathrm{above}}$ (see sections 3.4.2 and 3.4.3) .

3.15p(c,d); both total yield and mean size are used in the calculations. The CIr of above-ground competition is also calculated following Wilson and Tilman (1991) as in equation 3.3, using both total yield and mean plant size as measures of performance. CIr results are shown in Figures 3.15n(e) and (f), and 3.15p(e) and (f).

Across a soil N gradient, below-ground CIr decreases at the individual and population scale, while above-ground CIr increases with increasing soil N. The resulting 'switch' from below-ground to above-ground competition at the individual scale (Figure 3.15n(e)) supports the hypothesis of Wilson and Tilman (1991). There is no clear 'switch' across the equivalent soil P gradient (runs 32Ap and 32Bp): the intensity of above- and below-ground competition for individuals at low P levels are identical, and as soil P increases below-ground competition decreases in intensity while above-ground competition remains at the same intensity. It is suspected that such a switch similar to that found in the N simulation may occur over the P gradient, but at lower soil P levels. Hence, additional runs of above-and below-ground competition treatments are performed at P levels 10^{-1} times the normal P values. The CIr results for these additional runs are shown in Figure 3.21, from which it can be seen that no 'switch' occurs at any P level: CIr_{below} and CIr_{above} are identical until soil P values of around 0.005 mg P per *SOILcell*, where below-ground competition becomes less intense than above-ground competition. As soil P values approach zero, CIr_{above} and CIr_{below} also approach zero.

The marked difference of the relationship of above- and below-ground competition between N and P simulations can only be a result of the different supply properties of N and P. The difference in apparent inter-specific above-ground competition (determined from the above-ground only treatment) at low N and P levels is actually a reflection of differences in below-ground intra-specific competition, for the following reasons. Above-ground biomass is affected by nutrient supply properties, as yield and mean plant size are greater at low N levels than at equivalent P levels. This should result in a greater chance of shading (and therefore greater per-unit biomass above-ground competition intensity) in the N simulation, whereas $CIr_{above} = 0$ at low N levels, indicating that at such levels of biomass there is insufficient growth (occupancy of *ABOVEcells*) for shading to occur. Thus, as shading is removed at low N and P levels, the only possible interaction is below-ground intra-specific competition. Inter-specific below-ground competition (in isolation of above-ground competition) is more intense at low P levels than at the equivalent N levels (see section 3.4.8), therefore it seems plausible that intra-specific competition for P is more intense than for N: hence the higher intensity of competition 'above-ground'. This apparently contradicts the prediction concerning the intensity of competition for N and P made in section 3.2.1; this is resolved in section 3.4.8.

Effect of R supply properties on competition.

Competition for P, as determined by the below-ground only treatments, is generally more intense than for N. The supply properties of the nutrient also appear to affect measured competition above-ground, via intra-specific below-ground competition (see above, and section 3.4.8).

Above-ground CIr as calculated according to equations 3.3 and 3.8.

The values derived from the two methods of calculating CIr above-ground are approximately equal, but not identical, so strictly the assumption of Wilson and Tilman (1991; equations 3.5 and 3.6) is not supported here (Fig. 3.15n(f) and 3.15p(f)). However, in the N simulations their method gives a good approximation (Pearson's correlation values of 0.934 and 0.993 for yield and size based CIr respectively), but not for the P simulations (Pearson's correlation values of 0.640 and -0.313 for yield and size based CIr respectively), where their method is least accurate at low soil P values.

3.4.3.2 *a* × *b6* : moderate shoot allocation × high shoot allocation

The results of runs 33A and 33B are shown in Figures 3.16n and 3.16p. Species *b6* has high constant allocation to shoots (see section 3.3.3.1), while species *a* has moderate shoot allocation in comparison.

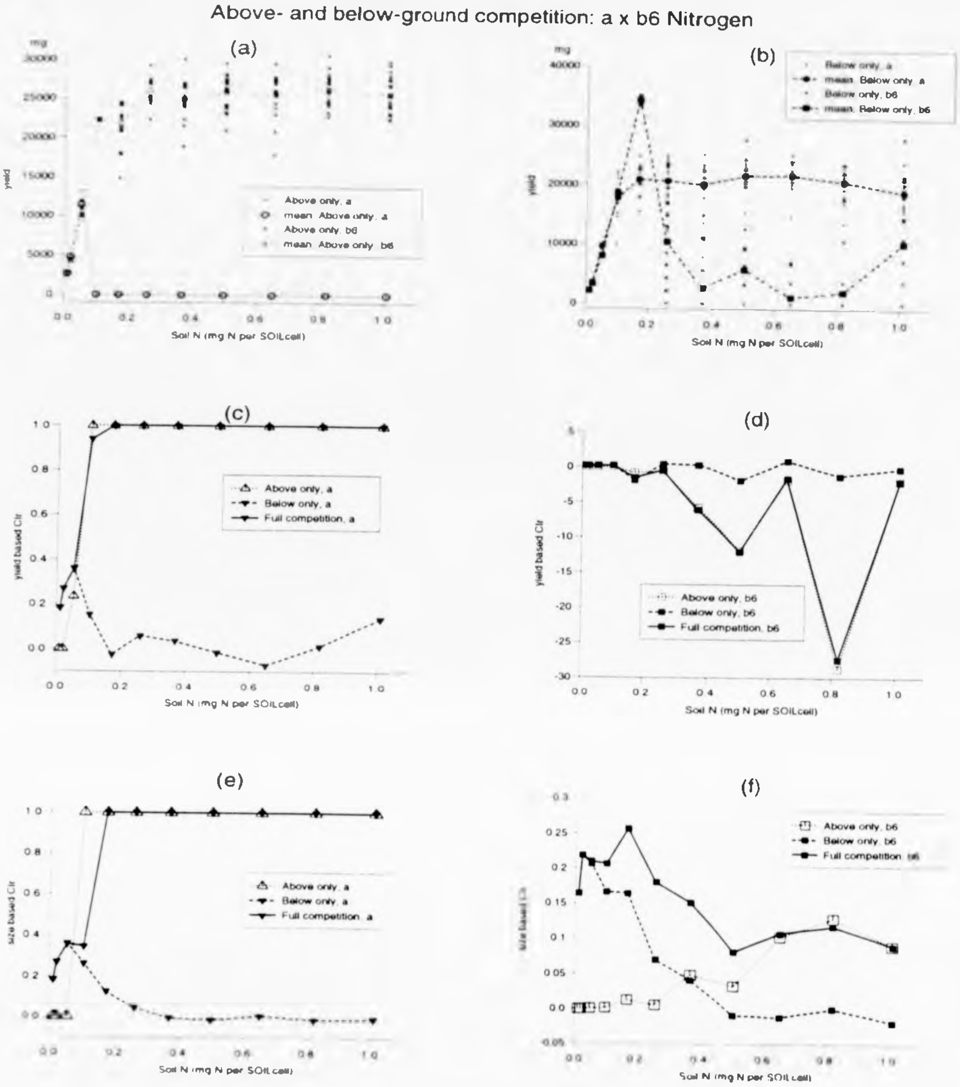


Figure 3.16n. Results of above- and below-ground competition between species *a* (moderate shoot allocation) and species *b6* (high shoot allocation) across Soil N gradient: (a) yields with no below-ground competition; (b) yields with no above-ground competition; (c) yield based CIr for *a*; (d) yield based CIr for *b6*; (e) size based CIr for *a*; (f) size based CIr for *b6*.

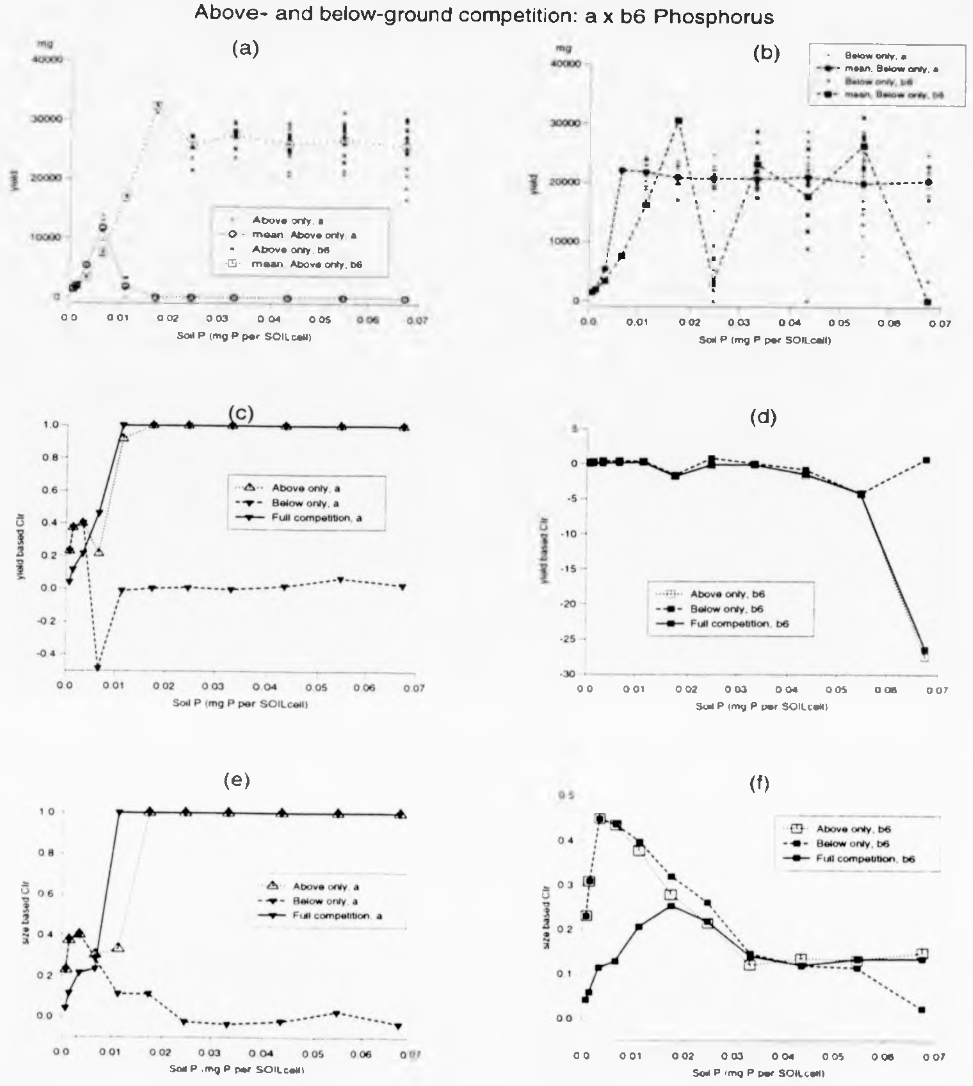


Figure 3.16p. Results of above- and below-ground competition between species *a* (moderate shoot allocation) and species *b6* (high shoot allocation) across Soil P gradient: (a) yields with no below-ground competition; (b) yields with no above-ground competition; (c) yield based CIr for *a*; (d) yield based CIr for *b6*; (e) size based CIr for *a*; (f) size based CIr for *b6*.

Yields

With above-ground competition only, *a* only survives in competition with *b6* at low soil R levels where *a* achieves a greater mean yield than *b6* (Figures 3.16n(a) and 3.16p(a)). With below-ground competition only, *a* is able to survive at all soil R levels, and achieves a greater mean yield than *b6* at several R levels. This indicates that *b6* is the superior above-ground competitor while *a* is the superior below-ground competitor for N, except at N level 5 where the allocation pattern of *b6* presumably facilitates a greater N uptake rate (see section 3.3.3.1 and below). There is no clear below-ground superior competitor for P.

Competitive ability of b6 above- and below-ground

The yield based and size based CA of *b6* above- and below-ground are shown in Figure 3.18(a) and (b). Increased allocation to shoot (relative to species *a*) generally confers a competitive advantage above-ground at higher R levels for both the individual and the population. There is a slight advantage to the particular allocation pattern of *b6* below-ground at soil N levels 3 and 4, due to increased transpiration and water uptake rate, and subsequent increased nitrogen interception.

Competition intensity above- and below-ground

Individuals of *a* experience decreasing CIr_{below} with increasing soil R levels; at low R levels this CIr_{below} is greater for P than N. At the scale of the population, *a* experiences decreasing CIr_{below} with increasing soil R, though at P level 4, *a* experiences negative competition intensity, as occurred in monoculture (section 3.4.3.1). Individuals of *b6* experience decreasing CIr_{below} with increasing soil R, for both N and P simulations. There is no clear trend of CIr_{below} of the population of *b6*.

The population of species *b6* experiences negative CIr for above-ground competition: this is most likely due to the suppressive effect of inter-specific competition on intra-specific competition (see section 3.3.5). Individuals of *b6* experience increasing CIr_{above} with increasing soil N, though they experience decreasing CIr_{above} with increasing soil P. The population and individuals of species *a* experience an increase in $\mathrm{CIr}_{\mathrm{above}}$ with increasing soil R, until $\mathrm{CIr}_{\mathrm{above}}$=1.0 where *a* does not survive in competition with *b6*. Both the population and individuals of *b6* experience less intense $\mathrm{CIr}_{\mathrm{above}}$ than *a*: this lends support to the conclusion that *b6* is the superior above-ground competitor.

Effect of R supply properties on competition

Individuals of both *a* and *b6* experience greater intensity of inter-specific below-ground competition for P than for N.

3.4.3.3 *a* × *c2* : non-plastic allocation × plastic allocation

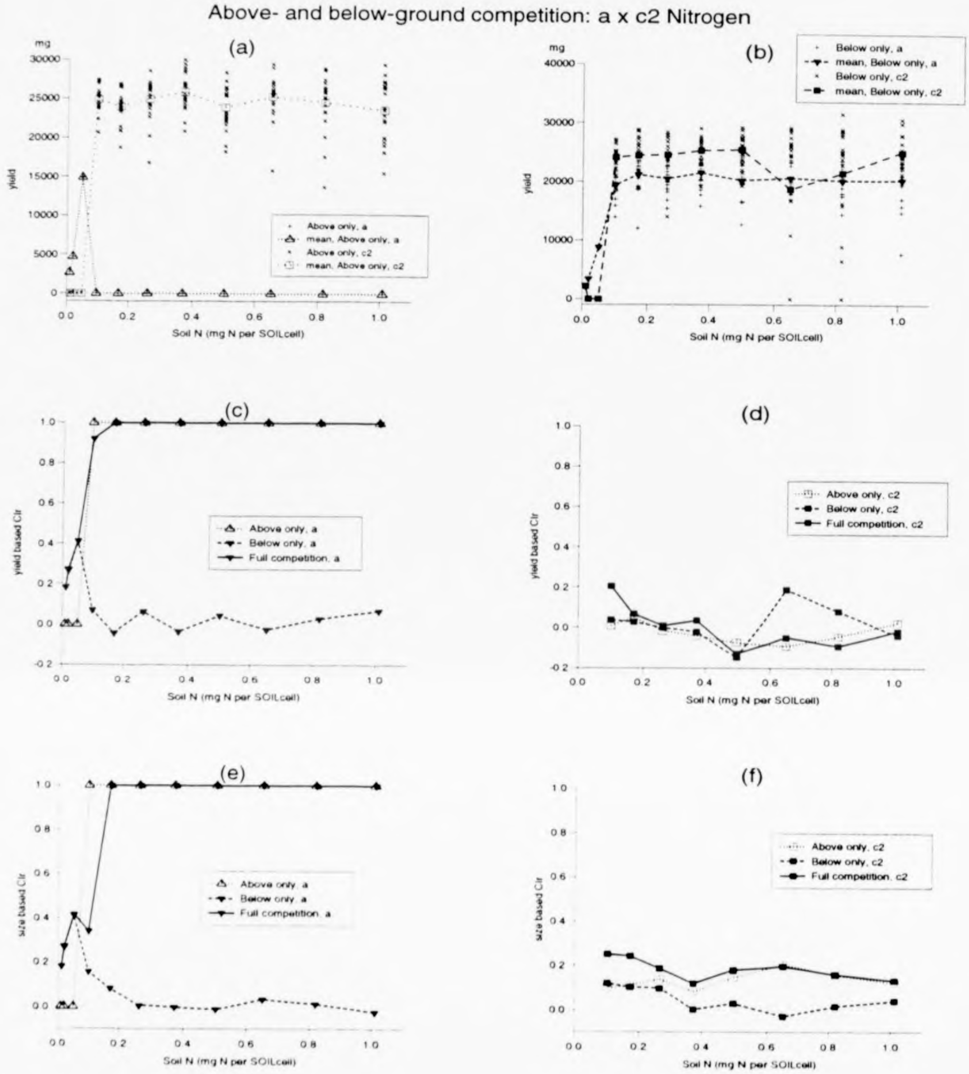
The results of runs 34A and 34B are shown in Figures 3.17n and 3.17p. Species *c2* has unbiased plastic allocation (see section 3.3.3.2), while species *a* has constant, unbiased allocation between root and shoot.

Yields

With above-ground competition only, *a* produces a greater yield than *c2* at low N and P levels; at greater N and P levels *c2* outcompetes *a* completely (*i.e.* yield of *a* = 0). With below-ground competition only, the yield of *a* is greater than that of *c2* for low N and P levels, but at greater N and P levels the yield of *c2* is greater than that of *a*. Thus, full mortality of *a* only occurs with light competition, whereas the full mortality of *c2* at low R levels is a reflection of the inviability of the highly plastic allocation pattern of *c2* at these levels (see *c2* monoculture yields and mortality in Figures 3.9n(a) and 3.9p(a)).

Competitive ability of c2 *above-and below-ground*

The above- and below-ground CA of *c2* are shown in Figure 3.18(c) and (d). A species with plastic allocation response would be expected to experience less intense competition than a species with fixed, unbiased allocation in a similar situation (section 3.3.3.2); *i.e.* CA[*c2*]>0. At the population scale, plastic allocation confers a competitive advantage below-ground at relatively low R levels (N level 3 and P level 4), and an



Above- and below-ground competition: a x c2 Nitrogen

Figure 3.17n. Results of above- and below-ground competition between species *a* (constant allocation) and species *c2* (highly plastic allocation) across Soil N gradient: (a) yields with no below-ground competition; (b) yields with no above-ground competition; (c) yield based CIr for *a*; (d) yield based CIr for *c2*; (e) size based CIr for *a*; (f) size based CIr for *c2*.

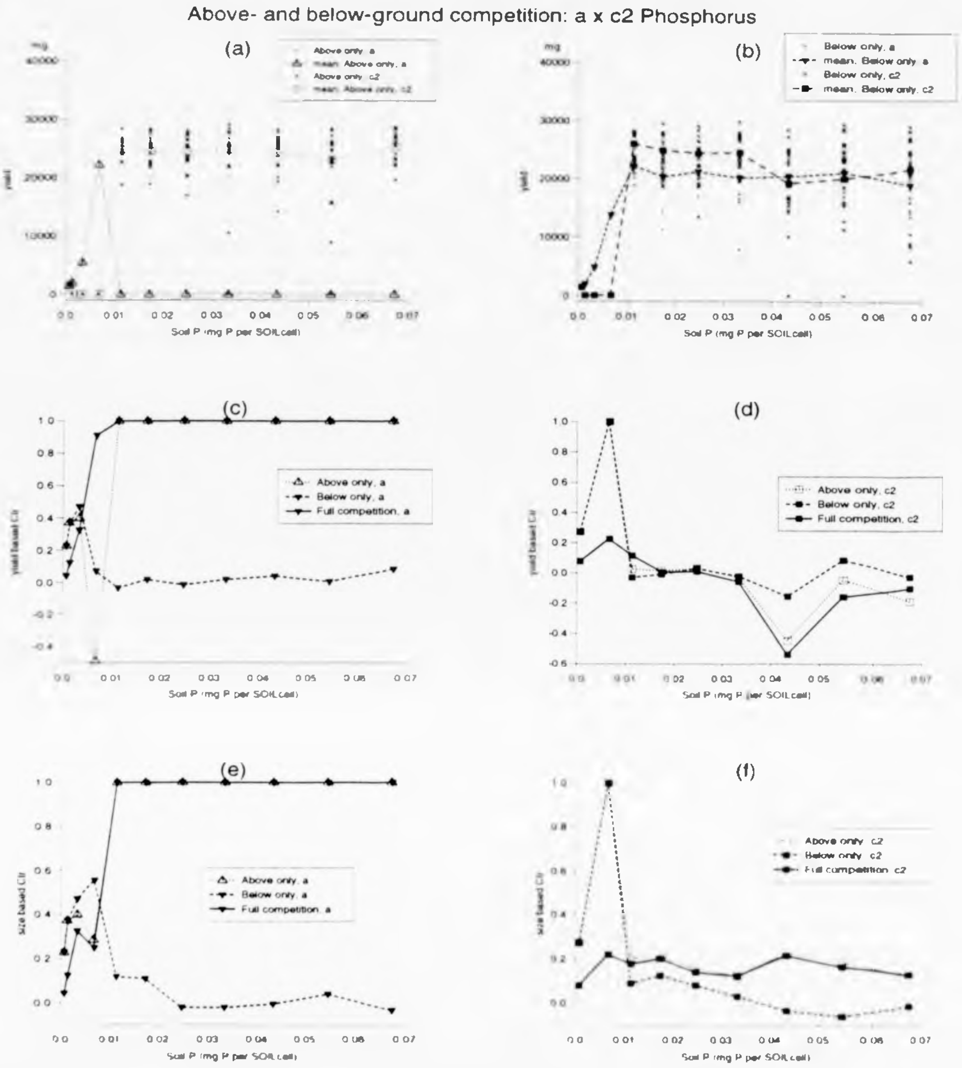
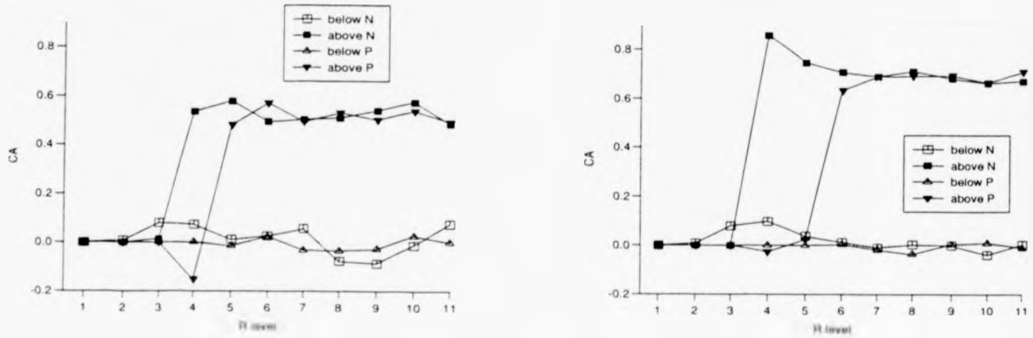


Figure 3.17p. Results of above- and below-ground competition between species *a* (constant allocation) and species *c2* (highly plastic allocation) across Soil P gradient: (a) yields with no below-ground competition; (b) yields with no above-ground competition; (c) yield based CIr for *a*; (d) yield based CIr for *c2*; (e) size based CIr for *a*; (f) size based CIr for *c2*.

(a) Yield based CA of b6

(b) Size based CA of b6



(c) Yield based CA of c2

(d) Size based CA of c2

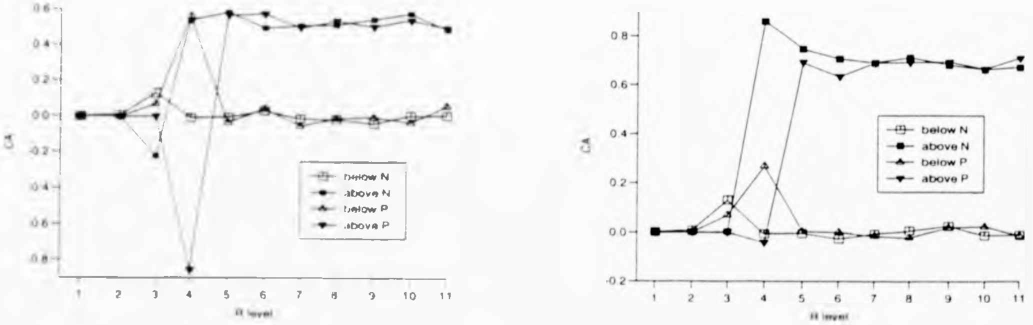


Figure 3.18. Above- and below-ground Competitive Abilities of species *b6*, (a) and (b), and species *c2*, (c) and (d), across Soil R gradient (both N and P).

advantage above-ground at higher R levels, though plasticity appears to be a disadvantage above-ground at low R levels (N level 3 and P level 4). However, this is probably an 'artifact' of the model's assumptions: plastic allocation in this model does not 'account' for the extra requirement of C for respiratory costs, only for inclusion into biomass (see the partitioning equations in section 2.2.12). At the individual scale, plasticity confers a competitive advantage below-ground at lower soil R levels, and above-ground at higher R levels, where $\mathrm{CIr}_{\mathrm{above}} > \mathrm{CIr}_{\mathrm{below}}$, but does not confer a significant disadvantage at any R level.

Competition Intensity above- and below-ground

Species *a* generally experiences greater competition intensity than *c2*: this is a reflection of the competitive advantage conferred by plastic allocation. $\mathrm{CIr}_{\mathrm{below}}$ decreases with increasing soil R for *a* and *c2* at the individual scale, and *a* at the population scale. With above-ground inter-specific competition only, individuals of *a* experience maximal $\mathrm{CIr}_{\mathrm{above}}$ at soil N levels > 3 and soil P levels > 4, while individuals of *c2* experience relatively constant $\mathrm{CIr}_{\mathrm{above}}$ across both N and P gradients. There is evidence of a qualitative change in competition from predominantly below-ground to predominantly above-ground (Wilson & Tilman 1991) in the CIr that individuals of *a* and *c2* experience with increasing soil N (Fig. 3.17n(e) and (f)). There is no 'switch' as such with increasing soil P: at low soil P levels the intensity of inter-specific below-ground competition is equal to the intensity of above-ground inter-specific competition (Fig. 3.17p(e) and (f)); while at higher soil P levels $\mathrm{CIr}_{\mathrm{above}}$ is much greater than $\mathrm{CIr}_{\mathrm{below}}$ (see section 3.4.8).

Effect of R supply properties on competition

The intensity of below-ground competition experienced by *a* and *c2* is greater across the P gradient than the N gradient.

3.4.3.4 *e* × *f* : coupled growth × uncoupled growth

The results for runs 35A and 35B are shown in Figures 3.19n and 3.19p. Species *e* has fully coupled growth, while *f* has uncoupled growth (see section 3.3.4).

Yields

With above-ground competition only (no inter-specific below-ground competition), there is a 'switch' in dominance as soil N and soil P increase; *e* has a greater yield than *f* at low soil R, while *f* produces a greater yield than *e* at higher R levels (Fig. 3.19n(a) and 3.19p(a)). This switch is qualitatively similar to that produced by full competition (runs 24n and 24p; see Fig. 3.12n and 3.12p). When above-ground inter-specific competition is removed (below-ground only treatment), no such switch in dominance occurs. This suggests that the shift in dominance between *e* and *f* along the soil R gradient is prompted by competition for light and not by nutrient competition (see below).

Competition Intensity above- and below-ground

At the population scale, there is a qualitative change in the CIr experienced by *e* and *f*. $\mathrm{CIr}_{\mathrm{below}}$ is greater than $\mathrm{CIr}_{\mathrm{above}}$ at low soil N, and this is reversed at higher N levels; at low P levels the intensities of above- and below-ground competition are identical, but at higher P levels $\mathrm{CIr}_{\mathrm{above}}$ is greater than $\mathrm{CIr}_{\mathrm{below}}$.

Individuals of species *e* experience a similar 'switch' with increasing soil N and 'divergence' with increasing soil P. However, individuals of species *f* only experience significant competition at low soil R levels, where $\mathrm{CIr}_{\mathrm{below}} > \mathrm{CIr}_{\mathrm{above}}$ in the N simulation but $\mathrm{CIr}_{\mathrm{below}} = \mathrm{CIr}_{\mathrm{above}}$ in the P simulation.

Effect of R supply properties on competition

Both the individuals and populations of *e* and *f* experience more intense below-ground competition in the P simulation than the N simulation, at low R levels.

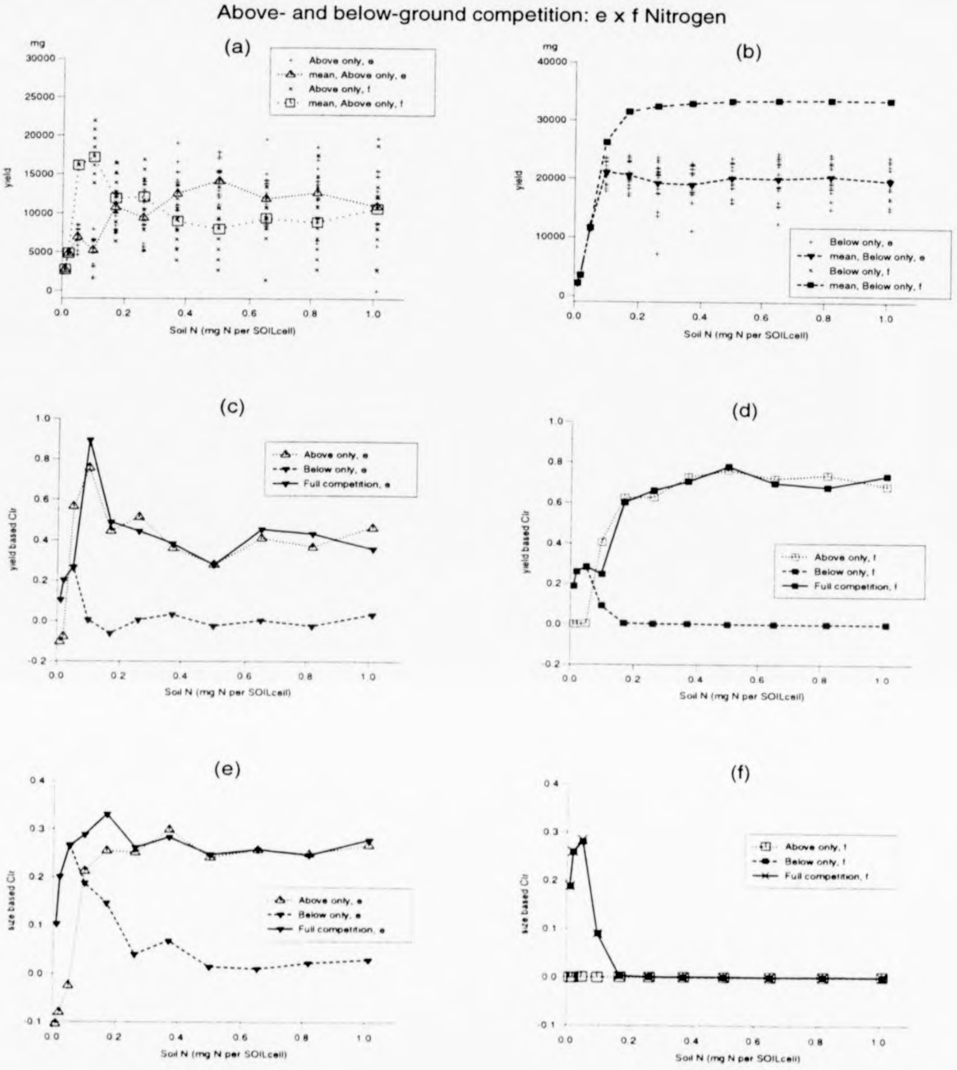


Figure 3.19n. Results of above- and below-ground competition between species *e* (coupled growth) and species *f* (uncoupled growth) across Soil N gradient: (a) yields with no below-ground competition; (b) yields with no above-ground competition; (c) yield based CIr for *e*; (d) yield based CIr for *f*; (e) size based CIr for *e*; (f) size based CIr for *f*.

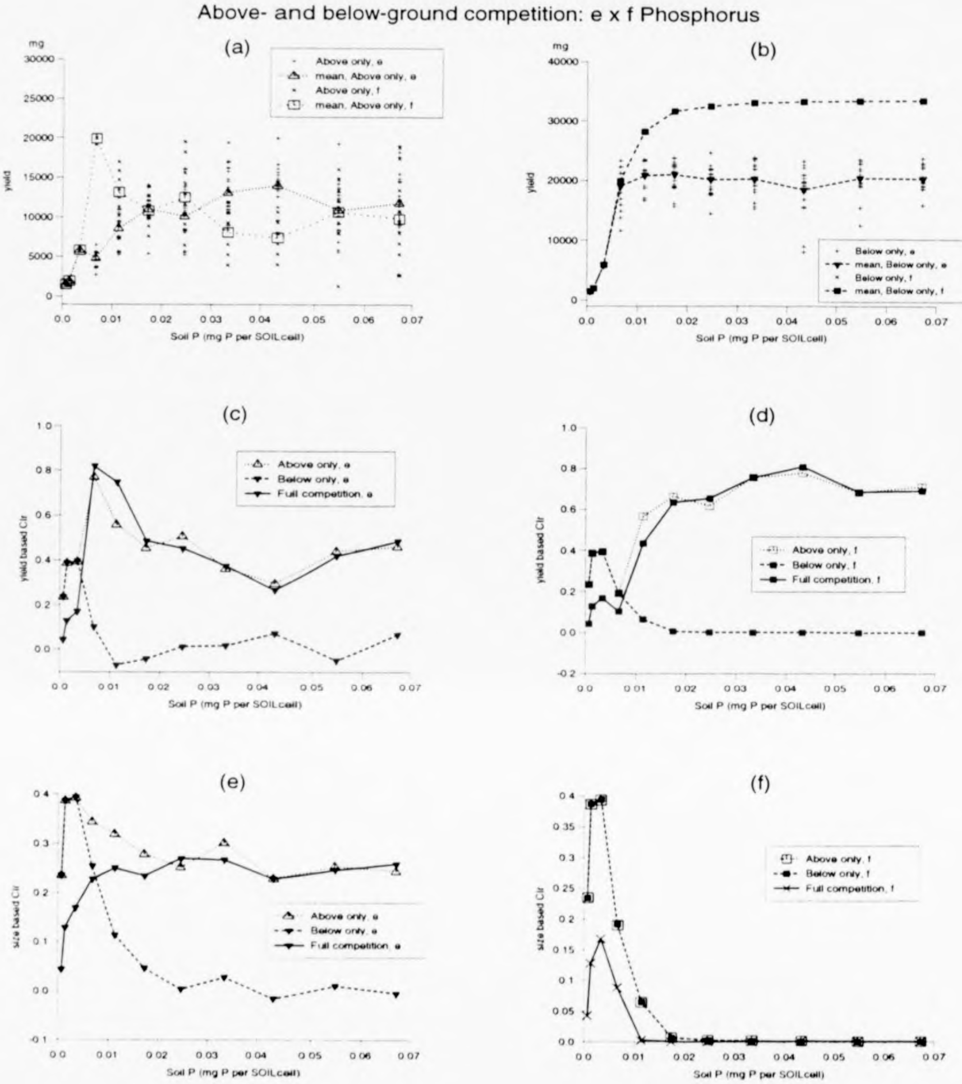


Figure 3.19p. Results of above- and below-ground competition between species *e* (coupled growth) and species *f* (uncoupled growth) across Soil P gradient: (a) yields with no below-ground competition; (b) yields with no above-ground competition; (c) yield based CIr for *e*; (d) yield based CIr for *f*; (e) size based CIr for *e*; (f) size based CIr for *f*.

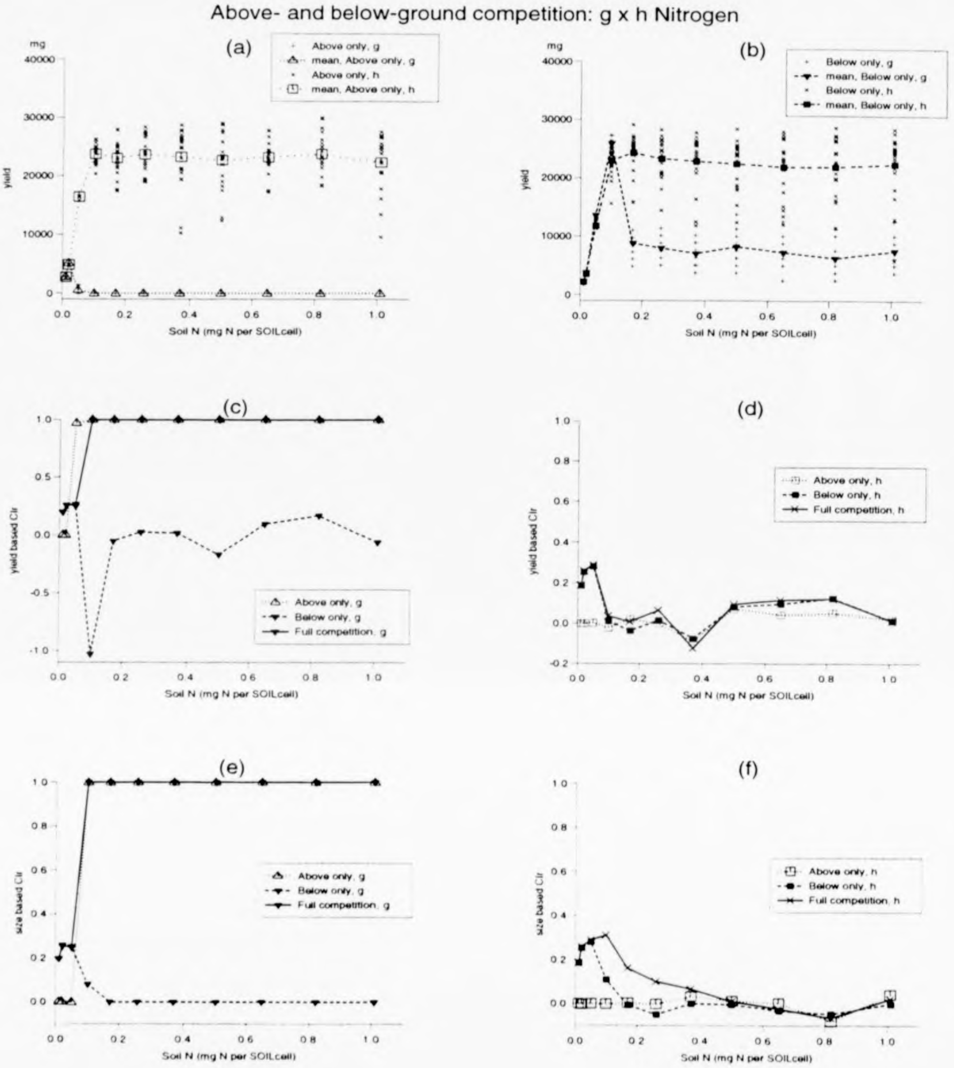


Figure 3.20n. Results of above- and below-ground competition between species *g* (high root allocation, uncoupled growth) and *h* (high shoot allocation, coupled growth) across Soil N gradient: (a) yields with no below-ground competition; (b) yields with no above-ground competition; (c) yield based CIr for *g*; (d) yield based CIr for *h*; (e) size based CIr for *g*; (f) size based CIr for *h*.

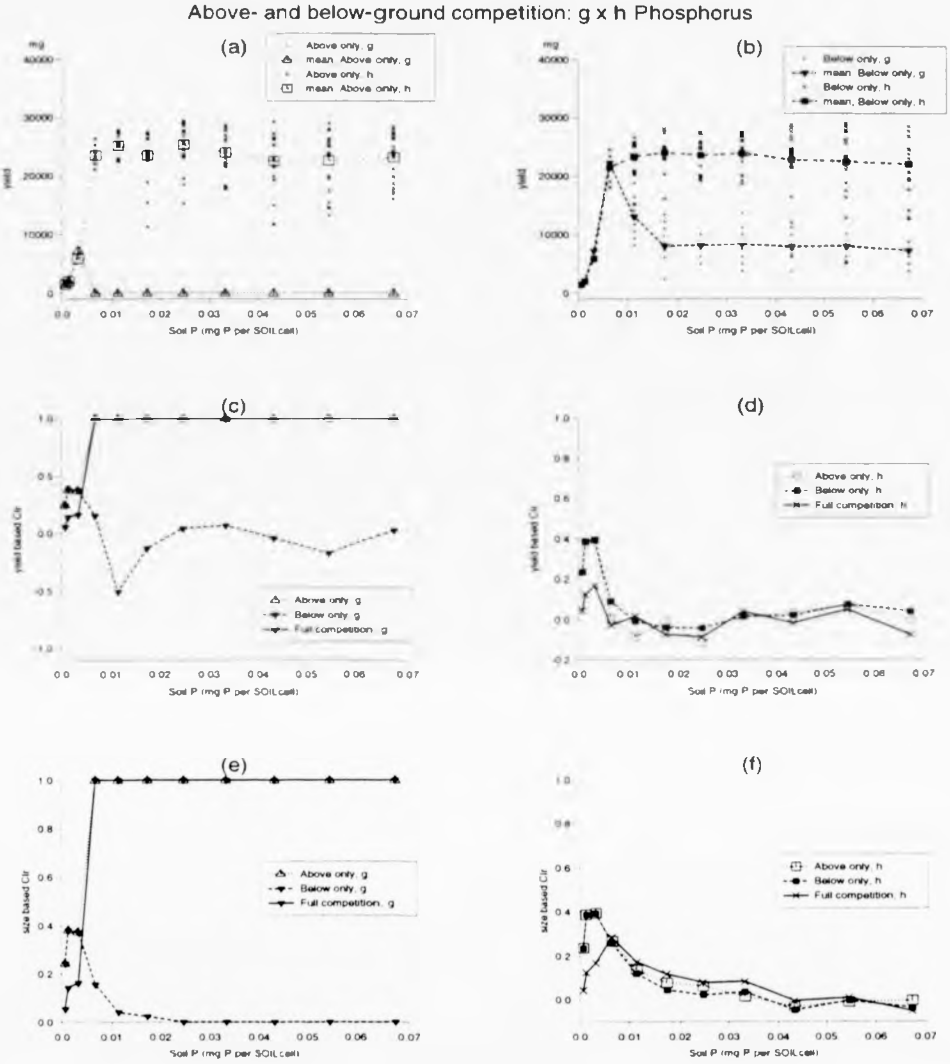


Figure 3.20p. Results of above- and below-ground competition between species *g* (high root allocation, uncoupled growth) and *h* (high shoot allocation, coupled growth) across Soil P gradient: (a) yields with no below-ground competition; (b) yields with no above-ground competition; (c) yield based CIr for *g*; (d) yield based CIr for *h*; (e) size based CIr for *g*; (f) size based CIr for *h*.

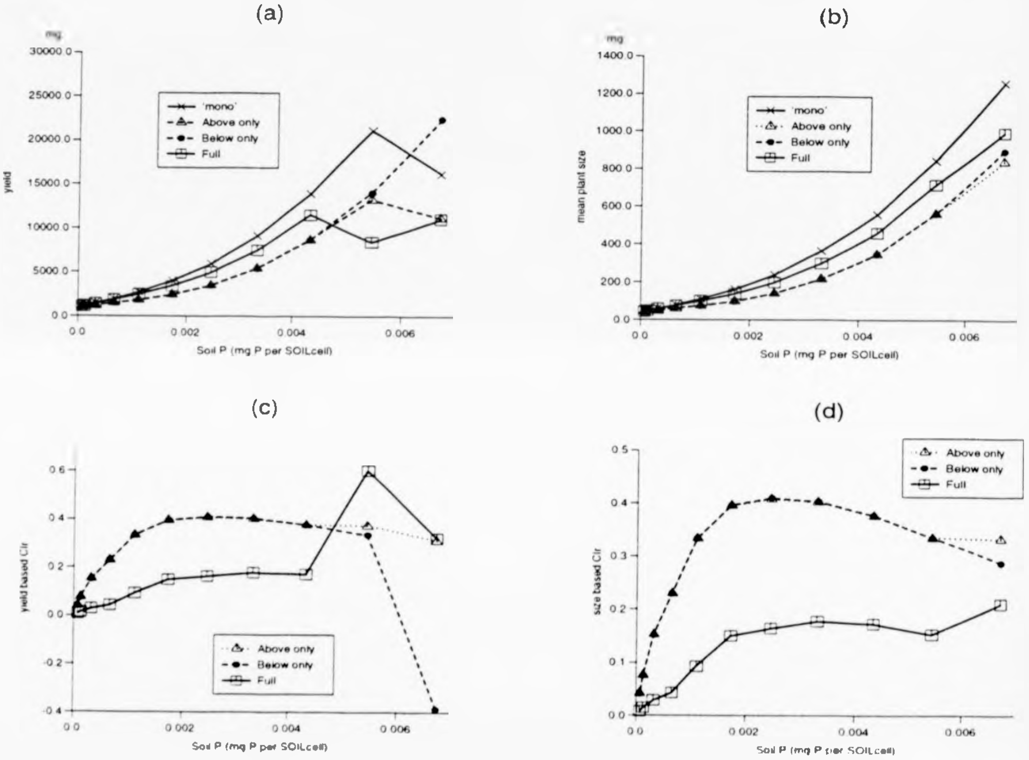


Figure 3.21. Results of above- and below-ground competition for reference species *a* across additional low Soil P gradient (see section 3.4.3.1): (a) yields; (b) mean size of surviving individuals; (c) yield based CIr; (d) size based CIr.

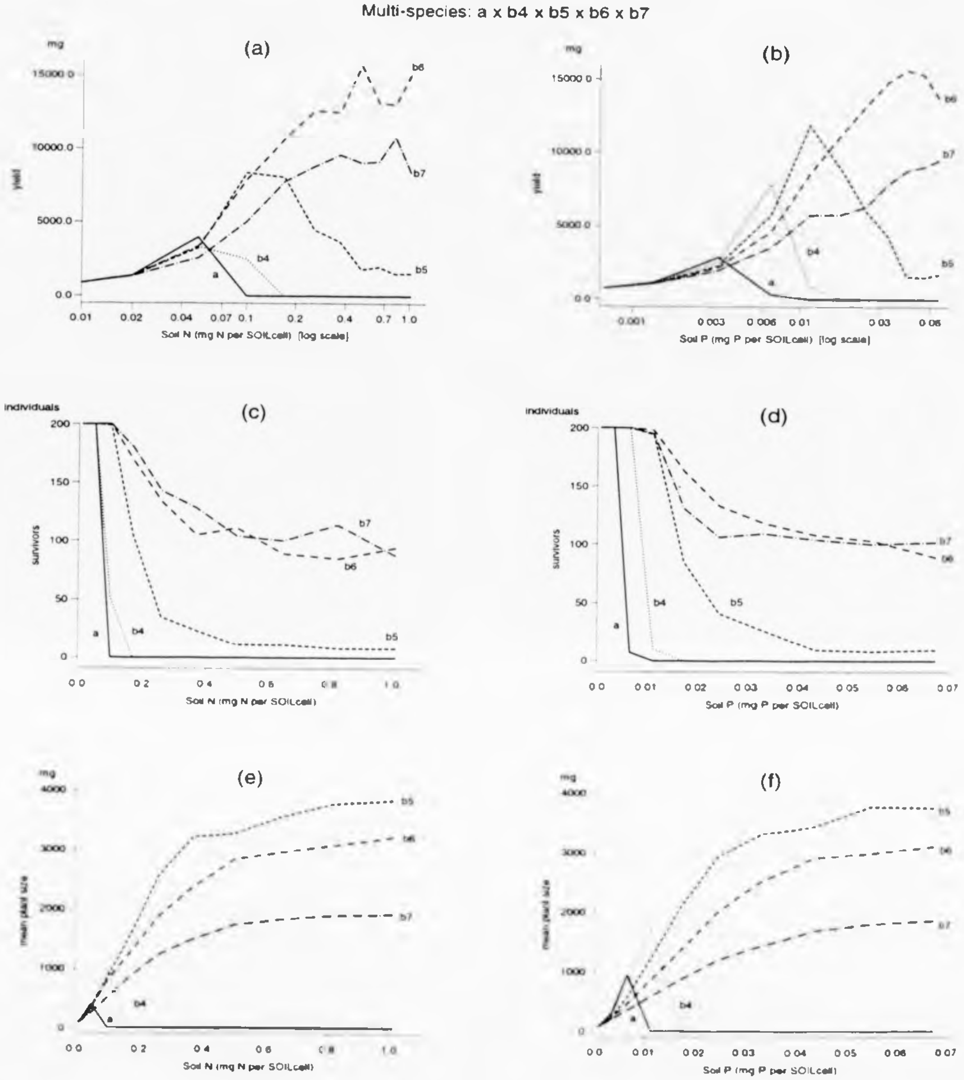


Figure 3.22. Results of multi-species competition with species *a*, *b4*, *b5*, *b6*, *b7* (in order of increasing shoot allocation); (a) yields in mixture across N gradient; (b) yields in mixture across P gradient; (c) number of surviving individuals across N gradient; (d) number of surviving individuals across P gradient; (e) mean size of surviving individuals across N gradient; (f) mean size of surviving individuals across P gradient.

3.4.3.5 *g* × *h* : uncoupled growth, high root allocation × coupled growth, high shoot allocation

The results of runs 36A and 36B are shown in Figures 3.20n and 3.20p. Species *g* has uncoupled growth and high allocation to roots, while species *h* has fully coupled growth and high allocation to shoots.

Yields

In the absence of inter-specific below-ground competition (above-ground only treatment) species *h* outcompetes *g* at N levels>3 and P levels>4 (yield of *g*=0; Fig. 3.19n(a) and 3.19p(a)), suggesting that *h* is a superior above-ground competitor to *g*. With inter-specific above-ground competition removed (below-ground only treatment) *g* is not outcompeted and produces a greater yield than *h* at low R levels (Fig. 3.19n(b) and 3.19p(b)) where below-ground competition is most intense (see section 3.4.3.1 and below), therefore *g* is a superior below-ground competitor to *h*.

Competition Intensity above- and below-ground

The population and individuals of *g* experience a 'switch' from predominantly below-ground to predominantly above-ground competition as soil N increases; at low soil P levels *g* experiences identical intensities of above- and below-ground competition, but at higher P levels above-ground competition intensity is greater than below-ground. The population of *g* experiences extremely negative below-ground CIr at several points, presumably due to the suppressive effect of inter-specific below-ground on growth and subsequent reduction of intra-specific above-ground competition.

The population and individuals of *h* experience minimal above-ground and decreasing below-ground competition with increasing soil N, but experience decreasing above- and below-ground competition with increasing soil P (Fig. 3.20n(f) and 3.20p(f)). There is no clear 'switch' from below-ground to above-ground competition with increasing soil N; the intensity of above- and below-ground competition are identical at low soil P levels.

Effect of R supply properties on competition

Species *g* and *h* experience greater CIr_{below} across the P gradient than across the N gradient.

3.4.8 Discussion

Calculation of above-ground competition intensity (CIr_{above})

As stated in section 3.4.2, the method of Wilson and Tilman (1991) to calculate above-ground competition intensity and employed in several studies, is not strictly comparable to the equivalent below-ground intensity. This is demonstrated in Figures 3.15n and 3.15p, and shows that the assumption of the calculation (equations 3.5 and 3.6) is false.

Competition below-ground as affected by resource supply properties

The CIr_{below} results are not wholly representative of below-ground competition as only inter-specific competition was removed, and intra-specific competition may still have affected yield and mortality; this is especially important when comparing with the results of studies which have separated above- and below-ground competition by removing both intra- and inter-specific competition. Within these simulations, competition below-ground is generally most intense at the lower end of the nutrient gradient, and it is here that competition for phosphorus is more intense than for nitrogen, at the population and individual scale: this is the opposite of the prediction made in section 3.2.4. However, this is not necessarily a contradiction for the following reason.

Competition for physical space, a necessary process of the model, is likely to have a greater effect on an individual's performance for phosphorus than for nitrogen, due to the modelled difference in mobility of N and P, *i.e.* at the spatial resolution of the model, roots acquire phosphorus mainly by direct interception whereas the bulk of acquired nitrogen may move through several *SOILcells* prior to interception (see section 3.2.3 and Fig. 3.3). At such low nutrient levels the root system of each individual only occupies a few *SOILcells*. With the supply differences of N and P described above, the presence of other root systems is more likely to affect the acquisition of P than N, as N is readily replaced from deeper soil layers by mass flow, whereas the immobility of P means that replacement of P is as likely to come from horizontal neighbouring *SOILcells* as from vertical *SOILcells*; this is manifested in the greater yield achieved with N in the below-ground only simulation than with P as the soil resource. Thus, where neighbouring root systems occupy adjacent cells, CIr_{below} is greater for P than for N, even though a greater yield is produced with N, and the overall (full competition) CIr with N (run 2n) is greater than that with P (run 2p; see section 3.3.2).

This greater CIr_{below} for P also affects CIr_{above} in the 'above-ground competition only' simulations: as only inter-specific below-ground competition is removed in these simulations, intra-specific competition for nutrients is still present and would have been more intense for P than for N, resulting in a greater apparent CIr_{above} in the P simulations.

Competition above- and below-ground

Competition at the individual scale across the N gradient always switches from predominantly below-ground to predominantly above-ground with increasing input of N, whereas across the P gradient competition above- and below-ground is of equal intensity at low P input and always 'diverges' with increasing P input, such that above-ground competition becomes more intense and below-ground competition becomes less intense at high P input levels. This suggests that intra-specific competition for N and P affects inter-specific competition for light to differing extents (see above). Thus, the supply properties of a resource can affect measured relationships with other resources across an environmental gradient.

At the individual scale, the position of the switch from competition below-ground to above-ground along the nutrient gradient is affected by the traits possessed by the species and the competing species. In the nitrogen simulations, while species *a* in competition with *a* experiences the switch between N levels 4 and 5, *b6* in competition with *a* experiences the switch between N levels 6 and 7. As *b6* has a greater allocation to shoots than *a* the relationship between CIr_{below} and CIr_{above} for *b6* is repositioned up the nitrogen gradient. Likewise, species *a* in competition with *b6* experiences the switch between levels 3 and 4. Species *c2* (highly plastic but unbiased) experiences the switch between N levels 4 and 5, the same point as species *a* did in monoculture, though the intensities of above- and below-ground competition that *c2* experiences in competition with *a* are much lower than those that *a* experiences in competition with *a*. Species *e* and *f* both experience this switch at similar N levels. Species *h* in competition with *g* experiences very little competition above-ground in the N simulation (due to the relatively high plastic allocation to shoot, in comparison with *g*) and experiences a switch in competition from below- to above-ground between N levels 4 and 5; *g* experiences this switch much more dramatically between N levels 3 and 4.

It is harder to obtain a clear picture of above- and below-ground competition across the phosphorus gradient because of the apparently greater intra-specific competition intensity for Soil P, discussed above.

In conclusion, a species will experience a switch in competition from below- to above-ground at different nutrient levels, depending on the CA above- and below-ground of the species (conferred by traits) and the CA above- and below-ground of competing species. High allocation to root appears to confer high CA below-ground where soil resources are most limiting; whereas high allocation to shoot appears to confer high CA above-ground where light is most limiting.

Chapter 4

Model Validation

4.1 Sensitivity Analysis of Selected Parameters

A sensitivity analysis is performed to compare the effects of different parameters on model performance. The sensitivity of the model output to the values assigned to various parameters is tested. The parameters *Imax* (equation 2.8), *Kb* (equation 2.15), *maintenanceRATE* (equation 2.18) and *PartR* (equations 2.35 and 2.36) are chosen as all affect nutrient and carbon acquisition and utilisation, and are therefore important determinants of the conclusion of Chapter 3. *CELLmass* determines the relationship between biomass and volume of space, and therefore determines the spatial resolution of the model: this parameter is also subject to a sensitivity analysis.

Sensitivity tests

These tests are designed to examine the sensitivity of the model output (yield) to variation in parameter values, therefore enabling the robustness of the model to parameter value to be evaluated.

All tests are conducted on a monoculture of 50 individuals, arranged spatially as for the 'mixture' density simulations of chapter 3, where all parameter values other than the one under examination are identical to those used for species *a* (see Tables 3.1 and 3.3). Therefore the yields attained from the sensitivity simulations may be compared directly to those attained in runs 2n and 2p (see Table 3.2).

Sensitivity analysis is performed at soil R levels 3, 4, 8 and 11, and for both nitrogen and phosphorus simulations. These soil R levels are chosen as they encompass the full range of competitive response, from predominately below-ground competition (level 3) to predominately above-ground competition (levels greater than 4); see section 3.4.

Twenty different parameter values are generated from a random number generator (Minitab statistical program), normally distributed around the usual parameter value with a standard deviation of ± 10%. The model is run separately with each of these parameter values. As the yield output of the model is variable, due to the stochastic element within the cell growth routines (see sections 2.2.13.2 and Appendix program), 10 replications (equivalent to *GROWTHreplications*; section 3.1.6) are performed for each parameter and soil R setting, and the mean value used in the sensitivity calculations described above. Whilst it is a simple process to substitute the normal values of *Imax*, *Kb*, *maintenanceRATE* and *CELLmass* for the randomly generated values, allocation pattern is linked to both *PartR* and *PartC* (equations 2.35 and 2.36), with the proviso that *PartR* + *PartC* ≤ 1.0 (see section 2.2.12), thus for the simulations where *PartR* is varied, constant allocation pattern is assumed, and *PartC* = 1 - *PartR*.

Sensitivity of the yield to parameter variation may be measured by S(*Yield*, *p*) (Thornley & Johnson 1990).

$$S(Yield,\ p) = \frac{\delta(Yield) \times p}{Yield \times \delta(p)} \tag{4.1}$$

such that

$$\delta(Yield) = Yield - Yield' \tag{4.2}$$

and

$$\delta(p) = p - p' \tag{4.3}$$

where *Yield* is the yield attained by the population of *a* in run 2n or 2p (depending on a nitrogen or phosphorus simulation) and *Yield'* is the yield attained by the population with changed parameter value, *p* is the normal parameter value and *p'* is the changed value of that parameter. S(*Yield*, *p*) is the relative change in yield divided by the relative change in parameter value. Thus if a change of +10% of the parameter value results in a +10% change of yield, S(*Yield*, *p*) = 1.0. This allows direct comparison of sensitivity between different parameters. This method is referred to as the *S*-test.

An alternative method of measuring the sensitivity to a parameter value is by calculating the coefficient of variance (*CV*) of the mean yields (in terms of *GROWTHreplications*) around the normal mean yield ($\underline{Y}$) from run 2n or 2p:

$$CV = \frac{1}{\underline{Y}}\sqrt{\frac{\sum (Y' - \underline{Y})^2}{(n-1)}} \qquad (4.4)$$

where Y' is the mean yield for each parameter setting and n is the number of different parameter values. The greater the value of *CV*, the greater the sensitivity of the yield to the value of the subject parameter. This method is referred to at the *CV*-test and the results for this test are shown in Table 4.1.

Given that the competition model contains a stochastic element in the growth routine and that replications (*GROWTHreplications*) are necessary to account for the variation this generates, the *CV*-test is perhaps a more appropriate sensitivity test for this model than the *S*-test. Even though replications are performed, small variation in yield is expected, due to the stochastic growth element. The variation caused by this may well be greater than that caused by very small parameter value changes. If so, the value of $S(Yield, p)$ would be very large where $\delta(p)$ is very small, simply due to the stochastic nature of the model, thus confounding the estimation of $S(Yield, p)$ and producing a erroneous result. However, both the *S*- and *CV*-tests are included, for comparison.

4.1.1 The absolute response of yield to parameter change

The plots of yield against relative change in *Imax* (Fig. 4.1a and 4.1c) show little general change in yield for the selected soil R level, except for Soil P level 4 (Fig. 4.1c). An increase in Imax value does not appear to increase yield, as would be expected given the importance that *Imax* has for acquisition of soil resource. The same plots for *Kb* (Fig. 4.2a and 4.2c) show that at higher Soil R levels (8 and 11, where competition is predominantly above-ground) yield is increased as the value of *Kb* increases, as would be expected. Yield is less affected by variation in *Kb* at lower R levels where the acquisition of carbon is non-limiting for plant growth (Fig. 4.2a and 4.2c). When the value of *maintenanceRATE* is changed, yield is relatively unaffected at lower R levels (N level 3,

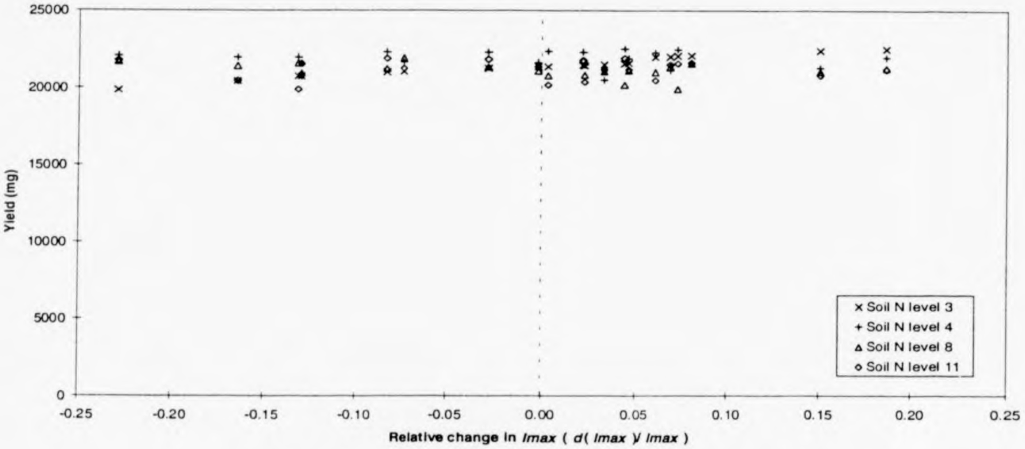


Fig. 4.1a Response of Yield to change in parameter value: *Imax* , Nitrogen. Dashed line marks normal parameter value.

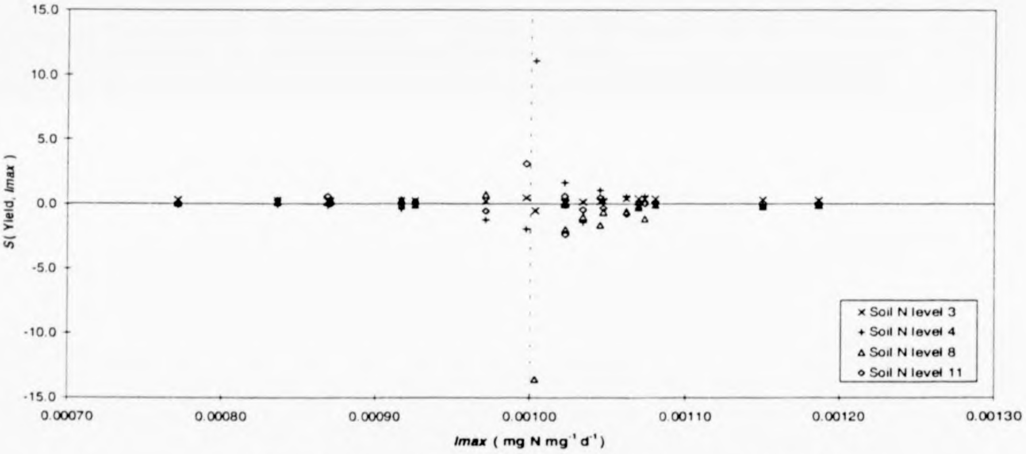


Fig. 4.1b Sensitivity of Yield to change in parameter value: *Imax*, Nitrogen. Dashed line marks normal paramter value.

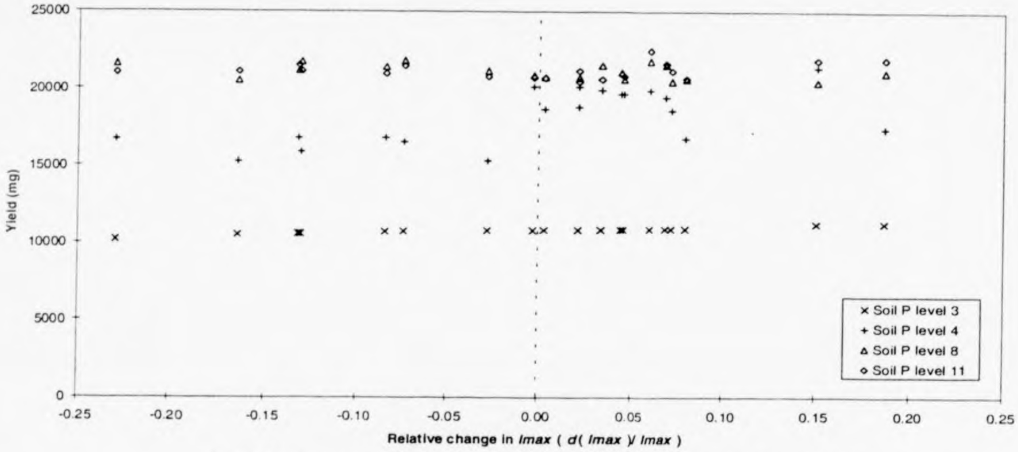


Fig. 4.1c Response of Yield to change in parameter value: *Imax* , Phosphorus. Dashed line marks normal parameter value.

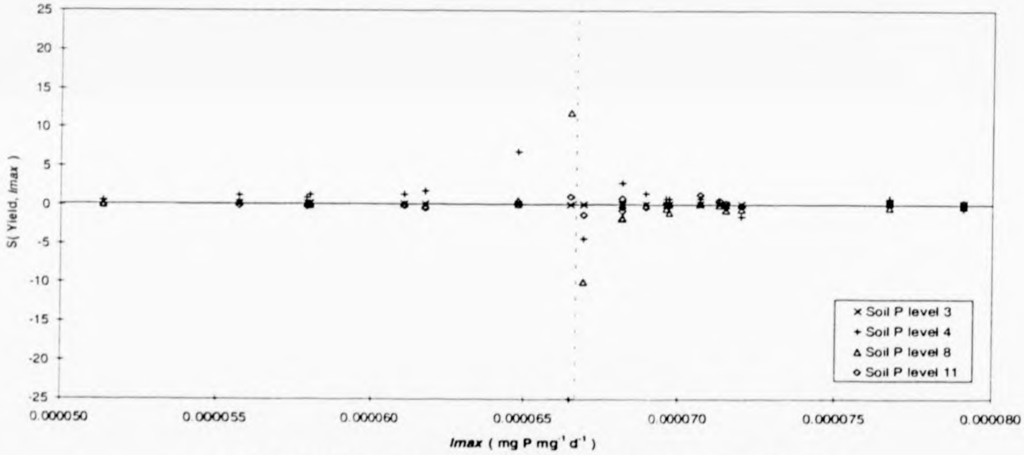


Fig. 4.1d Sensitivity of Yield to change in parameter value: *Imax*, Phosphorus. Dashed line marks normal parameter value.

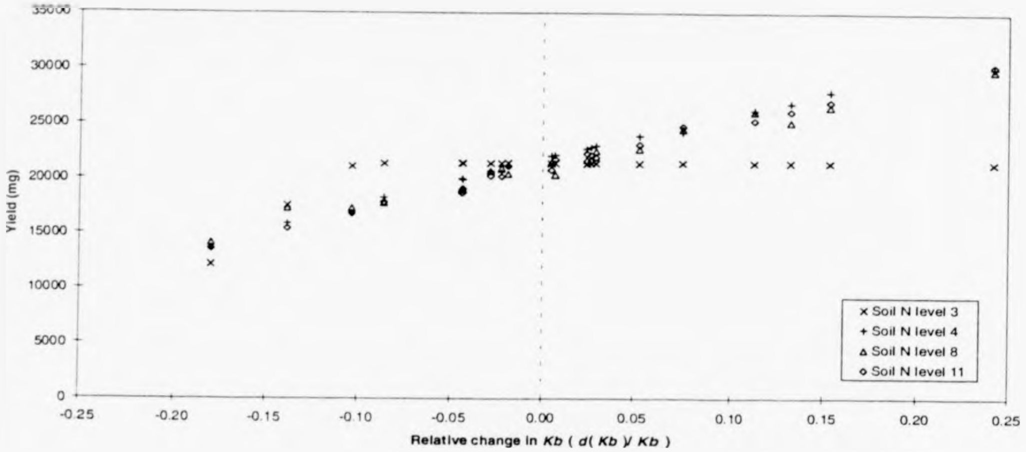


Fig. 4.2a Response of Yield to change in parameter value: ***Kb*** **, Nitrogen. Dashed line marks normal parameter value.**

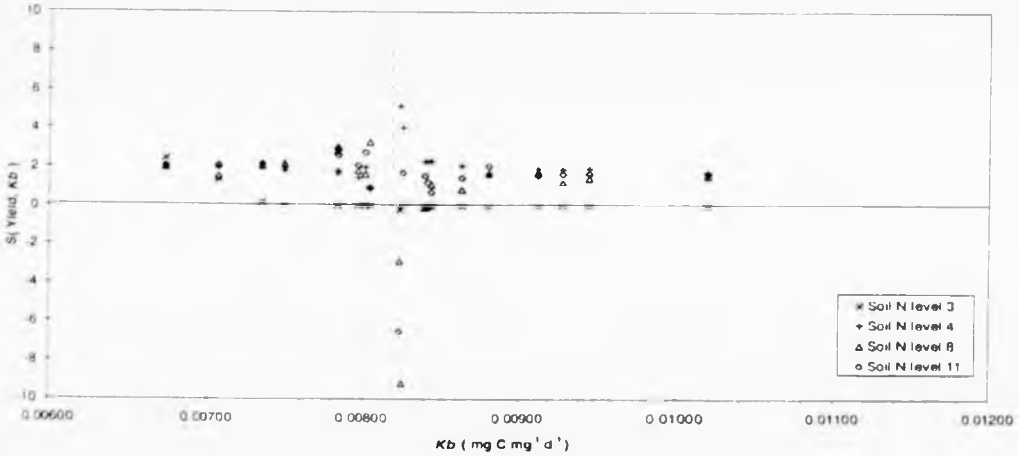


Fig. 4.2b Sensitivity of Yield to change in parameter value: ***Kb*****, Nitrogen. Dashed line marks normal parameter value.**

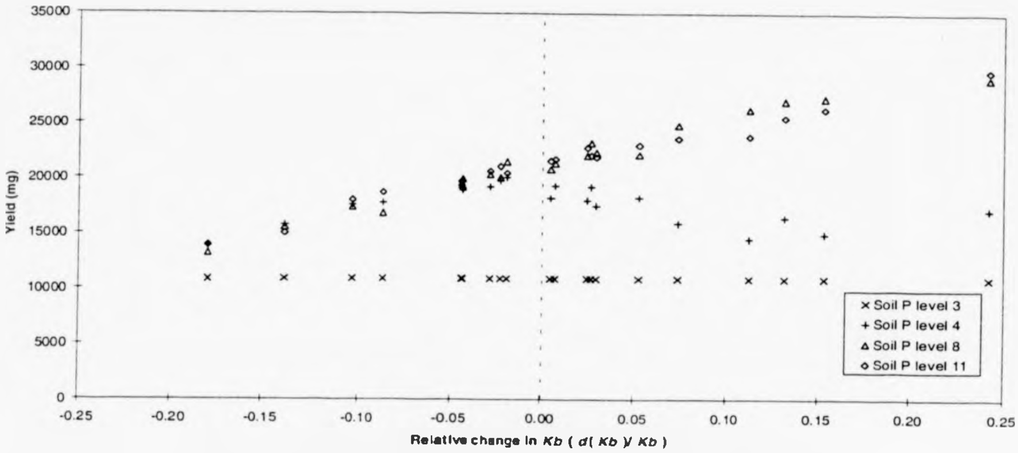


Fig. 4.2c Response of Yield to change in parameter value: *Kb* , Phosphorus. Dashed line marks normal parameter value.

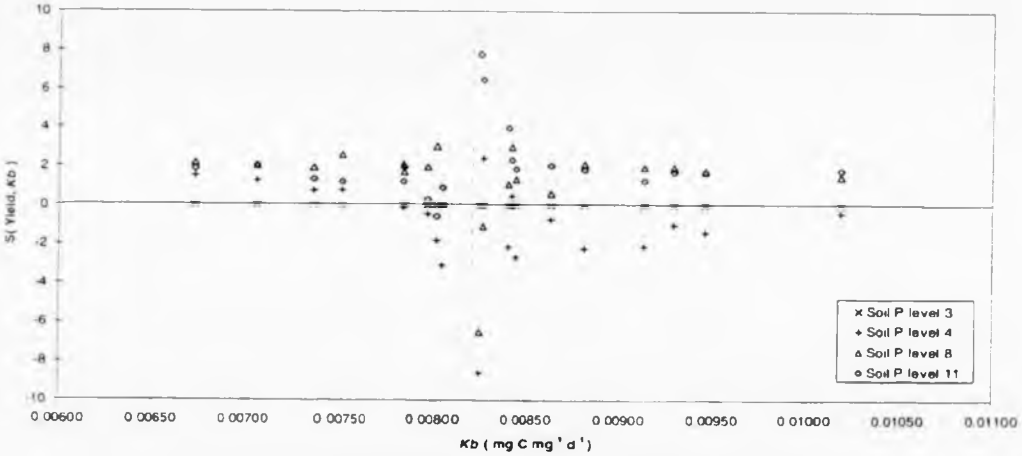


Fig. 4.2d Sensitivity of Yield to change in parameter value: *Kb*, Phosphorus. Dashed line marks normal parameter value.

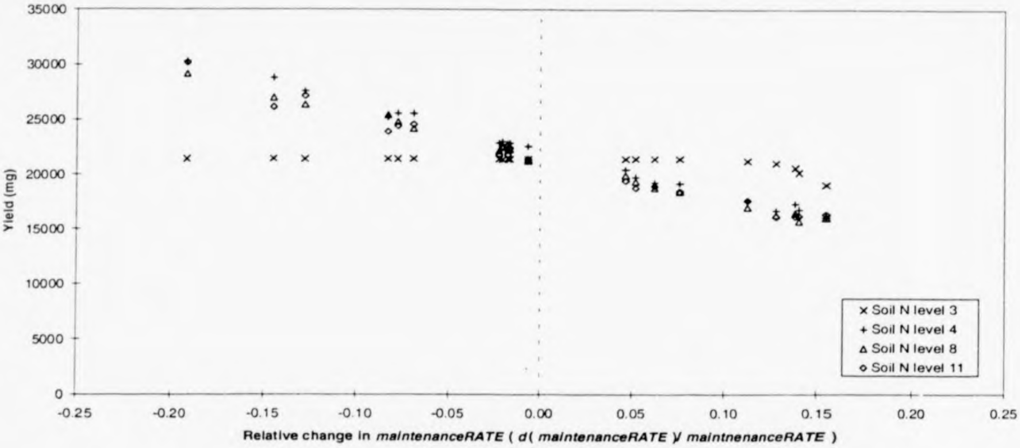


Fig. 4.3a Response of Yield to change in parameter value: *maintenanceRATE*, Nitrogen. Dashed line marks normal parameter value.

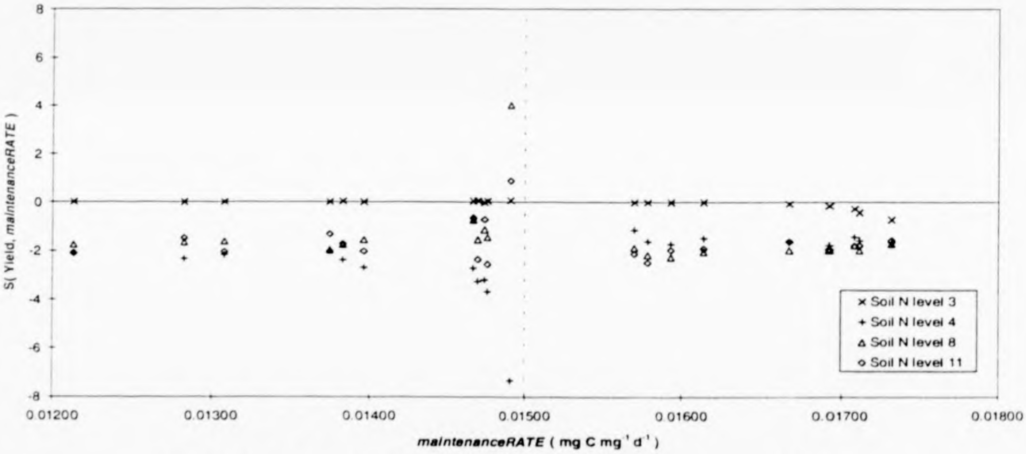


Fig. 4.3b Sensitivity of Yield to change in parameter value: *maintenanceRATE*, Nitrogen. Dashed line marks normal parameter value.

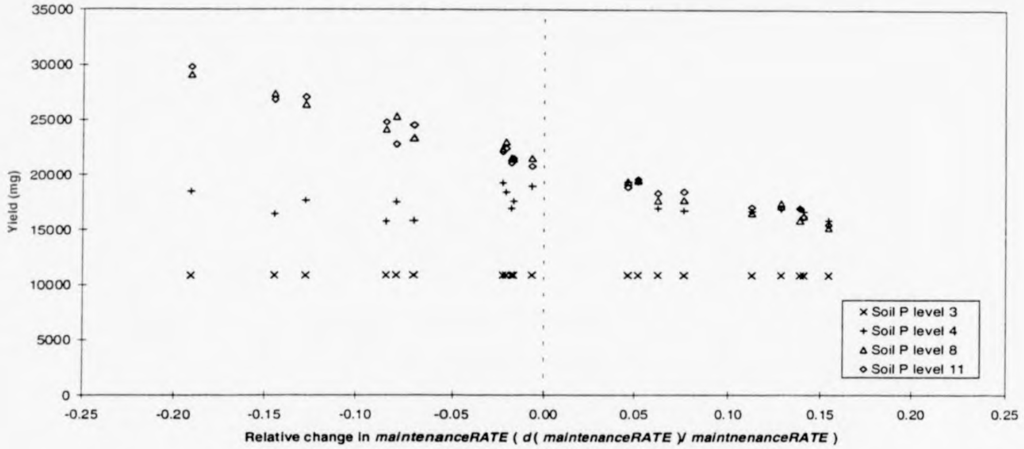


Fig. 4.3c Response of Yield to change in parameter value: *maintenanceRATE*, Phosphorus. Dashed line marks normal parameter value.

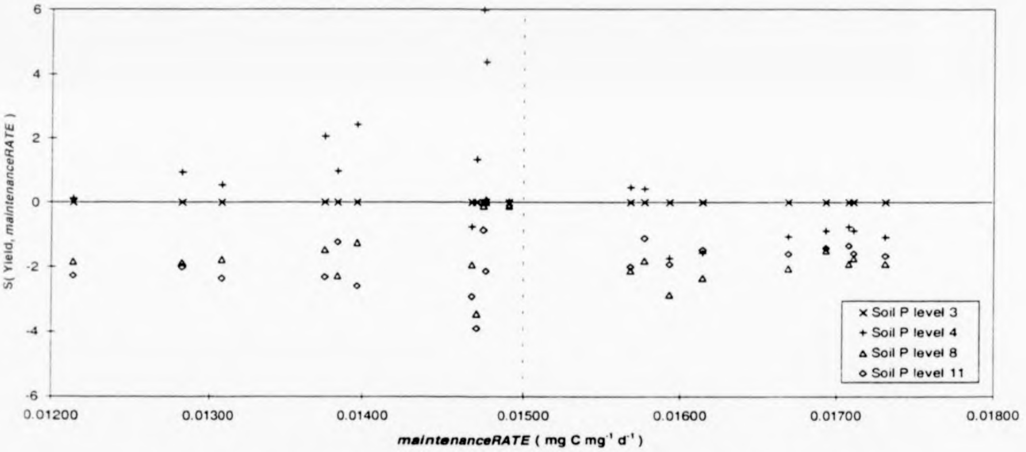


Fig. 4.3d Sensitivity of Yield to change in parameter value: *maintenanceRATE*, Phosphorus. Dashed line marks normal parameter value.

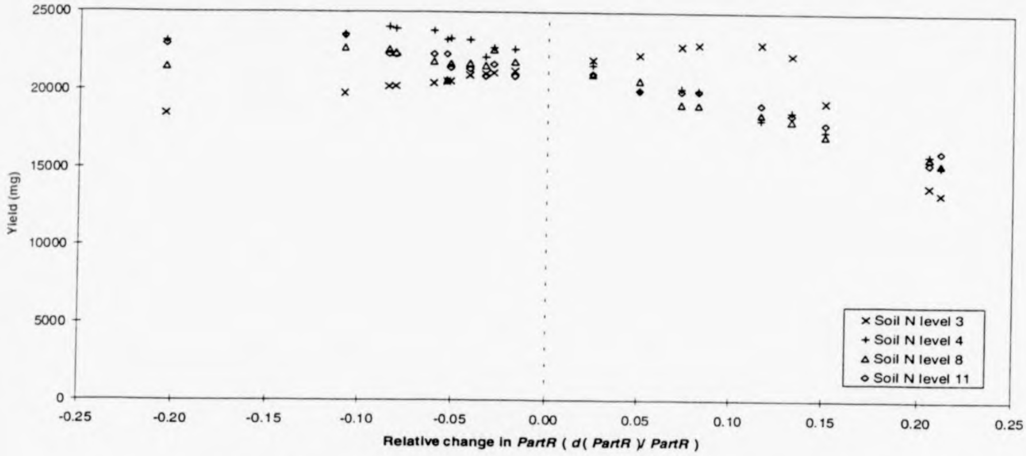


Fig. 4.4a Response of Yield to change in parameter value: *PartR*, Nitrogen.
Dashed line marks normal parameter value.

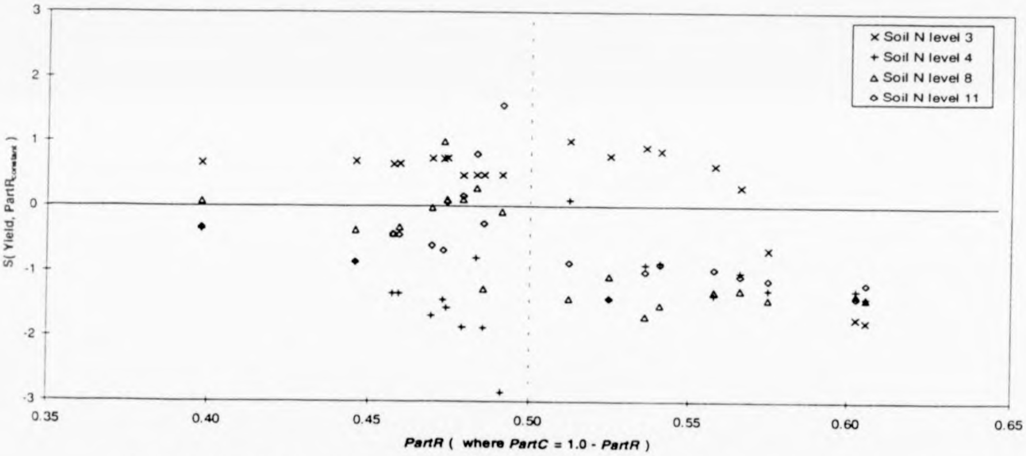


Fig. 4.4b Sensitivity of Yield to change in parameter value: PartR (constant allocation), Nitrogen.
Dashed line marks normal parameter value.

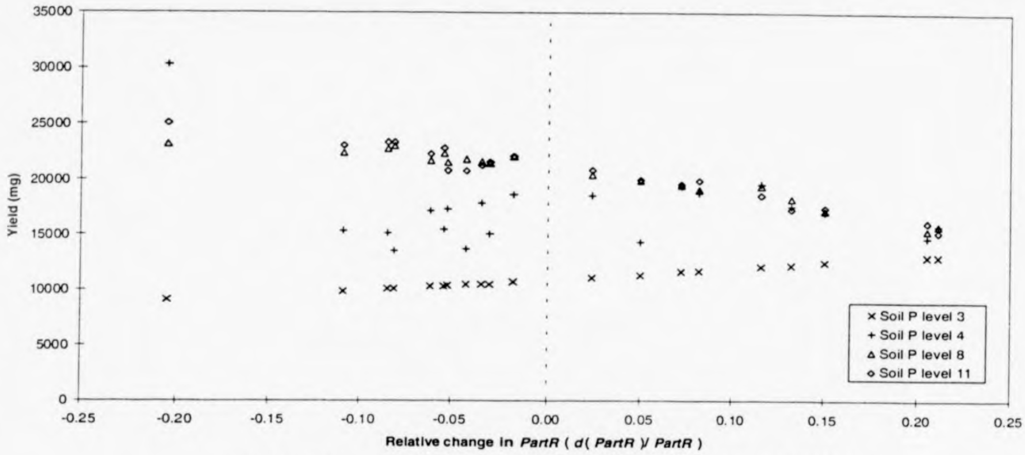


Fig. 4.4c Response of Yield to change in parameter value: *PartR*, Phosphorus. Dashed line marks normal parameter value.

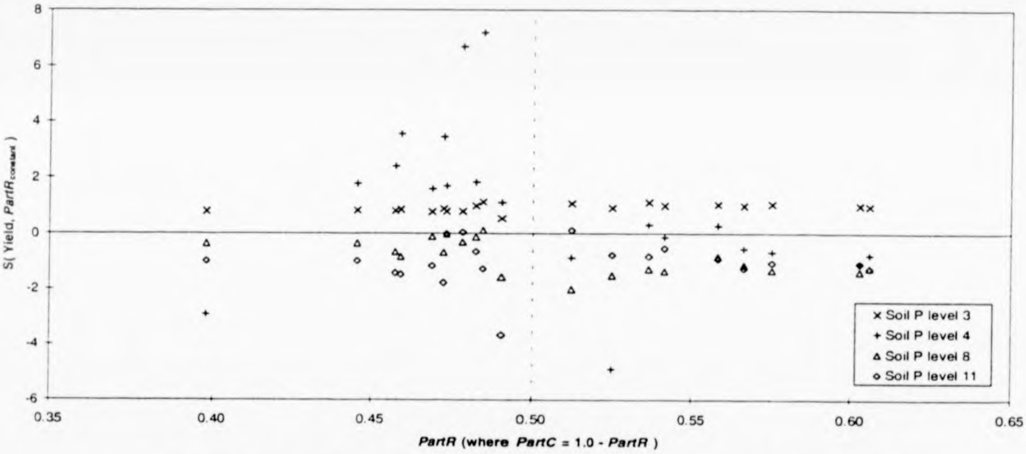


Fig. 4.4d Sensitivity of Yield to change in parameter value: *PartR* (constant allocation pattern), Phosphorus. Dashed line marks normal parameter value.

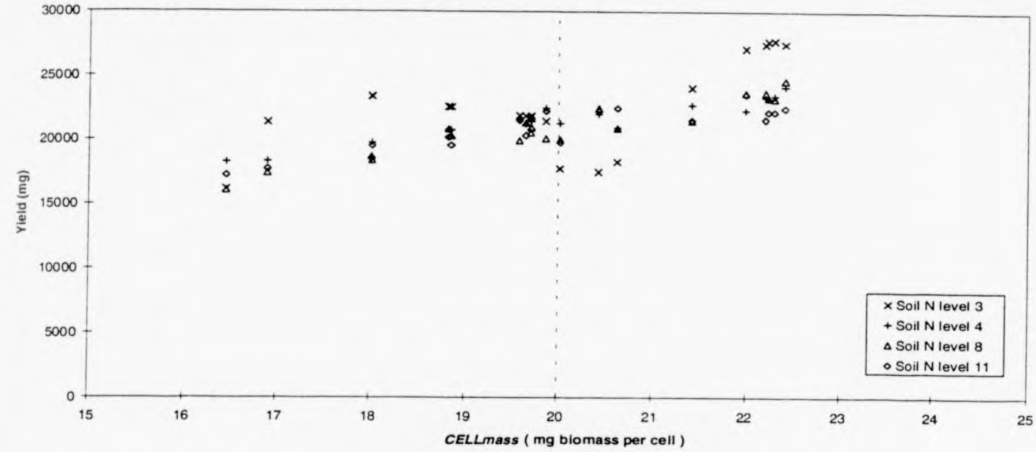


Fig. 4.5a Effect of *CELLmass* on Yield: Nitrogen.
Dashed line marks normal parameter value.

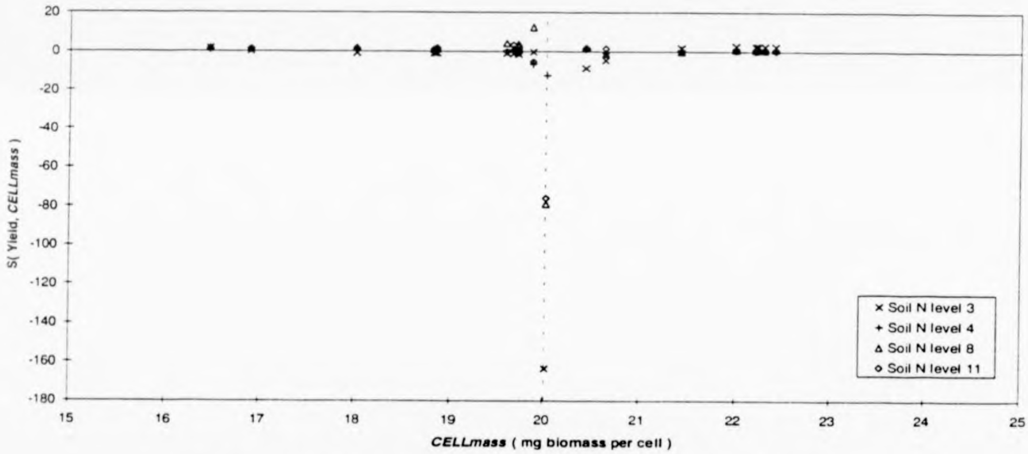


Fig. 4.5b Sensitivity of Yield to change in parameter value: *CELLmass* , Nitrogen.
Dashed line marks normal parameter value.

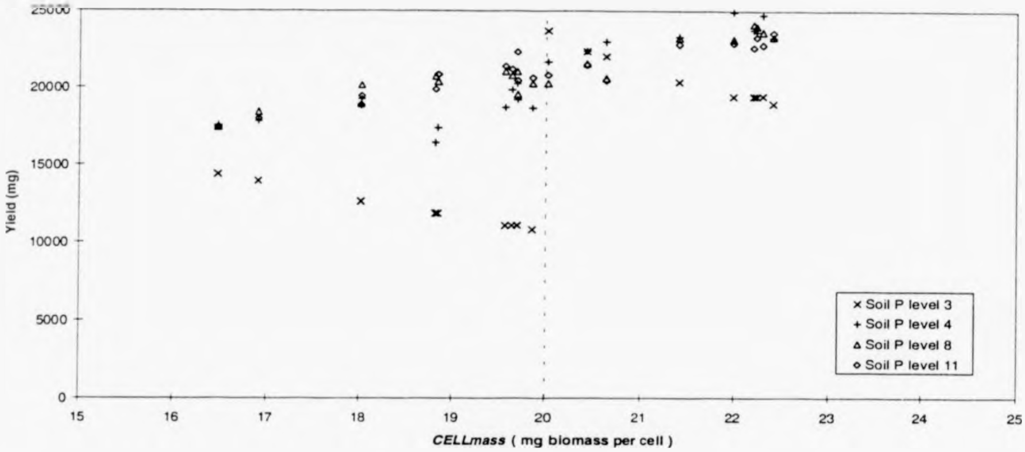


Fig. 4.5c Effect of *CELLmass* value on Yield: Phosphorus.
Dashed line marks normal parameter value.

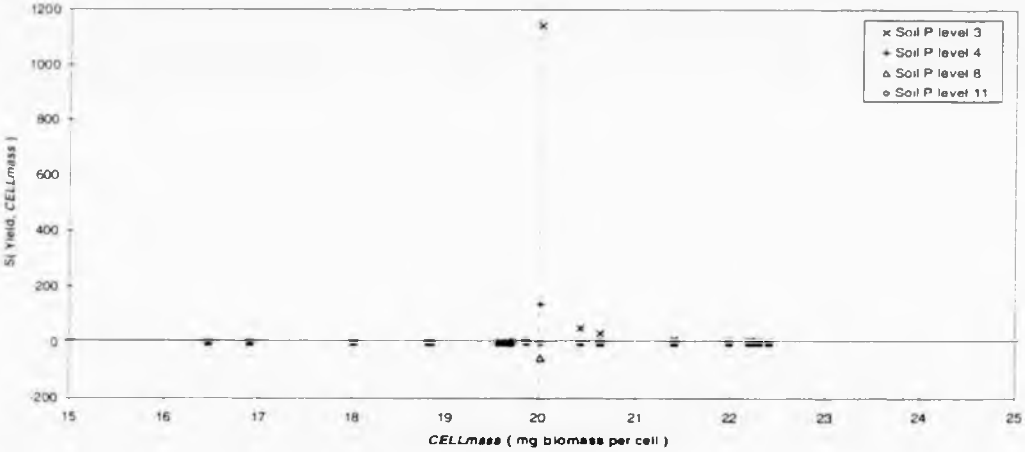


Fig. 4.5d Sensitivity of Yield to change in parameter value: *CELLmass*, Phosphorus.
Dashed line marks normal parameter value.

Fig 4.3a; P level 3 and 4, Fig. 4.3c) but at higher levels yield decreases as *maintenanceRATE* increases, as expected.

The response of yield to change in *PartR* (where allocation pattern is constant) is dependent on the soil R level at which the simulation is run (Fig. 4.4a and 4.4c). At soil R level 3, yield increases as *PartR* increases, as would be expected, given the greater acquisition of limiting soil R by a greater investment in root at this level (see section 3.3.3.1); Fig. 4.4a and 4.4c. At this soil R level, the respiratory cost of high root investment is reflected in a decrease in yield as *PartR* values > ~0.55 in the nitrogen simulation (Fig. 4.4a). At higher soil R levels, yield decreases as *PartR* (and investment in root) increase.

Yield appears to increase slightly as *CELLmass* increases for soil R levels 4, 8 and 11; however, for soil R level 3 yield varies greatly with changes in *CELLmass* (Fig. 4.5a and 4.5c).

4.1.2 *S*-tests

The results for the *S*-tests are shown in Figures 4.1b,d (*Imax*), 4.2b,d (*Kb*), 4.3b,d (*maintenanceRATE*), 4.4b,d (*PartR*) and 4.5b,d (*CELLmass*).

The *S*-tests for the five tested parameters all suggest that the model is most sensitive to very small changes in parameter value. However, this is most likely due to the stochastic output of the model, as described above, rather than the incredible sensitivity to parameter values the results suggest, as sensitivity is markedly reduced (*i.e.* *S*(Yield, parameter) approaches zero) as the relative change in parameter value is increased: for example, S(Yield, *Imax)* is within the range 0.0 to 1.0 when $\delta(Imax)/Imax > 0.2$ (Fig. 4.1b and 4.1d), where the stochastic effect would be least. This leads to the conclusion that the *S*-tests are not a reliable method of determining sensitivity to parameter values for this model.

4.1.3 *CV*-tests

The results for the *CV*-tests are shown in Table 4.1. These indicate that at soil R level 3, yield is most sensitive to *CELLmass* and least sensitive to *maintenanceRATE* and *Imax*, while at higher soil R levels (levels 8 and 11), yield is most sensitive to *maintenanceRATE* and *Kb*, and least sensitive to *Imax* and *CELLmass*. This is more intuitively correct than the *S*-test results, considering the effect on absolute yields (section 4.1.1).

Table 4.1 Coefficient of variances (equation 4.4) for each parameter, at each Soil R level.

	Soil N level 3	**Soil N level 4**	**Soil N level 8**	**Soil N level 11**	**Soil P level 3**	**Soil P level 4**	**Soil P level 8**	**Soil P level 11**
Imax	0.03118	0.02772	0.03735	0.03226	0.02203	0.10536	0.02994	0.0297
Kb	0.10779	0.18870	0.17031	0.18698	0.00004	0.12296	0.18897	0.1779
maintenanceRATE	0.03068	0.19788	0.18668	0.18815	0.00001	0.10556	0.19148	0.1927
PartR	0.13135	0.13062	0.12661	0.11285	0.10438	0.21145	0.11906	0.1252
CELLmass	0.17549	0.07893	0.10988	0.08484	0.63989	0.17094	0.08990	0.0845

4.1.4 Sensitivity of the model to parameter values

The apparent sensitivity of the model to parameter values is largely dependent upon the sensitivity test. The conventional *S*-test is inappropriate for testing this model, except with very large (more than ± 0.1) relative changes in parameter value where the model appears to be most sensitive to changes in *Kb* and *maintenanceRATE*, parameters both governing carbon acquisition and utilisation rates. The use of the *CV*-test also shows that the values of *Kb* and *maintenanceRATE* are relatively important, especially at high soil R levels, though this is not surprising considering that plant death (an important event, considering the large effect this has on yield) is ultimately controlled by these two parameters. This sensitivity therefore is a reflection of the assumption that plant death occurs the instant an individual has insufficient carbon for maintenance costs. The model would benefit from a relaxation of this assumption, such that negative growth may occur; this would also affect the self-thinning relationships and size hierarchy development of modelled monocultures (see section 4.2), and perhaps generate more realistic relationships (*e.g.* greater number of surviving individuals of small size). Also, the link between occupancy of space and plant material, primarily *CELLmass*, is most important at low soil R levels, where it effectively determines the growth rate of plants, *i.e.* the amount of resources required to generate more biomass and so initiate and sustain the positive feedback loop between growth and resource acquisition. Given that the sensitivity tests used a parameter variation of ± 10%, the model yield appears to be relatively insensitive to changes in *PartR* (determining allocation to root), compared to the higher *CV* values produced by the other parameters tested here.

4.2 Examination of model population results

Yield and plant size

The greatest total biomass yields from the simulations are in the region of 60,000 mg per 0.25 m^2, *i.e.* 240 g m^{-2}. The study by Bonser & Reader (1995) reports the biomass of old fields of herbaceous annuals where the mean above-ground biomass ranges from 64 (± 26) to 776 (± 184) g m^{-2}. The maximum shoot biomass within the simulation here is about 120 g m^{-2}. Estimated initial biomass of transplants in Wilson & Tilman's (1995) above- and below-ground experiments were 30 to 40 mg per individual: all model individuals begin with mass of 40 mg, 20 mg equally distributed above- and below-ground.

Yield and mean survivor size, for *a* in low density monoculture and the sub-population of *a* in high density monoculture at soil N level 11, through time are shown in Fig. 4.6a, and the relative growth rate (RGR) of the average individual from these simulations is shown in Fig. 4.6b. It can be seen that, at both densities, yield increases to a peak and quickly falls: this corresponds to the beginning of self-thinning and the death of individuals through insufficient carbon reserves for maintenance respiration (see section 2.2.14). Hence the reduction in yield, as biomass is removed via plant death. Subsequent to this, yield is relatively constant through time. Mean survivor size shows a smoother progression (Fig. 4.6a). The RGR of the mean individuals of the two populations (Fig.

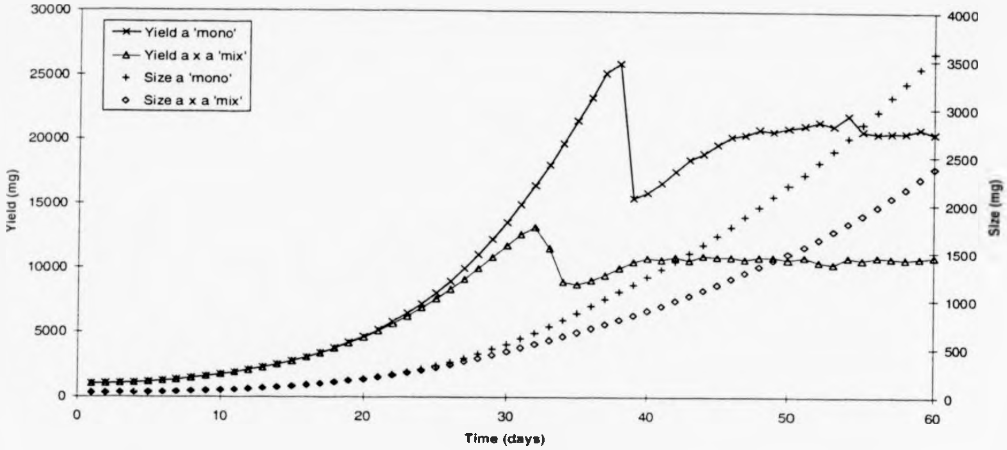


Fig. 4.6a Mean yield and surviving individual size through time for species *a* in low and high density monoculture, at soil N level 11.

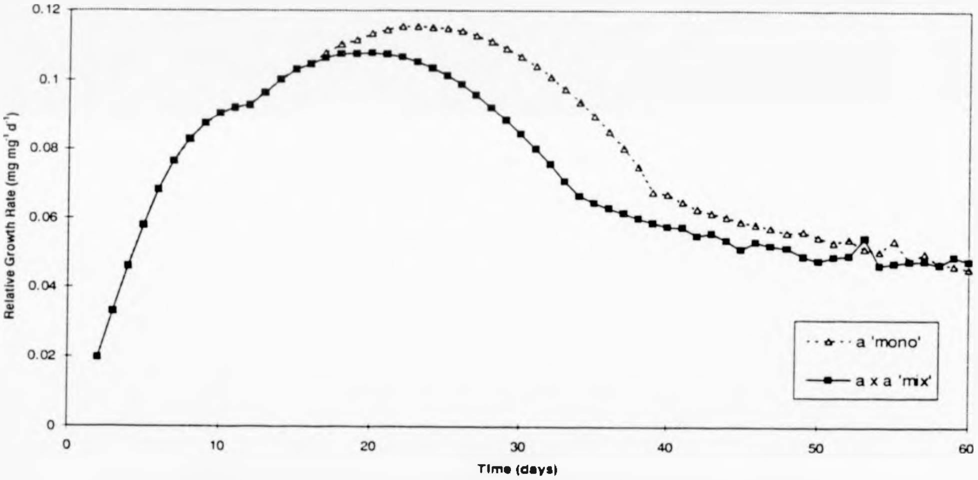


Fig. 4.6b Relative growth rate of the average individual in low and high density monoculture of species *a*, at Soil N level 11

4.6b) shows a typical RGR curve (Hunt & Lloyd 1987), the two curves departing where individuals are sufficiently large for competition (presumably mainly for light at this R level) to occur.

Variation in Yield

Variation in yield is an inevitable outcome of the stochastic element of the growth routine, and the reason why replications for each soil R level are performed. It is interesting to note that the random process by which each individual occupies space above and below-ground can lead to such variation in final yield; for example, in Fig. 3.4n(b), at soil N level 11 there is an approximate 7.6 fold difference in yield attained by *a* (though it must be remembered that this is only part of the population within that simulation: there is only a 1.3 fold difference in yield when the whole monoculture population of *a* is considered).

Self-thinning

Further validation of the model may be attained by considering self-thinning relationships of monocultures: for this purpose self-thinning within only the monocultures of species *a* are examined as this is the only model species that has monoculture simulations performed at more than one initial density. However, analysis is hampered due to the restricted densities attained and used.

Figures 4.7a-d shows the relationship at day 60 between $\log_e$(plant size) and $\log_e$(survivors) for the nitrogen (all values in Fig. 4.7a, mean values in Fig. 4.7c) and phosphorus simulations (all values in Fig. 4.7b, mean values in Fig. 4.7d). These plots are not strictly demonstrations of self-thinning, as the results from all the soil R levels are included, and all values were taken at day 60. However, they demonstrate how the relationship between mean plant size and number of survivors changes with increased nutrient availability. At low soil R levels, growth and competitive interaction is insufficient to generate any thinning; this is the vertical part of the curves in Fig. 4.7c and 4.7d shown in the plots. As soil R availability increases, there is little further increase in overall yield (above soil R level 4), and the relationship between $\log_e$(mean plant size) and $\log_e$(survivors) is approximates to a slope of -1.

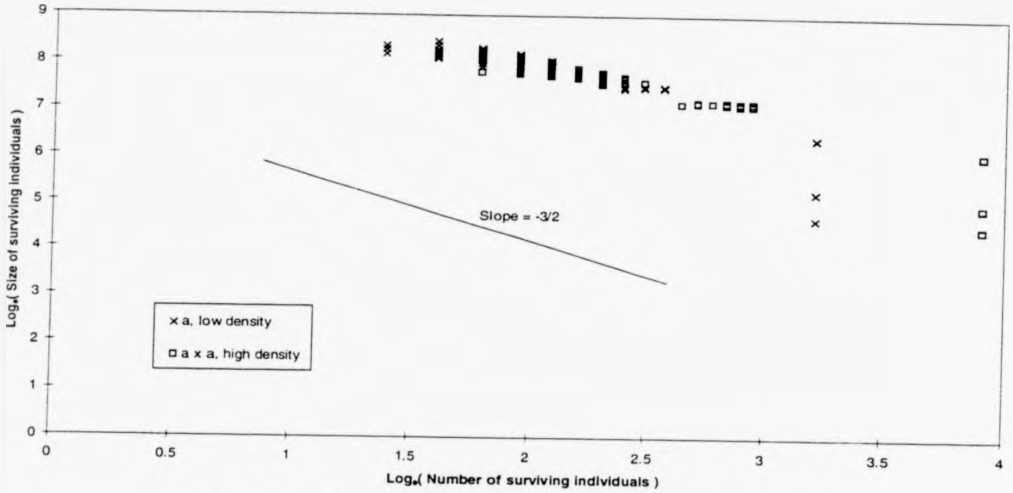


Fig. 4.7a Self-thinning relationship within the monocultures of species *a*: Nitrogen

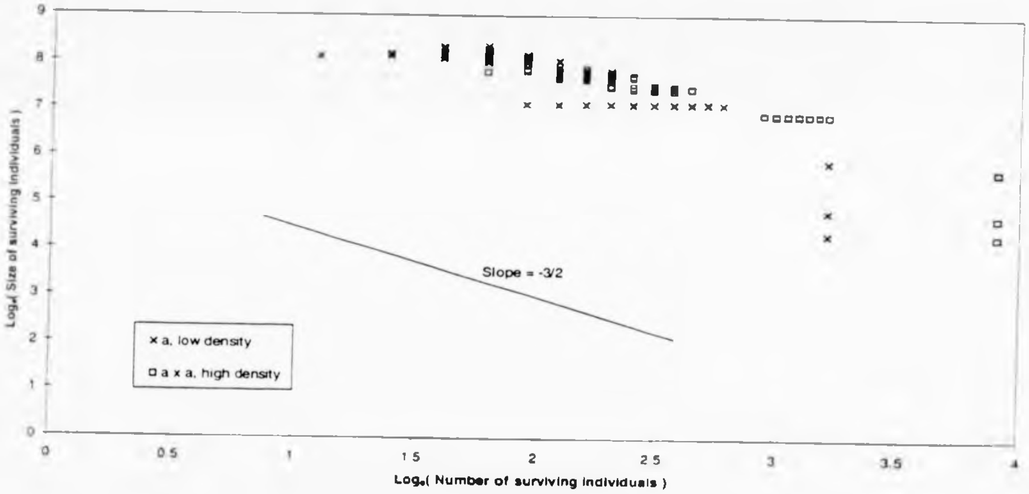


Fig. 4.7b Self-thinning relationship within the monocultures of species *a*: Phosphorus

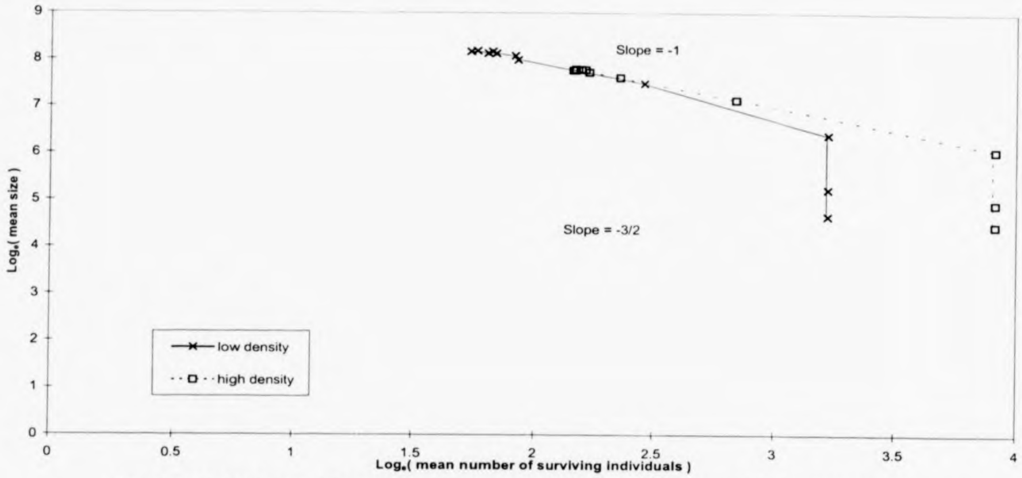


Fig. 4.7c Self-thinning relationship using the means of survivors and size within the monocultures of species *a* : Nitrogen

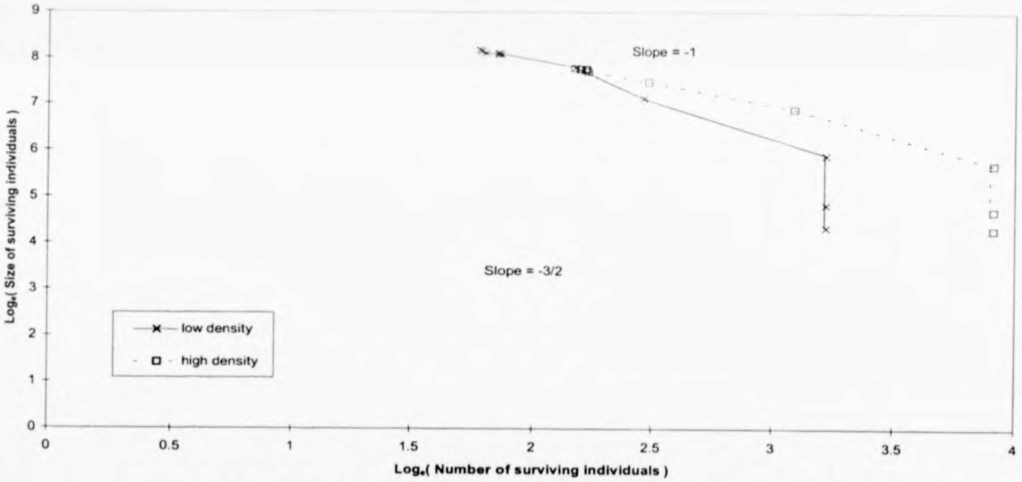


Fig. 4.7d Self-thinning relationship using the means of survivors and size within the monocultures of species *a* : Phosphorus

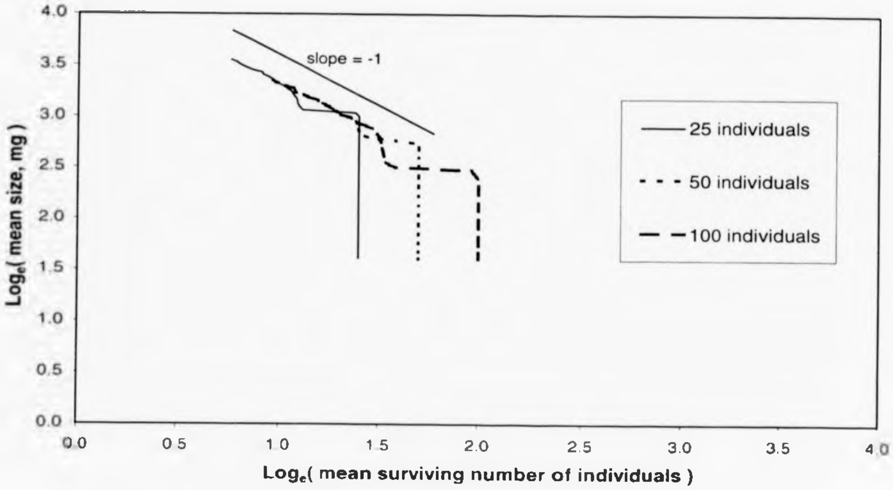


Fig. 4.7e. Self-thinning trajectories from simulations of monocultures of species *a*, at the highest soil N level. Values used are the means for 20 replicates.

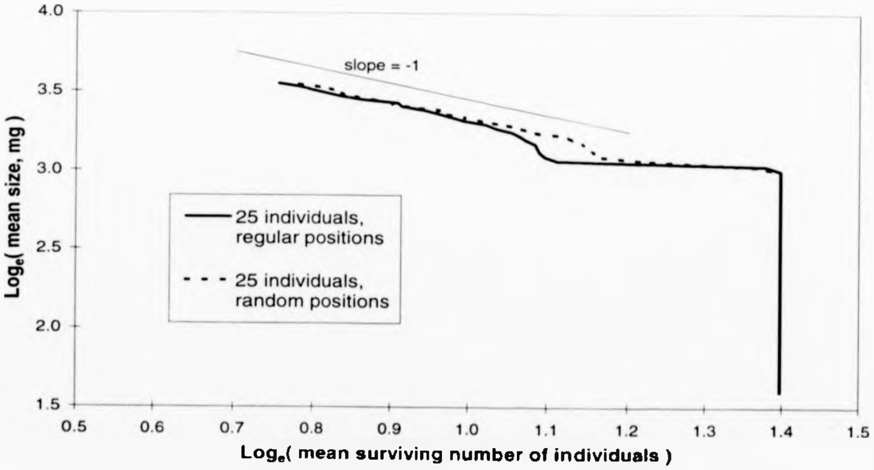


Fig. 4.7f. Self-thinning trajectories from simulations of monocultures of species *a*, at the highest soil N level, comparing the effect of individual arrangement.

Figure 4.7e shows the self-thinning trajectories through time for monocultures of species *a* at three different initial densities (25, 50 and 100 individuals per 0.25 m^2), at the highest soil nitrogen level (1.01 mg N per *SOILcell*); mean values calculated from 20 growth replicates are used. It can be seen that all three simulations converge on a similar line which has a slope of about -1, where maximum yield is attained; this phenomena has been reported for several thinning studies (Lonsdale & Watkinson 1982, Watkinson 1984, Westoby 1984), though the generality of it has been questioned (Weller 1987, Lonsdale 1990). However, the approach of the simulation's trajectories to where they converge is characterised by a rapid increase in mortality with little change in mean plant size corresponding to the onset of competition induced mortality; here self-thinning would be expected to conform to the reported -3/2 power law (Westoby 1984, Weller 1987, Lonsdale 1990). Therefore, the performance of the model monocultures for this period of establishment differs considerably from the published self-thinning studies.

It was suspected that this difference may be due, in part, to the regular distribution of individuals within the modelled area: hence, a further simulation was conducted using 10 different sets of random initial positions for individuals, at a density of 25 individuals per 0.25 m^2: the mean values for both mean plant size and density were calculated, and the thinning trajectory using these values is shown in Fig. 4.7f. Both simulations converge onto a line with a slope of about -1; random initial positions decreases the magnitude of the rapid mortality increase in the regular position simulations, but it is still present. Thus, the model is not corroborated by published work in terms of self-thinning before maximum yield (for that environment) is attained. However, the fact that all density trajectories eventually converge indicates that the model simulates self-thinning in a qualitative manner. The difference in quantitative terms (*i.e.* thinning slope is not steep enough) is probably due to the manner in which the occupancy of space and death are modelled as dictated by programming limitations, discussed further in section 5.1 and below.

The geometry of plant growth within the model, following the death of a neighbour, tends to be predominately lateral, *i.e.* plants tend to grow laterally into the spaces vacated by dead neighbours before allocating biomass in the vertically plane, due to the cell growth rules in section 2.2.13.2. The geometry of plant growth is expected to affect self-thinning relationships (Westoby 1984, Lonsdale 1990) and the geometry of the model plants is suspected to contribute to the discrepancies between the model's and recorded thinning relationships.

Morris and Myerscough (1991) presented evidence that self-thinning relationships (in terms of yield and density) for *Ocimum basilicum* are affected by nutrient availability, such that the intercept of the thinning increases with nutrient availability; similar effects of nutrient supply have been reported in *Fagopyrum esculentum* (cited in Morris & Myerscough 1991). The results of the model do not conform to this view; instead, it appears that self-thinning is slowed down and follows the same pattern at lower nutrient levels and at higher levels (not shown explicitly, but compare Figs. 4.7c and 4.7e). This phenomena has also been reported in studies by White and Harper (1970) and Bazzaz and Harper (1974), though it is debatable whether suitable data points were selected in these studies (Weller 1987).

Size hierarchies

The size distribution of surviving individuals of the high density (50 individuals) monoculture of species *a* in the nitrogen simulation (run 2n) at the end of the simulation (60 days) are shown in Fig. 4.8. The skewness of the distribution across the soil N gradient is as follows: there is a skewness value of 0.878 at soil N level 3, 0.014 at soil N level 4, 0.528 at soil N level 8, and 0.348 at soil N level 11. The inequality of sizes may be measured by the coefficient of variance of the survivors sizes, and the values for these simulations are: 0.042, 0.067, 0.125 , and 0.110 at soil N levels 3, 4, 8 and 11 respectively.

It can be seen that the distribution is uneven in that there are fewer large individuals in comparison to the number of smaller individuals (*i.e.* skew > 0) at the higher soil N levels especially. It is expected that the skewness and size inequality of monoculture populations increase with increasing productivity (Weiner 1985, Hutchings 1986, Weiner & Thomas 1986). This is not evident from the skewness results (the highest value is at soil N level 3), yet the coefficient of size variance does increase with increasing nutrient availability, which has been shown to occur in natural populations (Weiner 1985). The size inequality of survivors increases with an increase of density at all the above soil N levels. For the monoculture with 100 initial individuals the coefficient of variances are: 0.064, 0.089, 0.204 and 0.191 at soil N level 3, 4, 8, and 11 respectively. This has been

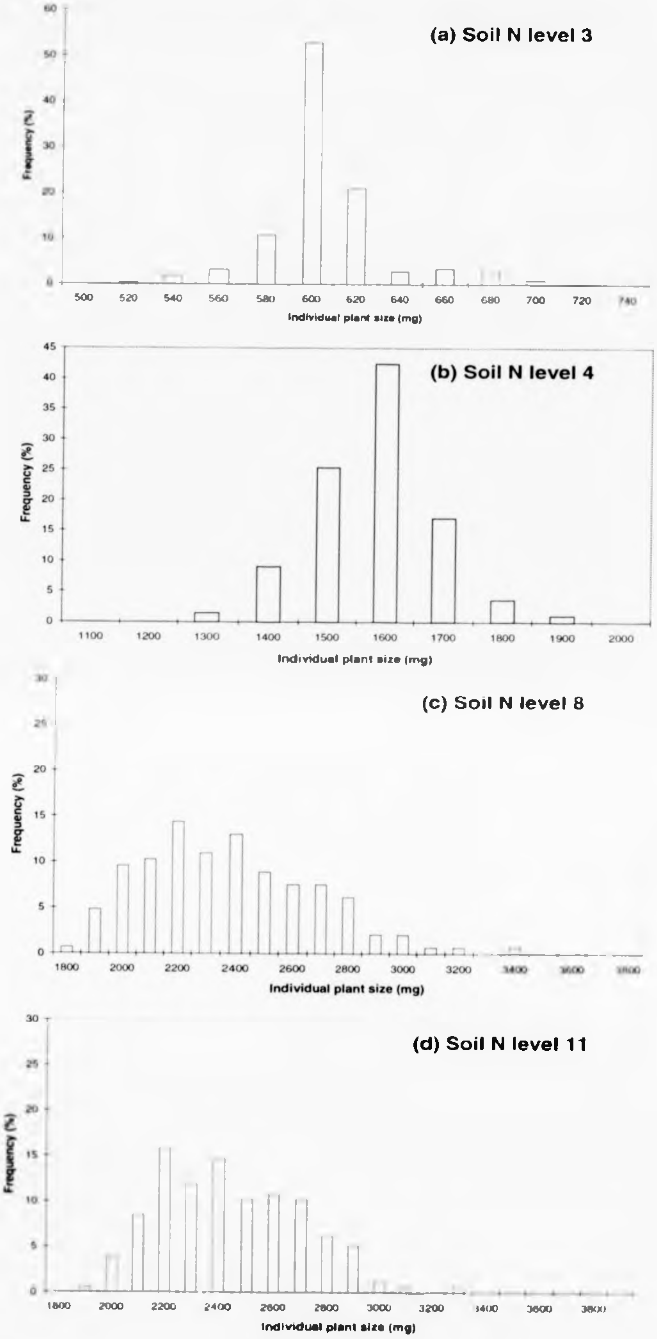


Fig. 4.8 Size hierarchy of surviving individuals in *a* x *a* nitrogen simulation. Values on x-axis refer to centre of size class.

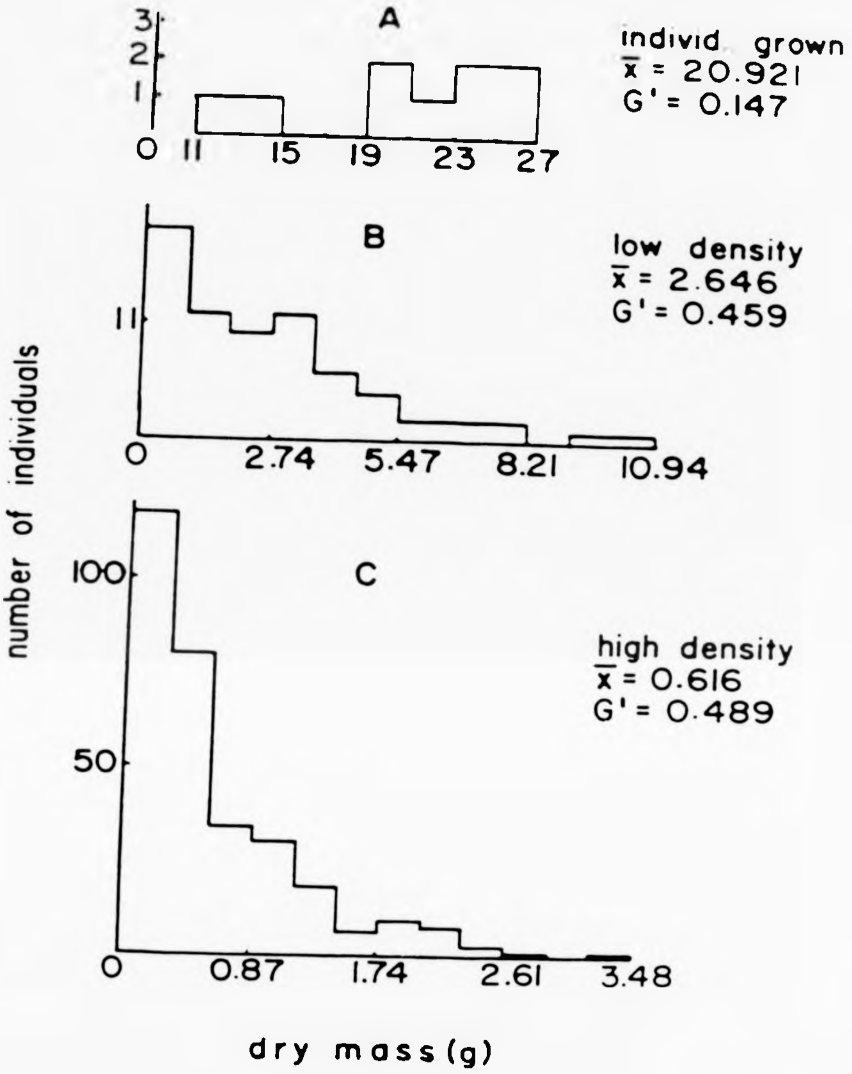


Fig. 4.9 Dry mass distributions of monocultures of *Lolium multiflorum* grown in high-fertility soil. (A) Individually grown; (B) low density (200 individuals per m^2); (C) high density (1200 individuals per m^2).
From Weiner (1985:Fig. 4)

demonstrated to occur in experimental populations (Weiner & Thomas 1986). Unfortunately, the size distribution of individuals was not recorded for the monoculture split above- and below-ground competition simulations of runs 32A and 32B for comparison with the study of Weiner (1986) on the size distribution with partitioned above- and below-ground competition in vine populations.

One notable feature of the size distributions shown in Fig. 4.8 is the absence of very small individuals and the weak skewness of the size distribution at the highest nutrient levels, where the distribution would be expected to be distinctly skewed (Weiner & Thomas 1986): for comparison see Fig. 4.9 taken from Weiner (1985). This lack of small sizes may be due in part to the absence of any variation in initial plant size. Perhaps the best explanation for the relative symmetry of the model sizes at high nutrient levels, is due to assumptions concerning plant growth: no negative growth (due to competition) is included within the model and that plant death results in the instantaneous removal of biomass. As the individuals in a very dense, productive simulation compete not only for light and nutrients but also for space, and due to the manner in which the cell growth algorithm operates (see above), individuals tend to die before being over-topped by larger neighbours. Hence, while the model's results demonstrate that the distribution of sizes conform qualitatively to published work, the extent of size hierarchy development suggests that light competition is less asymmetric within the model than in nature. This presents an obvious opportunity for the development of the model.

4.3 Validation of some aspects of the simulation results

In this section, the results from the simulations of Chapter 3 are compared against related published studies. Not all the results from simulations may be validated in this manner, as the model does not simulate explicitly any of the documented studies. Thus, it is probably more constructive to determine if the model results corroborate qualitatively with field and experimental results, and numerical values fall within the range encountered in nature, than to compare in a purely quantitative manner. The two aspects of the model results used for external comparison are root:shoot ratios and competition intensity across a soil nutrient gradient.

4.3.1 Comparison of model root:shoot ratios with published ratios

The sensitivity analysis of section 4.1 suggests that, generally, yield is not as sensitive to root:shoot ratio (at least where allocation is constant) as to the other tested parameters, though this is obviously dependent on the nutrient level. However, differences in allocation pattern have been demonstrated to produce markedly different results in the model (*e.g.* simulation m1, section 3.3.3.1). Therefore, it is worthwhile comparing the root:shoot ratios of the model species with published studies.

Viable allocation patterns

Although only a few of all possible allocation patterns from various values of *PartR* and *PartC* (which determine the allocation of growth to root or shoot and the degree of plasticity in allocation) were used in simulations, it is possible to make some generalisations concerning viability of species. Although not shown explicitly in Chapter 3, species with constant root:shoot ratio ≥ ~ 2.33 (RWR ≥ ~ 0.7) appear to be unviable at the simulated soil nutrient levels. Of the 68 herbaceous wetland species examined by Shipley and Peters (1990), the highest root:shoot ratio found was 2.23, though all the other species exhibited ratios between 0.1 (RWR ≈ 0.091) and 0.6 (RWR ≈ 0.375). It is unfortunate that Shipley and Peters do not record the nutrient status of the habitats in which the species are normally resident. The maximum root:shoot ratio of old-field species reported by Wilson & Tilman (1995) is about 2.4, and that was for *Poa pratensis* subjected to only below-ground competition and severe above-ground 'disturbance'. Some of the species in this study exhibited greater plasticity of root:shoot ratio (in the absence/presence of neighbours) than others. However, in another study Tilman and Wedin (1991*a*) found much higher ratios, values ranging from about 6 to 8 in *Schizachyrium* and *Andropogon* species at very low soil nitrogen availability, though it must be remembered that the simulation models represent general herbaceous species, and there is evidence that these old-field perennials have significantly different physiological adaptations to the other species in the studies which displayed much lower ratios (generally about 0.1 to 2).

Plastic allocation

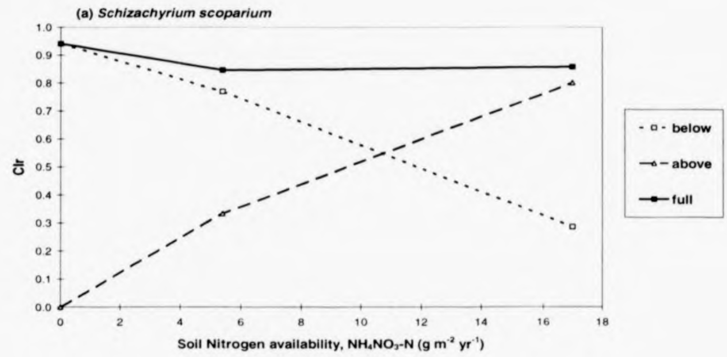
The results of monoculture simulations of species *c1* and *c2* (runs 15 and 16; section 3.3.3.2) which exhibit unbiased plastic allocation patterns may be used to examine the realism of plastic response of some model species. The range of root:shoot ratios shown by *c2* (the most plastic species) was from 2.33, at the lowest soil resource level, to 0.25, at high soil resource levels; this is narrower than the range the species is capable of, and therefore probably represents the most extreme allocations that are viable within the modelled system. This approximate 10-fold difference is just within the range (1.5 to 12-fold) cited by Chapin (1980), with an equivalent 100-fold difference in nutrient availability. The study of eight old-field species by Wilson and Tilman (1995) showed approximately 1 to 2.3-fold decreases of root:shoot ratios with an increase of nutrient supply; this is a smaller range than model species *c2* exhibits, but these species are likely to have adaptations other than root:shoot ratio to the very low nitrogen availability characteristic of their habitat.

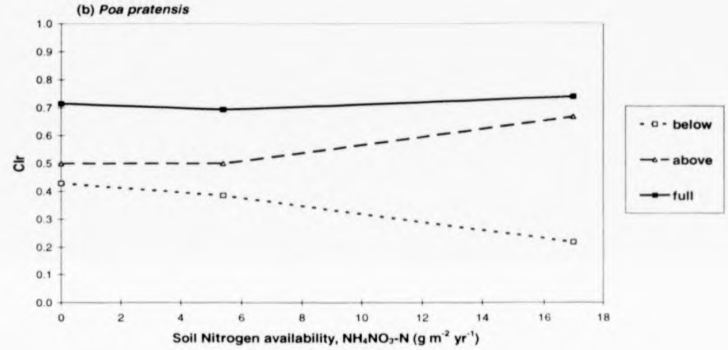
Ratios related to the environment

It is widely assumed that species adapted to nutrient poor habitats exhibit greater root:shoot ratios than species adapted to nutrient rich habitats (Chapin 1980, Tilman 1988). While the model presented within this thesis can conform to this axiom (see, for example, simulation run m1 within section 3.3.3.1), a prediction has not been made concerning specific root:shoot ratios and nutrient availability, as physiological differences (*e.g.*, per-unit mass nutrient acquisition rates) are identical for all model species, and other potentially important factors, such as the influence of mycorrhiza, are not included within the model. It is clear from several studies that allocation of biomass to resource acquisition organs alone does not necessarily confer an equivalent ability to acquire (and conserve) those resources (Berendse & Elberse 1990, Olff *et al.* 1991, Elberse & Berendse 1993).

4.3.2 Competition intensity in model simulations in comparison with published studies

The main prediction the model makes concerning competition shifting from below-ground to above-ground as soil nutrient availability increases remains untested in the great majority of natural annual and first-year perennial systems. Few studies have addressed the





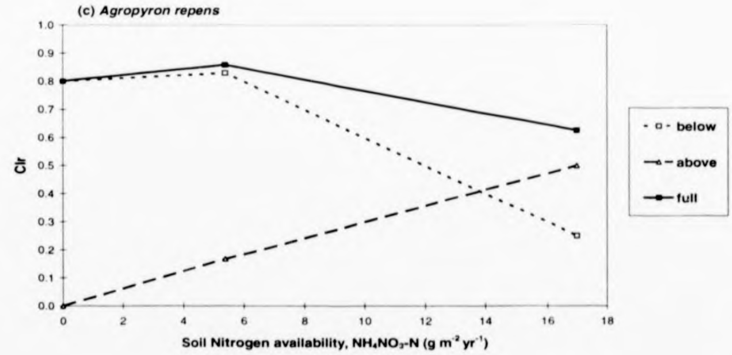


Fig. 4.10 Above- and below-ground competition intensity (CIr) experienced by the three grass species at three different nitrogen availabilities, in the study by Wilson & Tilman (1991). Values calculated from biomass estmiates from Wilson & Tilman 1991:Fig. 3.

issue of competition intensity (CIr) across a nutrient gradient with full (*i.e.* no partitioning of above and below-ground structures) competition (see section 5.3.2), only the work of Snaydon and Howe (1986) and most notably the experiments of Wilson and Tilman (1991, 1993, 1995) have investigated competition between roots and shoots with changes in nutrient availability, though Belcher *et al.* (1995) performed similar experiments on a soil depth gradient. Hence, it is not possible, because of the limited investigations and communities studied, to make categorical statements on the intensity of above- and below-ground competition across a nutrient gradient. However, all of these studies found that above- and below-ground competition differed in intensity and depended on nutrient availability, and that, generally, below-ground competition decreases and above-ground competition increases in intensity with increasing availability of nutrients. For example, Figure 4.10 shows the CIr (estimated from biomass measurements) for the three species in the study by Wilson and Tilman (1991:Fig. 3). Further research is required to examine the extent to which this phenomena occurs, but the model'sprediction conforms to the limited results available.

4.4 Discussion of the model validation

Haefner (1996) states that the criteria for determining a model's quality depends upon the objectives of the model. The term 'validity' is incomplete without reference to a purpose: one must state valid with respect to what purpose. It is, therefore, difficult to determine if a model is 'valid', given that this is a subjective notion depending on the purpose the user has in mind. For example, Haefner suggests that "generality, simplicity, increasing understanding, and qualitative correctness of model behaviour are concepts that are more relevant to purely theoretical studies" (Haefner 1996:152). These comments seem most relevant to the model presented within this thesis.

While the model is not particularly elegant or simple (though is competition between individuals simple? Presumably not from the vast amount of literature devoted to the subject), it does qualitatively display several features of competing annual and first-year perennial populations: self-thinning, competition density effects, size hierarchy development, increasing variation of surviving sizes with increases in density and nutrient availability, and the changes in relative competition shifting from below- to above-ground.

This suggests that the model is at least plausible in terms of modelling competition for nutrient and light. As discussed above in section 4.2, the model appears to understate the severity of light competition on population structure due to the manner in which individuals grow and occupy space and the subsequent characteristics of light interception by competing individuals. The model differs *quantitatively* from the published results of such features, perhaps as a direct consequence of this, though given the generality of the model's specification (*i.e.* the establishment of annual or first year perennial herbs in relation to the mechanism of light and nutrient competition between them, over a broad range of environmental productivity and densities) this result is not surprising.

It would be most useful to simulate a well researched particular community, if sufficient data (e.g. mechanistic resource acquisition, and allocation of those resources between tissues and within space) were available for parameter estimation. The absence of such data makes quantitative validation of the model difficult. Thus, it is more profitable to consider the model in terms of the qualitative similarity to known monoculture phenomena, described above, and the pattern of competition across a soil resource gradient. As the model does exhibit all of these phenomena, and as it has proved a genuinely useful tool for thinking about competition and placing the theories of Grime and Tilman within a common framework, it must, therefore, be considered valid with reference to the criteria stated above.

Chapter 5
Discussion

5.1 Discussion of the model

In light of the sensitivity of selected parameter values and validation of the model in Chapter 4, it is worth discussing the limitations imposed on model design by the programming of the model, and potential improvements which could be made to the model, to perhaps improve the realism of the model, though this may be at the expense of generality (Sharpe & Rykiel 1991).

5.1.1 Limitation on modelling competition processes by programming

Discrete occupancy of cells within the model was necessary as information on plant position was stored using array type variables (see Kemp 1987) in the implemented program (see Appendix Program): each cell was assigned an occupancy status of a single integer. The use of pointers (see Kemp 1987) instead would permit *n* number of plants to 'occupy' each cell. This would allow the overlapping occupancy of space, and corresponds to a greater degree of 'inter-mingling' of root and shoot systems, thereby removing competition for space, and is expected to affect resource competition between neighbouring individuals. Structuring the occupancy of space by individuals in this way would probably reduce the variation in yield generated by the present model and affect the self-thinning relationships. However, the disadvantages of using pointers are greater complexity of programming (making programming errors harder to trace), much longer running time of simulations, and increased memory usage.

5.1.2 Possible extensions to the model

Duration of the model is 60 days, and perhaps is not long enough to sufficiently allow competitive processes to reach 'equilibrium' (*sensu* Tilman 1988), though to satisfy equilibrium conditions the reproduction and regeneration of individuals are required to be incorporated into the model. The temporal scale of the model could be extended for long term (decades) simulation studies though huge computing power would be required (an example of the current model's computing time: 5 to 6 hours per simulation run at high priority on Hewlett Packard Model 712/60 machine). If regeneration were added to the model, then population and community dynamics, as well as long-term soil R dynamics could be simulated, and the influence of competition over extended periods of time (several generations) could be investigated. Also, 'tolerance' traits could be included within the model, though there exists a dearth of physiological data on such mechanisms; this would require the inclusion of 'loss' (*sensu* Tilman 1988) incorporating senescence: however, this presents problems relating senescence to the three-dimensional structure of the individual plants (*i.e. which* cells become unoccupied due to senescence?).

Water is treated within the model in a very rudimentary manner. No effect of gravity is imposed upon the distribution of water, and this would affect the distribution of nitrogen in the soil and the productivity of the vegetation for a given initial amount of nitrogen, depending on the level of leaching occurring (Cameron & Haynes 1986).

The aim of the model was to simulate the early growth of herbaceous individuals and their interaction with environmental resources above- and below-ground: while the model succeeds in doing this, some aspects of the model (notably the relationship between space and biomass) would benefit from the relaxation of some assumptions, which were mainly necessary to programming considerations. The model is certainly open to further development, and could be used to explore many aspects relevant to plant interactions and community structure (e.g. environmental heterogeneity, mycorrhizal networks). This model includes many features not considered in previous plant competition models, principally the explicit description of the spatial distribution of individuals and resources above- and below-ground and their interaction, as well as incorporating plant traits (such as plastic allocation, not considered in Tilman's ALLOCATE model).

5.2 Methodology of competition studies

As intimated by Keddy (1989), the development of an understanding of plant competition has been constrained to some extent by the design of experiments and the choice of subjects. For example, several studies designed to test competition theories have only measured above-ground biomass to determine competitive effects experienced by the subject species or individual (for examples see Campbell & Grime 1992, Reader *et al.* 1994, Turkington *et al.* 1993). This assumes a constant distribution of biomass, irrespective of the intensity and response to below-ground competition. These results derived from above-ground biomass may be spurious as the studies have ignored the possibility of plastic response of allocation to environment (and competition), although Wilson & Tilman (1991,1993,1995) have shown that qualitative results of competition studies were not affected by this. Experimental pair-wise competition studies are unlikely to enable the prediction of the outcome of multi-species interactions, unless a common reference measurement is made enabling the comparison of competitive ability, *e.g.* using a reference species like species *a* in chapter 3 to determine CA, or absolute measurements of the effect of a species on the environment such as R^* (Tilman 1982).

The consideration of competition processes across abiotic and biotic gradients has greatly enhanced the framework and context of competition studies, and such gradients are extremely valuable tools with which to investigate general patterns of vegetation (Keddy 1989, 1990). However, several recent studies (e.g. Reader et al. 1994, Belcher *et al.* 1995, Wilson & Tilman 1995) have used biotic productivity gradients in an attempt to ‘summarise’ the environmental conditions limiting plant growth, regardless of the physical elements (resources) pertaining to that level of productivity. Thus, very different environmental conditions (and processes) could produce identical productivity levels of the same vegetation: it would be impossible to determine this from productivity alone. If productivity is maximal at an intermediate level of a resource, for example low water availability limits growth yet high water availability (flooding) also limits growth, the use of a productivity gradient would confound any distinct competitive effects occurring at low productivity levels (see Austin & Smith 1989). Further problems arise when CIr is plotted against productivity: as CIr is derived from the amount of biomass present these two variables may be auto-correlated (J.B. Grace, *pers. comm.*; see Peters 1990). Hence, while productivity may be a useful concept where comparisons of competition are to be made between different habitats and ecosystems with different resource abundances, natural direct *abiotic* gradients (*i.e.* resource gradients *sensu* Austin 1990) should be measured wherever possible. In addition, where a study involves experimental manipulation of nutrient availability (*e.g.* Reader 1990, Wilson & Tilman 1993, 1995), the inclusion of more than two nutrient levels would facilitate a better understanding of the competitive processes occurring *along* a gradient.

Measurement of competition intensity has been addressed by Grace (1993, 1995*a*) and in the relativised form (CIr) has permitted the separation of the response of a species to competition from its response to environment, yet there is no clear picture of how CIr experienced by competing species depends on the species themselves and their traits, density, habitat (as opposed to productivity), resources, scale of measurement (individual/population, spatial and temporal); this also applies for competitive ability. The CIr results presented within chapter 3 suggest that competition intensity experienced is dependent upon the traits possessed by both the subject species and competitors, and this has been shown in field and experimental studies with competing species (see DiTommaso & Aarssen 1991, Campbell & Grime 1992, Turkington *et al.* 1993, Wilson & Tilman 1991,1995). Similarly, CA is dependent on traits, resource supply and scale (individual/population), and may very well depend on the choice of reference species (Belcher *et al.* 1995), though this was not tested.

5.3 Plant competition along a gradient of nutrient availability

5.3.1 Allocation of biomass

General allocation between root and shoot

The simulation results predict that allocation between organs of resource acquisition affect the ability of individuals to acquire those resources and this is reflected in the CIr experienced by competing individuals. For example, comparison of size-based CIr experienced by species *b6* (low root:shoot) at low soil R values is less intense in competition with species *a* (medium root:shoot) than with species *b2* (high root:shoot), whereas the opposite occurs at higher soil R values (see section 3.3.3.1 and

Fig. 3.7). Thus, the model predicts that a greater allocation to structures responsible for the acquisition of the most limiting resource (for that habitat) confers a competitive advantage by increasing the CA of that species, and increasing the intensity of competition experienced by competitors. This suggests that in natural vegetation where high levels of resource acquisition is more 'important' than tolerance to low resources (where soil resources are abundant and productivity is high), allocation to an organ responsible for resource acquisition should be positively correlated with competitive ability for that resource.

Gaudet and Keddy (1988) investigated the competitive ability (based on competitive performance in mixture with a reference species) of 44 herbaceous plants and concluded that total plant biomass was the best indicator of competitive ability, explaining 63% of the variation in competitive ability. This experiment was conducted at only one nutrient level representative of the highly productive environment where the species occur naturally, and where light is likely to be the most limiting resource. Therefore, it is hardly surprising that total biomass was the principal indicator of CA, given the size-asymmetric nature of competition for light (see Weiner 1990). It would be interesting to see whether this level of explanation would be achieved if the same experiment were conducted at a lower nutrient level (*i.e.* lower productivity), where nutrients would be more limiting than light. However, Goldberg (1987) found that the competitive effect a species exerted upon competitors was best explained by differences in size or abundance, at a lower productivity level than that studied by Gaudet and Keddy (1988). Aerts *et al.* (1991) investigated the cause of differential competitive ability below-ground among three perennial plants (where competition was shown to be predominantly below-ground) and found that below-ground competitive ability was associated with a root system efficient at acquiring below-ground resources (high allocation to roots and an extensive rooting volume system). Studies by Elberse and Berendse (1993) and Olff *et al.* (1991) showed that in some instances plants adapted to relatively nutrient-poor habitats allocate less dry matter to roots than plants adapted to nutrient-rich habitats. While this appears to refute the assertion made above, the study of Elberse and Berendse (1993) showed that the lower allocation to roots was compensated for by a higher specific root length and this was also suggested by Olff *et al.* (1991). Allocation pattern should therefore only be interpreted as one of several possible adaptive features that confer a high resource acquisition rate (see Berendse & Elberse 1990: Table 3).

If tolerance traits are assumed to be an important adaptive feature at low resource availability and if a trade-off is assumed between allocation of resource to organs of acquisition and allocation to physiological 'tolerance' mechanisms, there is unlikely to be a simple relationship between adaptive allocation pattern and resource availability. The inclusion of 'loss' of acquired resources (*sensu* Tilman 1988) into this hypothetical framework would also affect the predicted relationship between adapted allocation pattern and resource availability, especially if per-unit mass loss rates changed along a resource availability gradient. So instead of searching for allocation patterns correlated with productivity and light:nutrient gradients, and because the abundance of a species is the product of its ability to acquire and conserve resources, research should consider features that maximize the acquisition of resources for individuals where those resources are *most limiting* (see Chapin *et al.* 1987).

The significance of plasticity in biomass allocation

The results of the simulations indicate that plastic allocation of biomass between root and shoot confers a competitive advantage in terms of resource acquisition and maximum yield, though only where competition is predominantly for light at medium to high nutrient availability. The CIr experienced by individuals of species *c2* with very plastic response is almost constant along the nutrient gradients (see section 3.3.3.2 and Fig. 3.9n and 3.9p) which demonstrates that plasticity reduces the impact of competition. However, there is no cost associated with plasticity within the model, and this cost will limit the extensiveness of plasticity in natural systems (Tilman 1988), though it is unknown to what extent. Tilman & Cowan (1989) found that the response of root and shoot growth to environmental conditions was greater between species than within species: no one species had extreme plasticity in allocation between root and shoot. This suggests that plastic allocation is subject to selection in much the same way as constant allocation, as perceived by Tilman (1988), such that species differentiation along a nutrient:light gradient may still occur if all competing species exhibit limited plastic response. Limits to this response are necessary for differentiation otherwise a single species, with unlimited response, would be able to generate the optimum root:shoot ratio for all possible environmental conditions, *i.e.* a 'super-species', sensu Tilman (1988).

5.3.2 Intensity of competition along a nutrient gradient

CIr experienced by populations and individuals

The relationship between CIr and an environmental resource gradient is subject to the resource supply characteristics and the competing species response to and effect on that resource. CIr may well be affected by other mechanisms (*e.g.* resource loss, and damage or removal of resource acquiring tissue), and the introduction of 'tolerance' traits to the assumptions of this model may significantly affect the CIr experienced by vegetation at low resource levels.

The CIr experienced by both individuals and populations of the simulations (as determined by using either total yield or mean plant size) are not the same. This has crucial implications for competition studies and theories, as both must make a clear distinction between inter-individual competition and inter-specific competition, a point echoed by Goldberg (1994). Nearly all of the studies that have used CIr, or a related method to calculate the intensity of competition, have measured the performance of individuals (see Table 5.1). As yet, no studies of natural plant populations have compared competition intensity experienced by individuals and populations or species across environmental gradients.

As related in Chapter 1, there has been much debate regarding the relationship of intensity of competition across a gradient of productivity; this has arisen again recently with the results of Bonser and Reader (1995) which suggests that CIr increases most when productivity increases from low to medium levels, but remains relatively constant as productivity increases from medium to high levels, comparable to the 'full

Table 5.1. Studies which have measured the intensity of competition using CIr or related method. *I* indicates CIr is based on individual performance, *P* indicates CIr is based on performance of the population. Values in brackets refer to number of nutrient levels.

Study	**Performance indicator**	**Gradient**
Reader 1990	*P?* rosette number per-unit area	nutrient level (2)
DiTommaso & Aarssen 1991	*I* mean plant size	nutrient level (3)
Wilson & Tilman 1991	*I* above-ground growth rate of transplants	nutrient level (3)
Campbell & Grime 1992	*P* above-ground biomass	nutrient level (5)
Turkington *et al.* 1993	*P* percent cover (above-ground biomass)	nutrient level (5)
Wilson & Tilman 1993	*I* above-ground growth rate of transplants	nutrient level (2), soil N, light penetration
Reader *et al* 1994	*I* above-ground growth rate of transplants	productivity
Belcher *et al* 1995	*I* above-ground biomass of transplants	soil depth, productivity
Bonser & Reader 1995	*I* above-ground biomass of transplants	productivity
Wilson & Tilman 1995	*I* total growth rate of transplants	nutrient level (2), neighbour productivity

competition' CIr results of species *a* in monoculture (Fig. 3.4n(e) and 3.4p(e); section 3.3.2). This seems to add credence to both schools of thought regarding competition intensity across productivity levels: CI may both increase (Grime 1979, Keddy 1990) and remain constant (Newman 1973, Tilman 1988) with increasing productivity, depending on the range of productivity measured; Belcher *et al.* (1995) have also suggested just such a relationship. However, the range of productivity used by Bonser and Reader (1995) is within the range that other studies have reported (see Belcher *et al.* 1995), and further tests are required to ensure that this is not a spurious result stemming from auto-correlation problems associated with plotting CIr against total productivity (see above).

Competition above- and below-ground

The results from the split competition treatments (section 3.4) all show that at low nutrient levels, competition between individuals is more intense for nutrients than for light; this has been tested in only a few selected natural habitats (with relatively low productivity), and it was found that competition below-ground is more intense than competition above-ground (Belcher *et al.* 1995, Wilson & Tilman 1991, 1993, 1995). As a generalised model, as nutrient ability increases, competition intensity for the nutrient increases to a peak and then diminishes while the intensity of light competition increases asymptotically. This is very similar to the model proposed by Belcher *et al.* (1995:Figure 7). Snaydon and Howe (1986) found that below-ground competition between populations of established ryegrass and invading grass seedlings decreased in intensity with increased supply of the limiting nutrient, but did not detect any appreciable increase in above-ground competition with the increase in nutrient supply, though this was only performed at very low ryegrass densities, where shoot competition may be expected to be low.

The switch in competition from below- to above-ground with increasing nutrient availability is determined by the relative above- and below-ground competitive effect exerted by each species on other species present. For example, the CIr and the 'switch' experienced by the individuals of two species with different allocation above- and below-ground (species *a* × *b6*: section 3.4.3.2) is very much species dependent: the species with greater allocation above-ground has a greater CA above-ground and the 'switch' is experienced at a higher nutrient level relative to that experienced by the other species. Unbiased plasticity (*e.g.* species *c2*) had no effect on the position of the switch along the nutrient gradients, although the CIr experienced above- and below-ground by the species with plastic response was greatly reduced by plasticity (see section 3.4.3.3).

This switch in competition generally occurs at relatively low nutrient levels according to the simulation results. Higher nutrient levels almost exclusively led to complete dominance by one species (though most of the simulations involved only two species). This is found in many natural systems where the addition of fertilizer has decreased species diversity (DiTommaso & Aarssen 1989), and is represented in Grime's (1979) 'hump-back' model of species diversity; the size-asymmetric nature of light competition (Weiner 1990) is cited as an explanation (Huston & DeAngelis 1994, Belcher *et al.* 1995). A greater number of species survived at low nutrient levels (for example, see Fig. 3.5(e) and 3.5(f)), though species diversity might conceivably have reached a maximum at intermediate nutrient levels if death of modelled plants occurred from insufficient nutrient acquisition, in addition to insufficient light interception (see Huston & DeAngelis 1994).

Given that the presence of vegetation and consequent resource acquisition alters the annual availability of nutrients (either increase or decrease), then competition will shift between above- and below-ground depending on the current nutrient:light ratio. As has been shown by the simulations, above- and below-ground competition (at least for annuals and first-year perennial) will select for different traits and species; thus, vegetation change may be a consequence of a shift in competition between above- and below-ground, though this may be caused by many factors other than resource competition (*e.g.* herbivory). This is also the prediction of the Resource Ratio hypothesis of succession, in that the vegetation present and the resources available are interdependent and succession is driven by their interaction (Tilman 1985).

Competition in relation to the supply properties of resource

The results of the simulations contrasting nutrient supply properties (see chapter 3) suggest that the mobility of the nutrient does have an effect on competition: in the 'full' competition simulations where competition was predominantly below-ground, CIr experienced was always greater in the N (relatively mobile) simulations than in the P (relatively immobile) simulations, though in the 'below-ground only' competition simulations the reverse was true as a result of supply properties and the spatial positioning and packing of root systems (see section 3.4.8). This emphasizes the point made above that CIr experienced is dependent on circumstance (*i.e.* species present and the density and spatial arrangement of individuals) as well as the properties of the resource(s). The three-dimensional aspect of nutrient movement and competition is responsible for the decrease of CIr with increasing nutrient availability, where availability is greater than that which confers maximal CIr for nutrients, even though increases in nutrient availability confer larger, more expansive root systems. The unidirectional nature of light results in CIr for light increasing with the size of competing individuals. These properties and their consequences are also reported from a model by Huston and DeAngelis (1994), which also treats nutrient distribution and below-ground competition in an explicit manner at the scale of the individual (Huston & DeAngelis 1994, Grace 1995*b*), though their model does not treat spatial light distribution explicitly (Grace 1995*b*). Thus, both the availability and supply properties of a resource determine the competition intensity for that resource experienced by competing populations and individuals, though other factors (*e.g.* species traits, density of individuals) may also influence the intensity of competition (see above). This serves as a caution against assuming all resources may be treated identically in plant competition models (*e.g.* the Resource-Ratio and R^* models).

However, the current model ignores the possible transfer of resources (carbon, nitrogen and phosphorus) between individual plants via networks of mycorrhizal mycelium (Newman 1988), and the increased acquisition of nutrients associated with mycorrhizal infection of the roots (Allen & Allen 1990). Grime *et al.* (1987) have demonstrated the significance of mycorrhizal infection for the suppression of the dominant species in an artificial plant community, probably the result of carbon transfer from the dominant species to the subordinate species. The transfer of resources between competing individuals has important implications for competition: any transfer of resource from a high concentration to a lower concentration would be expected to decrease the CIr experienced by the subordinate species for that resource. However, the rate of transfer through the mycelium network may not be fast enough to have a significant effect on competition; this has been shown to be true for the transfer of phosphorus between competing tillers of *Lolium perenne* (Newman & Eason 1993). Mycorrhizal transfer of acquired resource down concentration gradients could be incorporated within the model, assuming that a uniform mycelium network exists within the soil. The values of *Cpool* and *Rpool* would therefore depend on acquisition, storage and assimilation (as before), and the flux (via mycorrhizal network) to or from neighbouring plants, according to the relative sizes of the plant resource pools and the distance between individuals or their root systems. Evidence for such relocation of resources is limited at present, and it is unclear how widespread this may be in naturally occurring communities.

Further implications for theories and ecology

The results of the simulations show that while most of the model species can survive in monoculture at all nutrient levels, species are displaced along the nutrient gradient according to competitive ability: this supports the 'competitive hierarchy model' of Keddy (1989).

The results imply that a central assertion of Grime's CSR model, that competition is primarily for light and occurs predominantly in productive habitats, is not true: while maximal competition intensity for light generally coincided with maximum production, competition between individuals below-ground could be just as intense at much lower productivity (section 3.4). The assumption of the CSR model concerning coupled and uncoupled growth is supported to some extent by the simulations of species *e* (coupled) and *f* (uncoupled), in that *f* achieved a greater yield than *e* at low nutrient availability (high 'stress', sensu Grime 1979); see sections 3.3.4 and 3.4.3.4. Also, the variation in CA of species along the nutrient gradient does not support the assumption of CSR model that competitive ability of a species is a fixed characteristic irrespective of environment. While the CSR model has stimulated much discussion and research, several of the assumptions upon which it is based have been shown to be incorrect, and there are self-contradictions within the conceptual framework (see Chapter 1). The non-mechanistic structure of the CSR model has rendered it non-operational and while it succeeds in describing herbaceous types in terms of certain physiological attributes, it omits several important proven aspects of competition: notably asymmetry of competition (*sensu* Weiner 1990) and an appreciation of above- and below-ground competition.

While supporting Tilman's Resource Ratio theory (the model shares some fundamental assumptions with the Resource Ratio theory) in terms of allocation of biomass to plant compartments, the model and simulation results cannot test the long-term predictions of the Resource Ratio and R^* theories, as their biomass and population equilibrium requirements cannot be met due to the short time period of the model. However, the assertion of Wilson & Tilman (1991, 1993, 1995) concerning the nature of above- and below-ground competition is supported by this work (see above). In contrast to the CSR model, the Resource Ratio and R^* theories have been made unambiguous by Tilman, and the mechanistic approach has yielded testable (*i.e.* operational) predictions.

5.4 Future research directions

The obvious extensions possible to the model have been detailed in section 5.1. However, models are only as good as the data available, and further work is needed to determine the role of plant competition in community ecology. Methodological tools, like CIr and 'productivity' gradients, need to be assessed, while the problem of spatial, temporal and ecological (individual/population/community) scale requires consideration and investigation.

The split competition treatments employed by Wilson and Tilman (1991, 1993, 1995) and Belcher *et al.* (1995) are an important contribution to understanding competition above- and below-ground processes: more competition studies should employ this approach as above- and below-ground competition processes appear to be very different and interdependent. The hypothesis of Huston and DeAngelis (1994) concerning 'coexistence' along a nutrient gradient also requires testing in a natural system: neighbour removal and monitoring of individuals and populations may shed light on the displacement of species along a natural environmental (non-biotic) resource gradient. Further work is required to test if competition (as measured by CIr) is indeed different for individuals and populations.

What is really needed is a test of various community organization theories, to determine the role (if any) of competition (both above- and below-ground), herbivory and mycorrhizae in the development and structuring of communities. Such a study would, ideally, include several different habitats and different species. While the separation of above- and below-ground competition has been achieved successfully for individuals (*e.g.* Wilson & Tilman 1991), there is no satisfactory method to remove above- or below-ground for plant populations in the field or under controlled conditions.

Goldberg's null community model (Goldberg 1994) is an appropriate method to determine the role of competition in structuring communities: rather than assuming that only one species will exist, the null hypothesis is that *all* species will co-exist. Artificial, experimental habitats are useful, but proper tests of competition theories must be performed on naturally occurring communities in natural habitats. Likewise, knowledge of pair-wise interactions along environmental gradients will not enable construction of community models, where the effect of each species on all other species tends to be assumed or ignored. There is nothing in the results from pair-wise competition of species *b1* to *b7* with a (section 3.3.3.1) that suggests the outcome of the multi-species simulation (m1; section 3.3.3.1, Fig. 3.22).

5.5 Conclusions

Ambiguity in the definition of terms and conditions within the plant competition theories of Grime (CSR model) and Tilman (Resource Ratio and R* hypotheses) has generated much debate and apparent contradiction: these are resolvable when a common context and rigorous definition are introduced. Plant resource competition is a passive process: plants respond to changes in environmental resources mediated by competitors, not the presence of competitors *per se*. Competition may either be determined by acquisition of resources and/or tolerance of low resource levels, and it is important that this distinction be recognised in competition studies, as both will affect the measurable intensity of competition.

The model presented here attempts to relate competition between individual plants to the environment, in terms of resource availability, distribution in space, and the acquisition and allocation of these resource by the individuals. The generality of the model prevents it from being quantitatively validated against published studies of plant competition, but the model does qualitatively display several important phenomena reported from plant competition studies. The model has been used to explore some of the predictions made by the theories of Grime and Tilman, and this process has generated further hypotheses.

Competition appears to act differently on populations and individuals: this also is an important consideration for studies. The intensity of resource competition (CIr) between individual annuals or first-year perennials depends on the supply properties of the resource (*e.g.* size-symmetry and mobility), the abundance of the resource, the relationship of that resource to other potentially limiting resources, the allocation and growth patterns of the plants, and the density of individuals. The competitive ability (CA as defined in section 1.5.4) of an individual is dependent on the environment (absolute and relative resource abundance), and the traits possessed. Even so, this does not necessarily imply that a universal pattern of CIr across resource gradients does not exist, but variation between species and ecosystems may be significant.

Allocation of biomass to resource acquiring organs is predicted by the model to increase CA and resource acquisition: the potential for positive feedback between acquisition and allocation is the cause of competitive exclusion, but is predicted to be greater for light than for nutrients because of the difference in size-symmetry. Plastic allocation facilitates greater competitive ability (resource acquisition) at nutrient (and productivity) levels where competition is predominantly for light. Tolerance traits and per-unit mass effects on acquisition are predicted to affect this relationship. Growth uncoupled from resource acquisition is predicted to be advantageous in nutrient poor habitats, while growth coupled to resource acquisition is predicted to be advantageous in nutrient rich habitats.

Below-ground competition intensity for a soil resource, in the absence of light competition, is predicted to be higher for a highly mobile resource than for a relatively immobile resource, and competition intensity in the presence of light competition is also predicted to be greater for the more mobile resource (this assumes that mycorrhiza are not present). Competition for light is predicted to be most intense in habitats with high nutrient levels, while competition for nutrients is expected to be most intense at low to medium levels of nutrient availability; thus, plant adapted to a low nutrient (low productivity) environment should possess a high CA below-ground, while plants adapted to a high nutrient (high productivity) environment should possess a high CA above-ground.

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Parameter Values

Range of *InitialSoilR* values

The range of *InitialSoilR* for nitrogen is 0.01 to 1.01 mg N per *SOILcell* (equivalent to 0.00577 to 0.57714 mM NO_3^-), while for phosphorus the range 0.00067 to 0.06733 mg P per *SOILcell* (0.00017 to 0.01738 mM $H_2PO_4^-$), *i.e.* 1/15 of the nitrogen values. Fitter and Hay (1987) report soil solution P concentrations of maximum 0.09 mM H_2PO_4, minimum 0.00 mM H_2PO_4, and mean of 0.02 mM H_2PO_4: the chosen values are within this range.

Proportion of nutrient movement by diffusion (*a*) and mass flow (*b*); equation 2.6

The contribution of mass flow to nutrient movement for nitrogen is reported to be 100% (sugarbeat and spring barley, Marschner 1986), 40% (spring wheat, Marschner 1986) and 79% (corn, Barber 1984). For phosphorus, Barber (1984) reports that 5% moves through mass flow, while Marschner (1986) estimates that 2 to 3% moves by mass flow. The following values are assigned to a and b: for nitrogen, a=0.21, b=0.79; for phosphorus, a=0.98, b=0.02 .

Diffusion coefficient, *d*; equation 2.2

Diffusion coefficient, d, values of 10 and 1000 for nitrogen and phosphorus respectively were chosen to represent the difference in mobility of the two nutrients (i.e. 100 fold difference in diffusion rate).

CELLmass

CELLmass may be estimated from

$$CELLmass = \frac{ShootBiomass}{80 \times ShootHeight}$$

where *ShootBiomass* is the density of shoot material (g m^{-2}) and *ShootHeight* is the height of the shoot material (cm). However, this assumes that the whole of volume of space (*ShootHeight* × 1 m^2) is uniformly occupied by shoot material, unrealistic in mixture plots.

A better estimation of *CELLmass* may be attained when this value is multiplied by the actual proportion of shoot material present within the area of space:

$$CELLmass = \frac{ShootBiomass^2}{80 \times ShootHeight \times TotalBiomass}$$

where *TotalBiomass* is the total amount of shoot biomass present of all species (g m^{-2}). This assumes that biomass present is distributed uniformily throughout the space occupied by each species. CELLmass can be determined in this fashion for each of the grass species described by Tilman and Wedin (1991), and an overall mean calculated across all nitrogen levels and species: 20.1 mg biomass per cell (i.e. mg biomass 0.00025 m^{-3}). Thus a value of 20 mg biomass per cell is assigned to both above and below ground tissues: therefore a square metre of shoot material with height 50 cm and uniform biomass distribution would have a density of 80 g m^{-2}.

Imax and *Km*; equation 2.8

Imax and *Km* values for nitrogen are derived from the nitrate absorption curves for 20 day old annual grass species in Huffaker & Rains (1978), given in the tables below.

Species	Estimated nitrate V_{max} (μmoles NO_3 g^{-1} hr^{-1})	Nitrogen *Imax* value (mg N mg^{-1} d^{-1})
Bromus mollis (L.)	2.5	0.00084
Avena fatua (L.)	2	0.000672
Lolium multiflorum (Lam.)	9	0.003024

Species	Nitrate Km (mM)	Nitrogen *Km* value (mg N per cell)
Bromus mollis (L.)	0.015	0.02625
Avena fatua (L.)	0.02	0.035
Lolium multiflorum (Lam.)	0.03	0.0525

Calculation of nitrogen *Imax* is given by

$$(Nitrogen)\ Imax \ = V_{\max} \times 10^{-6} \times 14 \times 24$$

where V_{max} is the estimated value from the absorption curves within Huffaker and Rains (1978). It is assumed that nutrient uptake occurs 24 hours each day. Calculation of nitrogen *Km* is given by

$$(Nitrogen)\ Km \ = S \times 1000 \times 10^{-6} \times 14 \times 0.000125$$

where *S* is the Km (mM) value given by Huffaker and Rains (1978), and the size of a single SOILcell is 0.000125 m^{3}. Values of 0.001 and 0.04 were chosen for the standard nitrogen values of *Imax* and *Km* respectively. Phosphorus values of *Imax* and *Km* are set at 1/15 the nitrogen values to avoid confounding the effect of supply properties on competition.

Ka and *Kb*, equation 2.15; *LAD*, equation 2.12

Larcher (1980) reports ranges of maximum CO_2 uptake rates per unit mass of dry leaf for heliophytes (0.03 - 0.06 g CO_2 g^{-1} dry weight hr^{-1} or 0.1312 - 0.2618 g C g^{-1} d^{-1}), sciophytes (0.01 - 0.03 g CO_2 g^{-1} dry weight hr^{-1} or 0.0436 - 0.1312 g C g^{-1} d^{-1}) and wild grasses and sedges (0.008 - 0.035 g CO_2 g^{-1} dry weight hr^{-1} or 0.0349 - 0.1527 g C g^{-1} d^{-1}); the value of *Kb* was chosen as 0.1312. *Ka* was assigned a value of 0.5, in the absence of experimental evidence. LAD is a measure of the fraction of light an occupied *SHOOTcell* will absorb. This is effectively the same as the light extinction coefficient, *k*, in the Bouguer-Lambert law of light penetration through a canopy; Tremmel and Bazzaz (1993) report some values of *k* for the forbs *Abutilon theophrasti*, *Datura stramonium* and *Polygonum pensylvanicum* (mean values throughout canopy of 0.4, 0.41 and 0.55 respectively) and the grass *Setaria faberii* (mean value throughout canopy of 0.31).

respirationRATE and *maintenanceRATE*, equations 2.30 and 2.18

Studies on white clover gave values of 0.25 and 0.015 g C g^{-1} d^{-1} for *respirationRATE* and *maintenanceRATE* respectively (McCree 1970). Other studies have calculated growth and maintenance component rates of respiration: soyabean has calculated values between 0.04 - 0.065 g C g^{-1} d^{-1} for *respirationRATE* and 0.01 - 0.035 g C g^{-1} d^{-1} for *maintenanceRATE* (Bunce & Ziska 1996); a study by Bunce (1987) on the maintenance respiration of various herbaceous species (*Amaranthus hybridus, Chenopodium album, Glycine max*) gives mean values of 0.0173 at high light intensity (1000 μmol m^{-2} s^{-1} photon flux density) and 0.025 at lower light intensity (500 μmol m^{-2} s^{-1} photon flux density), though all are fast growing species. While the *maintenanceRATE* value of 0.015 may be low compared with these species, it is not unreasonable.

transpirationRATE; equation 2.9

The value of 10 mg water mg^{-1} biomass d^{-1} is an estimate assigned to *transpirationRATE*, though the actual value is irrelevant to the results generated by the model, as *transpirationRATE* is the same for all shoot biomass regardless of light intensity and species, and only relative gradients of water distribution (and not the absolute values) throughout the soil are required for the calculation nutrient movement by mass flow (section 2.2.4).

Rcontent and *Ccontent*; equations 2.34 and 2.46

Reynolds and Thornley (1982) suggest values of 0.03 and 0.45 for *Rcontent* (nitrogen) and *Ccontent* respectively, following experiments on tomato plants; *Rcontent* for phosphorus was derived as 1/15 the value for nitrogen, *i.e.* 0.002. These values seem reasonable given the average concentrations of N and P within 3 neutral grassland herbaceous species (*Centaurea jacea, Vicia sepium, Urtica dioica*) are 0.023 and 0.002 mg nutrient mg^{-1} dry leaf tissue (Fitter & Hay 1987). Thornley & Johnson (1990) report a value of 0.002 g P g-1 dry biomass for *Zea mays* (maize).

```
program NITROGEN(   input,  PLANTdata,ROOTrnd,SHOOTrnd,PROBrnd,
                   output,  PLANTres,GRADres,SPECIESres,DETAILS,
                            Rres,ROOTres,SoilRres,relSoilRres,Lightres,SHOOTres,
                            timeA,timeB,timeC );

const

 {*** GENERAL constants ***}
 REPLICATIONS = 20 ; {number of replications}
 TIMEEND = 60 ; {days}
 PLANTnumber = 50 ; {number of individual plants}
 SPECIESnumber = 2 ; {number of different species}
 SHOOTCELLmass = 20.0 ; {mg biomass cell-1}
 ROOTCELLmass = 20.0 ; {mg biomass cell-1}
 {horizontal area modelled...}
 MAXx = 10 ;
 MAXy = 10 ;

 {*** PLANT constants ***}
 { photosynthesis }
 Ka = 0.5 ;
 Kb = 0.0082 ;
 { respiration }
 GROWTHrespirationRATE = 0.25 ; { mg Carbon mg-1 CarbonProduced day-1 }
 SHOOTmaintenanceRATE = 0.015 ; { mg Carbon mg-1 DRYweight day-1 }
 ROOTmaintenanceRATE = SHOOTmaintenanceRATE ;
 { assimilation ratio between C and R }
 CRratio = 15 ; {g C g-1 R}
 Ccontent = 0.45 ; {fraction of biomass that is C}
 Rcontent = Ccontent / CRratio ;
 {loss}
 RlossRATE = 0 ; {g R g biomass per day}
 { initial plant values }
 InitialRpool = 0.0 ; {mg Resource}
 InitialCpool = 0.0 ; {mg Carbon }
 InitialAssimilates = 0.0 ; { mg Organic Material }

 {*** SOIL constants ***}
 { depth }
 MAXdepth = 20 ;
 { water }
 TotalInitialWater = 1000000 ; {mg water per m-3}
 InitialWater = TotalInitialWater / 8000 ; {mg water cell-1}
 { return of OrganicP to SoilR }
 InitialDecomp = 0.0 ; {mg unavailable SoilR cell-1}
 decayRATE = 0.0 ; { fraction of OrganicP released day-1 }
 { SoilR movement }
 a = 0.2 ; { Diffusion }
 b = 0.8 ; { Mass Flow. NB a + b = 1.0 }
 d = 10 ; { N diffusion coeff. }
```

```
 n = 6 ; { Neighbour number; int. }
 WD = 1 ; { Water diffusion coeff. }
 Nt = 1 ; { Iteration number Water:N }

 {*** ABOVE-GROUND constants ***}
 { height }
 MAXheight = 20 ;
 { light intensity }
 SunLIGHT = 1.0 ; {unitless}
 DAYlength = 16 ; {hours of light}
 { transpiration }
 TranspirationRATE = 10.0 ; { mg Water mg-1 shoot biomass day-1 }

 {*** graphical output constants (see PICTURE proc's) ***}
 STRIPlength = 5 ;
 SPACEsize = 2 ;

{*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&}

type
 SoilcellREAL = array[ 0..(MAXdepth+1), 0..(MAXx+1), 0..(MAXy+1) ] of real ;
 SOILcellINT = array[ 0..(MAXdepth+1), 0..(MAXx+1), 0..(MAXy+1) ] of integer ;
 ABOVEGROUNDcellINT = array[ 0..(MAXheight+1), 0..(MAXx+1), 0..(MAXy+1) ] of integer ;
 ABOVEGROUNDcellREAL= array[ 0..(MAXheight+1), 0..(MAXx+1), 0..(MAXy+1) ] of real ;
 eachPLANTreal = array[ 1..PLANTnumber ] of real ;
 eachPLANTint = array[ 1..PLANTnumber ] of integer ;

{*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&}

var
 PLANTdata, ROOTrnd, SHOOTrnd, PROBrnd, PLANTres, GRADres, SPECIESres, DETAILS, Rres,
        ROOTres, SoilRres, relSoilRres, Lightres, SHOOTres, timeA, timeB, timeC : text ;
 SoilR, SoilWater, SoilOrgMat : SoilcellREAL ;
 Light : ABOVEGROUNDcellREAL ;
 ROOTcell : SOILcellINT ;
 SHOOTcell : ABOVEGROUNDcellINT ;
 deadPLANT, PlantX, PlantY, ROOTtimeout, SHOOTtimeout,CaptGroCOUPLED, Height, Depth,
        ROOTcellnumber,SHOOTcellnumber, Species : eachPLANTint ;
 gcP, gcC, PsubRATE, CsubRATE, PartP, PartC, ROOTincrease, SHOOTincrease, ROOTbiomass,
        SHOOTbiomass, Ruptake, Cproduction, Rpool, Cpool, Assimilates, ROOTdensity, RootImax,
        RootKm, LAD, WaterUptake, TotalR, TotalC, propROOT, propSHOOT, propBIOMASS,
        PREVIOUSbiomass : eachPLANTreal ;
 InitialResource : real ;
 repl, P, TIME, STOP, LAYER, x, y, plant, alive, PlantTooDeep, PlantTooHigh : integer ;
```

```
{*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&}
                {PROCEDURES}
{*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&}
             {***** General TOOL procedures *****}
{*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&}

procedure calcROOTcellnumber( plant : integer ; var number : integer ) ;

var
 CELLtype, LAYER, x, y : integer ;

begin {calcROOTcellnumber}

 {*** set number to zero ***}
 number := 0 ;
 {*** search through ROOTcell and count the number of cells occupied by 'plant' using 'number' ***}
 for LAYER := 1 to Depth[plant] do
  begin {LAYER}
  for x := 1 to MAXx do
   begin {x}
   for y := 1 to MAXy do
    begin {y}
    CELLtype := ROOTcell[LAYER,x,y] ;
    if CELLtype = plant then
     begin
     number := number + 1
     end
   end {y}
  end {x}
 end {LAYER}

end ; {calcROOTcellnumber}

{&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*}
```

```
procedure calcSHOOTcellnumber( plant : integer ; var number : integer ) ;

var
 CELLtype, LAYER, x, y : integer ;

begin {calcSHOOTcellnumber}

 {*** set number to zero ***}
 number := 0 ;
 {*** search through SHOOTcell and count the number of cells occupied by 'plant' using 'number' ***}
 for LAYER := 1 to Height[plant] do
 begin {LAYER}
  for x := 1 to MAXx do
  begin {x}
   for y := 1 to MAXy do
   begin {y}
    CELLtype := SHOOTcell[LAYER,x,y] ;
    if CELLtype = plant then
    begin
     number := number + 1
    end
   end {y}
  end {x}
 end {LAYER}

end ; {calcSHOOTcellnumber}

{&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*}
```

```
procedure PlantDeath(  plant : integer ;
                       var ROOTbiomass, SHOOTbiomass : eachPLANTreal ;
                       var ROOTcell : SOILcellINT ;  var SHOOTcell : ABOVEGROUNDcellINT ;
                       var SoilOrgMat : SoilcellREAL ) ;

 {***    PlantDeath procedure performs the following:
         (1) Empties all SHOOTcells previously occupied by plant and
                 directs this organic matter to the surface layer of
                 SoilOrgMat - ie. leaf + stem collapse and decay on floor.
         (2) Empties all ROOTcells previously occupied by plant and
                 directs the organic matter to the corresponding SoilOrgMat
                 cell - ie. roots decay in situ. ***}

var
 OrganicMatter : real ;
 LAYER, x, y : integer ;

begin {PlantDeath}
 writeln('Plant Death -- plant no.=',plant:3,' TIME=',TIME:4) ;
 {*** Remove all SHOOT material belonging to plant ***}
 for LAYER := 1 to MAXheight do
 begin {LAYER}
  for x := 1 to MAXx do
  begin {x}
   for y := 1 to MAXy do
   begin {y}
    if SHOOTcell[LAYER,x,y]=plant then
    begin
     {*** clear cell of plant ***}
     SHOOTcell[LAYER,x,y] := 0 ;
     {*** determine OrganicMatter ***}
     if SHOOTbiomass[plant]<SHOOTCELLmass then
       OrganicMatter := SHOOTbiomass[plant]
      else
       OrganicMatter := SHOOTCELLmass ;
     {*** add matter to SoilOrgMat at soil surface ***}
     SoilOrgMat[1,x,y] := SoilOrgMat[1,x,y] + OrganicMatter
    end
   end {y}
  end {x}
 end ; {LAYER}
```

```
 {*** remove all ROOT material belonging to plant ***}
 for LAYER := 1 to MAXdepth do
 begin {LAYER}
  for x := 1 to MAXx do
  begin {x}
   for y := 1 to MAXy do
   begin {y}
    if ROOTcell[LAYER,x,y]=plant then
    begin
     {*** clear cell of plant ***}
     ROOTcell[LAYER,x,y] := 0 ;
     {*** determine OrganicMatter ***}
     if ROOTbiomass[plant]<ROOTCELLmass then
       OrganicMatter := ROOTbiomass[plant]
      else
       OrganicMatter := ROOTCELLmass ;
     {*** add matter to SoilOrgMat at that position ***}
     SoilOrgMat[LAYER,x,y] := SoilOrgMat[LAYER,x,y] + OrganicMatter
    end
   end {y}
  end {x}
 end ; {LAYER}

 {*** Reset Biomass and resource pools ***}
 ROOTbiomass[plant] := 0 ;
 SHOOTbiomass[plant] := 0 ;
 Rpool[plant] := 0 ;
 Cpool[plant] := 0

end ; {PlantDeath}
```

```
{*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&}

                    {***** More Specific DEDICATED procedures *****}

{*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&}

procedure PLANTsetup(          var deadPLANT, PlantX, PlantY, ROOTtimeout, SHOOTtimeout,
                                CaptGroCOUPLED, Species : eachPLANTint ;
                               var ROOTdensity, RootImax, RootKm, LAD, Assimilates,
                                PREVIOUSbiomass : eachPLANTreal ;
                               var ROOTcell : SOILcellINT ;
                               var SHOOTcell : ABOVEGROUNDcellINT ) ;
var
 tempP, tempC : real ;
 plant : integer ;

begin {PLANTsetup}

 reset( PLANTdata ) ;
 for plant := 1 to PLANTnumber do
 begin {plant}
  {*** Read in plant details from PLANTdata file ***}
  readln( PLANTdata, Species[plant], ROOTbiomass[plant], SHOOTbiomass[plant],deadPLANT[plant],
          PlantX[plant], PlantY[plant], ROOTtimeout[plant], ROOTdensity[plant],
          RootImax[plant], RootKm[plant], SHOOTtimeout[plant], LAD[plant], tempP,
          tempC, CaptGroCOUPLED[plant], PartP[plant], PartC[plant] ) ;
  {*** Occupy intial ROOT/SHOOTcells ***}
  ROOTcell[ 1, PlantX[plant], PlantY[plant] ] := plant ;
  SHOOTcell[ 1, PlantX[plant], PlantY[plant] ] := plant ;
  {*** Initialize some PLANT variables ***}
  {these two are excluded to allow biomass < CELLmass...}
  {ROOTbiomass[plant]:=ROOTCELLmass; SHOOTbiomass[plant]:=SHOOTCELLmass ;}
  Rpool[plant] := InitialRpool ;
  Cpool[plant] := InitialCpool ;
  Assimilates[plant] := InitialAssimilates ;
  ROOTincrease[plant] := 0 ;
  SHOOTincrease[plant] := 0 ;
  TotalR[plant] := 0 ;
  TotalC[plant] := 0 ;
  PREVIOUSbiomass[plant] := ROOTbiomass[plant] + SHOOTbiomass[plant] ;
  if CaptGroCOUPLED[plant]=0 then
    begin {uncoupled growth}
     PsubRATE[plant] := tempP ;
     CsubRATE[plant] := tempC
    end
   else
    begin {coupled growth}
     gcP[plant] := tempP ;
     gcC[plant] := tempC
   end ;
```

```
  {*** Check if plant alive ***}
  if deadPLANT[plant]=1 then
    begin
     {*** Plant Death! ***}
     PlantDeath( plant, ROOTbiomass, SHOOTbiomass, ROOTcell, SHOOTcell, SoilOrgMat )
    end
 end {plant}

end ; {PLANTsetup}

{*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&}

procedure SOILsetup( var SoilR, SoilWater, SoilOrgMat : SoilcellREAL ) ;

var
 LAYER, x, y : integer ;

begin {SOILsetup}

 for LAYER := 1 to MAXdepth do
 begin {LAYER}
  for x := 1 to MAXx do
  begin {x}
   for y := 1 to MAXy do
   begin {y}
    SoilR[LAYER,x,y] := InitialResource ;
    SoilWater[LAYER,x,y] := InitialWater ;
    SoilOrgMat[LAYER,x,y] := InitialDecomp
   end {y}
  end {x}
 end {LAYER}

end ; {SOILsetup}

{*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&}
```

```
procedure ROOTcellsetup( var ROOTcell : SOILcellINT ; var Depth : eachPLANTint ) ;

var
 LAYER, x, y, plant : integer ;

begin {ROOTcellsetup}

 {*** set ALL cells (including boundary cells) to -1 ***}
 for LAYER := 0 to (MAXdepth+1) do
 begin {LAYER}
  for x := 0 to (MAXx+1) do
  begin {x}
   for y := 0 to (MAXy+1) do
   begin {y}
    ROOTcell[LAYER,x,y] := -1
   end {y}
  end {x}
 end ; {LAYER}
 {*** set all central cells to 0 ***}
 for LAYER := 1 to MAXdepth do
 begin {LAYER}
  for x := 1 to MAXx do
  begin {x}
   for y := 1 to MAXy do
   begin {y}
    ROOTcell[LAYER,x,y] := 0
   end {y}
  end {x}
 end ; {LAYER}
 {*** set Depth[plant] to 1 ***}
 for plant := 1 to PLANTnumber do Depth[plant] := 1 ;
 {*** set PlantTooDeep to 0 (No plants have reached Maximum rooting depth, MAXdepth + 1) ***}
 PlantTooDeep := 0 ;

end ; {ROOTcellsetup}

{*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&}
```

```
procedure SHOOTcellsetup(      var Light : ABOVEGROUNDcellREAL ;
                               var SHOOTcell : ABOVEGROUNDcellINT ;
                               var Height : eachPLANTint ) ;

var
 LAYER, x, y, plant : integer ;

begin {SHOOTcellsetup}

 {*** set ALL cells (including boundary cells) to -1 ***}
 for LAYER := 0 to (MAXheight+1) do
 begin {LAYER}
  for x := 0 to (MAXx+1) do
  begin {x}
   for y := 0 to (MAXy+1) do
   begin {y}
    SHOOTcell[LAYER,x,y] := -1
   end {y}
  end {x}
 end ; {LAYER}
 {*** set all central cells to 0 ***}
 for LAYER := 1 to MAXheight do
 begin {LAYER}
  for x := 1 to MAXx do
  begin {x}
   for y := 1 to MAXy do
   begin {y}
    SHOOTcell[LAYER,x,y] := 0 ;
    {*** set all shoot cells to full light level ***}
    Light[LAYER,x,y] := SUNlight
   end {y}
  end {x}
 end ; {LAYER}
 {*** set Height[plant] to 1 ***}
 for plant := 1 to PLANTnumber do Height[plant] := 1 ;
 {***     set PlantTooHigh to 0. No plants have reached Maximum shoot height,
          MAXheight + 1. If they do PlantTooHigh switches to 1. ***}
 PlantTooHigh := 0 ;

end ; {SHOOTcellsetup}

{*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&}
```

```
procedure Conditions ;

var
 plant : integer ;

begin {Conditions}

 rewrite(DETAILS) ;
 writeln(DETAILS,'Nitrogen Time Simulation run ') ;
 writeln(DETAILS,' TimeEnd = ',TIMEEND:4,' days') ;
 writeln(DETAILS,' Replications = ',REPLICATIONS) ;
 writeln(DETAILS,' PlantNo = ',PLANTnumber:4) ;
 writeln(DETAILS,' ROOTCELLmass = ',ROOTCELLmass:4:3,' mg biomass cell-1') ;
 writeln(DETAILS,' SHOOTCELLmass = ',SHOOTCELLmass:4:3,' mg biomass cell-1') ;
 writeln(DETAILS,' Resource = ',InitialResource:5:7,' mg N CELL-1') ;
 writeln(DETAILS,' ',a:1:3,' diffusion - ',b:1:3,' mass flow ') ;
 writeln(DETAILS,' diff.coeff.=',d:5 ) ;
 writeln(DETAILS,' ROOTcell -> z:',MAXdepth:3,' x:',MAXx:3,' y:',MAXy:3) ;
 writeln(DETAILS,'SHOOTcell -> z:',MAXheight:3) ;
 writeln(DETAILS,' decayRATE= ',decayRATE:1:5,' g Inorganic N released g-1 Organic N day-1') ;
 writeln(DETAILS,' InitialDecomp = ',InitialDecomp:3:5,' mg Organic Matter cell-1 ') ;
 writeln(DETAILS,' Sunlight = ',SunLIGHT:3:3,' (unitless) ') ;
 writeln(DETAILS,'SHOOTcell -> z:',MAXheight:3,' x:',MAXx:3,' y:',MAXy:3) ;
 writeln(DETAILS,' ### PLANT details ###') ;
 writeln(DETAILS,' *** Health & Position ***') ;
 writeln(DETAILS,' plant dead coordinates') ;
 for plant := 1 to PLANTnumber do
  writeln(DETAILS,' ',plant:2,' ',deadPLANT[plant]:1,' x:', PlantX[plant]:2, ' y:',PlantY[plant]:2 ) ;
 writeln(DETAILS,' *** Absorption Rates *** ') ;  writeln(DETAILS,' plant RAD Imax Km LAD') ;
 for plant := 1 to PLANTnumber do
  writeln(DETAILS,' ',plant:2,' ',ROOTdensity[plant]:4:3,' ',ROOTImax[plant]:3:3,' ',
         ROOTKm[plant]:3:3,' ',LAD[plant]:4:3) ;
 writeln(DETAILS,' *** Growth Rates *** ') ;
 writeln(DETAILS,' plant PsubRATE CsubRATE CaptGroCOUPLED ') ;
 for plant := 1 to PLANTnumber do
 begin
  write(DETAILS,' ',plant:2,' ',PsubRATE[plant]:4:3,' ', CsubRATE[plant]:4:3, ' ') ;
  if CaptGroCOUPLED[plant]=0 then
    writeln(DETAILS,' No ')
   else
    writeln(DETAILS,' Yes')
 end ;
 writeln(DETAILS,' *** Allocation ***') ;  writeln(DETAILS,' plant PartP PartC') ;
 for plant := 1 to PLANTnumber do writeln(DETAILS,' ',plant:2,' ',PartP[plant]:4:3,' ',PartC[plant]:4:3) ;
 writeln(DETAILS,' *** Architecture *** ') ;  writeln(DETAILS,' plant ROOTtimeout SHOOTtimeout ') ;
 for plant := 1 to PLANTnumber do
  writeln(DETAILS,' ',plant:2,' ',ROOTtimeout[plant]:3,' ', SHOOTtimeout[plant]:3 ) ;

end ; {Conditions}
```

```
{*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&}

procedure calcWaterUptake(      var ROOTcellnumber,  SHOOTcellnumber : eachPLANTint ;
                                var WaterUptake : eachPLANTreal ) ;

 {*** procedure to determine the number of ROOT/SHOOTcells occupied by
 each plant. Values stored in ROOTcellnumber & SHOOTcellnumber.
 From these, transpiration rate for each plant can be found ***}

var
 transpiration : real ;
 plant : integer ;

begin {calcWaterUptake}

 for plant := 1 to PLANTnumber do
 begin {plant}

  if deadPLANT[plant] = 0 then
   begin {plant alive}
    calcROOTcellnumber( plant, ROOTcellnumber[plant] ) ;
    calcSHOOTcellnumber( plant, SHOOTcellnumber[plant] ) ;
    transpiration := transpirationRATE * SHOOTbiomass[plant] ;
    WaterUptake[plant] := transpiration/ROOTbiomass[plant] ;
   end {plant alive}
 end {plant}

end ; {calcWaterUptake}

{*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&}

procedure calcMassFlow(         LAYER,x,y,nLAYER,nx,ny : integer; SoilWaterFlux : real ;
                                NutrientCOPY : SoilcellREAL ;  var MassFlowFlux : real ) ;

begin {calcMassFlow}

 if SoilWaterFlux > 0 then
   MassFlowFlux := ( b*NutrientCOPY[nLAYER,nx,ny] )/(n*d) ;
 if SoilWaterFlux < 0 then
   MassFlowFlux := ( -1*b*NutrientCOPY[LAYER,x,y] )/(n*d) ;
 if SoilWaterFlux = 0 then
   MassFlowFlux := 0 ;

end ; {calcMassFlow}

{*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&}
```

```
procedure SoilRmovement( var Nutrient, SoilWater : SoilcellREAL ) ;

var

 SoilWaterCOPY, NutrientCOPY : SoilcellREAL ;

 TOTALNutrient, newTOTALNutrient, DfluxA, DfluxB, DfluxC, DfluxD, DfluxE, DfluxF, WfluxA,
  WfluxB, WfluxC, WfluxD, WfluxE, WfluxF, MassFlowFluxA, MassFlowFluxB, MassFlowFluxC,
  MassFlowFluxD, MassFlowFluxE, MassFlowFluxF, NETfluxA, NETfluxB, NETfluxC, NETfluxD,
  NETfluxE, NETfluxF : real ;
 LAYER,x,y,xx,yy,iteration : integer ;

begin {SoilRmovement}

 for iteration := 1 to Nt do
 begin {iteration}
  {*** Make COPY's of Nutrient and SoilWater sheets ***}
  NutrientCOPY := Nutrient ;
  SoilWaterCOPY := SoilWater ;
  for LAYER := 1 to MAXdepth do
  begin {LAYER}
   for x := 1 to MAXx do
   begin {x}
    for y := 1 to MAXy do
    begin {y}


     {*** setup BORDER cells the same as neighbour cells ***}
     {*** NB. corners are excluded because they have NO neighbours ***}
     {*** if cell is at edge of space either wrap-round or equal the 'spare' cell as neighbour ***}
     if LAYER = 1 then NutrientCOPY[LAYER-1,x,y] := NutrientCOPY[LAYER,x,y] ;
     if LAYER = MAXdepth then NutrientCOPY[LAYER+1,x,y] := NutrientCOPY[LAYER,x,y] ;
     if x = 1 then NutrientCOPY[LAYER,x-1,y] := NutrientCOPY[LAYER,MAXx,y] ;
     if x = MAXx then NutrientCOPY[LAYER,x+1,y] := NutrientCOPY[LAYER,1,y] ;
     if y = 1 then NutrientCOPY[LAYER,x,y-1] := NutrientCOPY[LAYER,x,MAXy] ;
     if y = MAXy then NutrientCOPY[LAYER,x,y+1] := NutrientCOPY[LAYER,x,1] ;
     {*** Do the same for Water ***}
     if LAYER = 1 then SoilWaterCOPY[LAYER-1,x,y] := SoilWaterCOPY[LAYER,x,y] ;
     if LAYER = MAXdepth then SoilWaterCOPY[LAYER+1,x,y] := SoilWaterCOPY[LAYER,x,y] ;
     if x = 1 then SoilWaterCOPY[LAYER,x-1,y] := SoilWaterCOPY[LAYER,MAXx,y] ;
     if x = MAXx then SoilWaterCOPY[LAYER,x+1,y] := SoilWaterCOPY[LAYER,1,y] ;
     if y = 1 then SoilWaterCOPY[LAYER,x,y-1] := SoilWaterCOPY[LAYER,x,MAXy] ;
     if y = MAXy then SoilWaterCOPY[LAYER,x,y+1] := SoilWaterCOPY[LAYER,x,1] ;
```

```
      {*** Calculate flux of SoilR and Water by diffusion ***}
      DfluxA := a*( (NutrientCOPY[ LAYER,x,y+1 ]-NutrientCOPY[ LAYER,x,y ]) / ( 2*n*d ) ) ;
      DfluxB := a*( (NutrientCOPY[ LAYER,x+1,y ]-NutrientCOPY[ LAYER,x,y ]) / ( 2*n*d ) ) ;
      DfluxC := a*( (NutrientCOPY[ LAYER,x,y-1 ]-NutrientCOPY[ LAYER,x,y ]) / ( 2*n*d ) ) ;
      DfluxD := a*( (NutrientCOPY[ LAYER,x-1,y ]-NutrientCOPY[ LAYER,x,y ]) / ( 2*n*d ) ) ;
      DfluxE := a*( (NutrientCOPY[ LAYER+1,x,y ]-NutrientCOPY[ LAYER,x,y ]) / ( 2*n*d ) ) ;
      DfluxF := a*( (NutrientCOPY[ LAYER-1,x,y ]-NutrientCOPY[ LAYER,x,y ]) / ( 2*n*d ) ) ;
      WfluxA := ( SoilWaterCOPY[ LAYER,x,y+1 ] - SoilWaterCOPY[ LAYER,x,y ] ) / ( 2*n*WD) ;
      WfluxB := ( SoilWaterCOPY[ LAYER,x+1,y ] - SoilWaterCOPY[ LAYER,x,y ] ) / ( 2*n*WD) ;
      WfluxC := ( SoilWaterCOPY[ LAYER,x,y-1 ] - SoilWaterCOPY[ LAYER,x,y ] ) / ( 2*n*WD) ;
      WfluxD := ( SoilWaterCOPY[ LAYER,x-1,y ] - SoilWaterCOPY[ LAYER,x,y ] ) / ( 2*n*WD) ;
      WfluxE := ( SoilWaterCOPY[ LAYER+1,x,y ] - SoilWaterCOPY[ LAYER,x,y ] ) / ( 2*n*WD) ;
      WfluxF := ( SoilWaterCOPY[ LAYER-1,x,y ] - SoilWaterCOPY[ LAYER,x,y ] ) / ( 2*n*WD) ;
      {*** Calculate flux of SoilR by mass flow ***}
      calcMassFlow(LAYER,x,y, LAYER,x,(y+1), WfluxA,NutrientCOPY,MassFlowFluxA) ;
      calcMassFlow(LAYER,x,y, LAYER,(x+1),y, WfluxB,NutrientCOPY,MassFlowFluxB) ;
      calcMassFlow(LAYER,x,y, LAYER,x,(y-1), WfluxC,NutrientCOPY,MassFlowFluxC) ;
      calcMassFlow(LAYER,x,y, LAYER,(x-1),y, WfluxD,NutrientCOPY,MassFlowFluxD) ;
      calcMassFlow(LAYER,x,y, (LAYER+1),x,y, WfluxE,NutrientCOPY,MassFlowFluxE) ;
      calcMassFlow(LAYER,x,y, (LAYER-1),x,y, WfluxF,NutrientCOPY,MassFlowFluxF) ;
      {*** Calculate net movement of SoilR by diffusion and mass flow ***}
      NETfluxA := DfluxA + MassFlowFluxA ;
      NETfluxB := DfluxB + MassFlowFluxB ;
      NETfluxC := DfluxC + MassFlowFluxC ;
      NETfluxD := DfluxD + MassFlowFluxD ;
      NETfluxE := DfluxE + MassFlowFluxE ;
      NETfluxF := DfluxF + MassFlowFluxF ;

      {*** Determine the new values for the cell ***}
      SoilWater[ LAYER,x,y ] := SoilWaterCOPY[ LAYER,x,y ] + WfluxA + WfluxB + WfluxC + WfluxD
           + WfluxE + WfluxF ;
      Nutrient[ LAYER,x,y ] := NutrientCOPY[ LAYER,x,y ] + NetfluxA + NETfluxB + NETfluxC +
           NETfluxD + NETfluxE + NETfluxF

    end {y}
   end {x}
  end {LAYER}
 end {iteration}

end ; {SoilRmovement}

{&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&* &*&*&*&*&*&*}
```

```
procedure Uptake( var SoilR, SoilWater : SoilcellREAL ; var Ruptake : eachPLANTreal ) ;

var

 TotalSoilR, P, ROOTmass,relativeRATE, celluptake : real ;
 CELLtype, LAYER, x, y : integer ;

begin {Uptake}

 TotalSoilR := 0 ;
 for LAYER := 1 to MAXdepth do
 begin {LAYER}
  for x := 1 to MAXx do
  begin {x}
   for y := 1 to MAXy do
   begin {y}
    CELLtype := ROOTcell[LAYER,x,y] ;
    TotalSoilR := TotalSoilR + SoilR[LAYER,x,y] ;
    {*** check if cell is occupied ***}
    if CELLtype > 0 then
      begin {rootcell occupied}
       {*** check if plant is alive ***}
       if deadPLANT[CELLtype] = 0 then
         begin {uptake}
          if ROOTbiomass[CELLtype] < ROOTCELLmass then
            {*** ROOTmass is the proportion of the cell occupied by the root ***}
            begin {*** Root smaller than full cell ***}
             ROOTmass := ROOTbiomass[CELLtype]
            end
           else
            begin {*** Root is at least one cell in size ***}
             ROOTmass := ROOTCELLmass
            end ;

          {*** SoilR UPTAKE ***}
          P := SoilR[LAYER,x,y] ;
          relativeRATE := (RootImax[CELLtype]*P)/(RootKm[CELLtype]+P) ;
          celluptake := ROOTmass * ROOTdensity[CELLtype] * relativeRATE ;
          {check if uptake if > available...and linearize if so}
          if celluptake>P then celluptake:=P ;
          {*** Remove celluptake from soil ***}
          SoilR[LAYER,x,y] := P - celluptake ;
          {*** Add uptaken P to Ruptake pool ***}
          Ruptake[CELLtype] := Ruptake[CELLtype] + celluptake;
```

```
          {*** WATER UPTAKE ***}
          if SoilWater[LAYER,x,y] <= WaterUptake[CELLtype] then
            begin {*** take up all of cell's water ***}
             SoilWater[LAYER,x,y] := 0 ;
            end
           else
            begin {*** only take up part of cell's water ***}
             SoilWater[LAYER,x,y] := SoilWater[LAYER,x,y]-WaterUptake[CELLtype]
            end
         end {uptake}
      end {rootcell occupied}
   end {y}
  end {x}
 end ; {LAYER}
 writeln( Rres, TIME:3,' ',TotalSoilR,' ', ((MAXdepth*MAXx*MAXy*InitialResource)-TotalSoilR) ) ;

end ; {Uptake}

procedure shade( var Light : ABOVEGROUNDcellREAL ) ;

{determines Light value for each AboveGround cell based on shading from
above -- the Light value is the amount of light REACHING a cell (NOT
passing through)}

const
 f = 1 ;  d = 0.01 {m} ; {the height of a single cell}
var
 LAYER, x, y, CELLtype : integer ;  Ptransmittance : real ;

begin {shade}

 for LAYER := (MAXheight-1) downto 0 do
 begin {LAYER}
  for x := 1 to MAXx do
  begin {x}
   for y := 1 to MAXy do
   begin {y}
    CELLtype := SHOOTcell[(LAYER+1),x,y] ;
    if CELLtype > 0 then
      Ptransmittance := exp( -1*f*LAD[CELLtype] )
     else
      Ptransmittance := 1 ;
    Light[LAYER,x,y] := Light[(LAYER+1),x,y] * Ptransmittance
   end {y}
  end {x}
 end {LAYER}

end ; {shade}
```

```
{&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*}

procedure Photosynthesis( var Cproduction : eachPLANTreal ) ;

var
 SHOOTmass, LIGHTintercepted, PhotosyntheticRATE, Photosynthate : real ;
 LAYER, x, y, CELLtype : integer ;

begin {Photosynthesis}

 {*** for every cell ***}
 for LAYER := 1 to MAXheight do
 begin {LAYER }
  for x := 1 to MAXx do
  begin {x}
   for y := 1 to MAXy do
   begin {y}

    {check if cell occupied...}
    CELLtype := SHOOTcell[LAYER,x,y] ;
    if CELLtype > 0 then
     begin {cell is occupied by plant}
      {*** check if plant is alive ***}
      if deadPLANT[CELLtype] = 0 then
       begin {plant alive}

        if SHOOTbiomass[CELLtype]<SHOOTCELLmass then
          begin {*** Shoot is smaller than full cell ***}
           SHOOTmass := SHOOTbiomass[CELLtype] ;
          end
         else
          begin {*** Shoot is at least one full cell in size ***}
           SHOOTmass := SHOOTCELLmass
          end ;
        {determine the amount of light intercepted by cell}
        LIGHTintercepted := Light[LAYER,x,y] * LAD[CELLtype] ;
        {determine the per-unit mass hourly rate of photosynthesis}
        PhotosyntheticRATE := ( LIGHTintercepted * Kb ) / ( LIGHTintercepted + Ka ) ;
        {determine the absolute amount of photosynthate produced}
        Photosynthate := SHOOTmass * DAYlength * PhotosyntheticRATE ; {mg C}
        {add cell's photosynthate contribution to cummulative total of today's production}
        Cproduction[CELLtype] := Cproduction[CELLtype] + Photosynthate

      end {plant alive}
    end {cell is occupied by plant}

 end {y}  end {x}  end {LAYER}

end ; {Photosynthesis}
```

```
{&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*}

procedure ResourcePooling(            var deadPLANT : eachPLANTint ;
                                      var Cproduction,  Ruptake, Cpool, Rpool : eachPLANTreal ) ;

 {***    Cproduction (from Photosynthesis) and Ruptake are added to the C and N pools in place.
         If Cproduction is -ve (after Respiration), then this deficit is subtracted from Cpool. If Cpool <
         0 then PlantDeath occurs.  ***}
var
 plant : integer ;

begin {ResourcePooling}

 for plant := 1 to PLANTnumber do
 begin {plant}

  if deadPLANT[plant]=0 then
   begin {plant alive}

    TotalR[plant] := TotalR[plant] + Ruptake[plant] ;
    TotalC[plant] := TotalC[plant] + Cproduction[plant] ;
    Cpool[plant] := Cpool[plant] + Cproduction[plant] ;
    Cproduction[plant] := 0 ;
    Rpool[plant] := Rpool[plant] + Ruptake[plant] ;
    Ruptake[plant] := 0 ;
    if Cpool[plant]<0 then
     begin
      {*** Plant Death! ***}
      deadPLANT[plant] := 1 ;
      PlantDeath( plant, ROOTbiomass, SHOOTbiomass,  ROOTcell, SHOOTcell, SoilOrgMat ) ;
      writeln(' Plant has a C deficit too great for Cpool: Cpool<0 ')
     end
   end

 end {plant}

end ; {ResourcePooling}

{&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*}
```

```
procedure Assimilation(          var deadPLANT : eachPLANTint ;
                                 var Rpool, Cpool, Assimilates : eachPLANTreal ) ;

 {***    This procedure deals with the assimilation of C and N directed to growth from Cpool and
         Rpool, into fresh biomass. Growth respiratory costs are included in this procedure and take
         the form of efficiency of conversion of raw carbon into fresh biomass.
         CaptGroCOUPLED determines whether Resource Capture is linked to Growth. If
         CaptGroCOUPLED[plant]=0 then it is NOT linked, and Nsub and Csub are used as rates of N
         and C put foreward for assimilation. If CaptGroCOUPLED[plant]=1 then it IS linked, and
         Nsub and Csub are used as proportions of Npool and Cpool (respectively) to foreward N and
         C for assimilation. ***}

var
 Rsubstrate, Csubstrate, respiratoryCOST, temp : real ;
 plant : integer ;

begin {Assimilation}

{FLAG}
 for plant := 1 to PLANTnumber do
 begin {plant}
  if deadPLANT[plant]=0 then
   begin {plant alive}

    {***Determine growth type, and construct subtrate pools accordingly ***}
    if CaptGroCOUPLED[plant]=0 then

      begin
       {*** GROWTH UNCOUPLED TO RESOURCE CAPTURE ***}
       {*** Create substrate pools ***}
       if Rpool[plant] < PsubRATE[plant] then
         begin {less than required}
          Rsubstrate := Rpool[plant] ;
          Rpool[plant] := 0 ;
         end
        else
         begin {adequate R}
          Rsubstrate := PsubRATE[plant] ;
          Rpool[plant] := Rpool[plant] - PsubRATE[plant] ;
         end ; {adequate R}
       if Cpool[plant] < CsubRATE[plant] then
         begin {less C available than required}
          writeln(' plant',plant:2,' has < adequate C' ) ;
          Csubstrate := Cpool[plant] ;
          Cpool[plant] := 0 ;
         end {less C available than required}
        else
         begin {adequate C}
          Csubstrate := CsubRATE[plant] ;
```

```
           Cpool[plant] := Cpool[plant] - CsubRATE[plant] ;
          end {adequate C}
       end
      else
       begin
        {*** GROWTH COUPLED TO RESOURCE CAPTURE ***}
        Rsubstrate := gcP[plant]*Rpool[plant] ;
        Rpool[plant] := (1-gcP[plant])*Rpool[plant] ;
        Csubstrate := gcC[plant]*Cpool[plant] ;
        Cpool[plant] := (1-gcC[plant])*Cpool[plant]
       end ;

     {*** Growth Respiration: determine respiratory cost of growth, and deduct this from Csubstrate ***}
     respiratoryCOST := Csubstrate * GROWTHrespirationRATE ;
     Csubstrate := Csubstrate - respiratoryCOST ;
     {*** shift the C deficit to Cpool ***}
     if Csubstrate<0 then Cpool[plant]:=Cpool[plant]+Csubstrate ;
     {*** Put in C:R determination & return of excess R or Csub to pool ***}
     if (Csubstrate/Rsubstrate) > CRratio then
       begin {XS Carbon}
        temp := Rsubstrate * CRratio ;
        Cpool[plant] := Cpool[plant] + (Csubstrate-temp) ;
        Csubstrate := temp
       end {XS Carbon}
      else
       begin {XS Resource}
        temp := Csubstrate / CRratio ;
        Rpool[plant] := Rpool[plant] + (Rsubstrate-temp) ;
        Rsubstrate := temp
       end ; {XS Resource}

    {*** Assimilation ***}
    Assimilates[plant] := Assimilates[plant] + Csubstrate * ( 1/Ccontent ) ;
    {** OR **** = Assimilates[plant] + Rsubstrate * ( 1/Rcontent ) ***}

   end {plant alive}
 end ; {plant}


end ; {Assimilation}

{&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*}
```

```
procedure Maintenance(          ROOTcellnumber, SHOOTcellnumber : eachPLANTint ;
                                var Assimilates : eachPLANTreal ; var deadPLANT : eachPLANTint ) ;

 {***   Procedure to calculate the Respiration Maintenance cost for each whole plant based on a
        constant cost per cell occupied, NOT per unit biomass as this would bring further
        discrepances in to the model between REAL biomass and INTEGER biomass (based on cells).
        N Uptake and Photosynthesis are calculated on a cellwise basis and so is respiration. ***}
 {***   MaintenanceCost (the maintenance cost for the whole plant) is subtracted from the Assimilates
        pool. Thus, the plant may cease to grow, but can still live. ***}
var
 ROOTmaintenanceCOST, SHOOTmaintenanceCOST, MaintenanceCost : real ;
 totalCELLnumber,plant : integer ;

begin {Maintenance}

 for plant := 1 to PLANTnumber do
 begin {plant}
  if deadPLANT[plant]=0 then
   begin {plant alive}
    totalCELLnumber := ROOTcellnumber[plant] + SHOOTcellnumber[plant] ;
    if ROOTbiomass[plant] < ROOTCELLmass then
      ROOTmaintenanceCOST := ROOTbiomass[plant]*ROOTmaintenanceRATE
     else
      ROOTmaintenanceCOST := ROOTcellnumber[plant] * ROOTCELLmass * ROOTmaintenanceRATE;
    if SHOOTbiomass[plant] < SHOOTCELLmass then
      SHOOTmaintenanceCOST := SHOOTbiomass[plant] * SHOOTmaintenanceRATE
     else
      SHOOTmaintenanceCOST := SHOOTcellnumber[plant] * SHOOTCELLmass *
           SHOOTmaintenanceRATE ;
    MaintenanceCost := ROOTmaintenanceCOST + SHOOTmaintenanceCOST ; {mg C}
    Cpool[plant] := Cpool[plant] - MaintenanceCost ;
    {*** Chcek if plant has insufficient C for Maint. ***}
    if Cpool[plant] < 0 then
     begin  {*** Plant Death! ***}
      writeln(' plant=',plant,' has not enough C for Maint.') ;
      deadPLANT[plant] := 1 ;
      PlantDeath( plant, ROOTbiomass, SHOOTbiomass, ROOTcell, SHOOTcell, SoilOrgMat )
     end ;
    {*** Now to convert for R maint costs}
    Rpool[plant] := Rpool[plant] - ( (RlossRATE * ROOTcellnumber[plant]*ROOTCELLmass)
                  + (RlossRATE * SHOOTcellnumber[plant]*SHOOTCELLmass) ) ;
    {*** Check if plant has insufficient R to survive ***}
    if Rpool[plant] < 0 then
     begin {plant death}
      writeln(' plant=',plant,' has not enough R for Maint. ',TIME) ;   deadPLANT[plant] := 1 ;
      PlantDeath( plant, ROOTbiomass, SHOOTbiomass, ROOTcell, SHOOTcell, SoilOrgMat )
     end ;
   end {plant alive}
 end {plant}
end ; {Maintenance}
```

```
{&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*}

procedure Partition(     Assimilates : eachPLANTreal ;  var deadPLANT : eachPLANTint ;
                         var ROOTincrease, SHOOTincrease : eachPLANTreal ) ;

 {***     Partition procedure determines the allocation of Assimilates between ROOT and SHOOT.
           Assimilates going towards growth.

          NB. ROOTallocate and SHOOTallocate (the proportions of Assimilates directed towards root
          and shoot respectively) are calculated from relative Rpool and Cpool levels AFTER the N+C
          subtrate pools have been created ***}

var
 ROOTallocate, SHOOTallocate : real ;
 plant, p : integer ;

begin {Partition}

 for plant := 1 to PLANTnumber do
 begin {plant}
  {*** check if plant alive ***}
  if deadPLANT[plant] = 0 then
   begin {plant alive}

    {*** ALLOCATION ***}
    if (Cpool[plant]+Rpool[plant]) > 0 then
      begin {Both C & N available}
       ROOTallocate := ( Cpool[plant]  + (CRratio*PartP[plant]*Rpool[plant]) -
                     (PartC[plant]*Cpool[plant]) ) / ( (CRratio*Rpool[plant])+Cpool[plant] ) ;
       SHOOTallocate := ( (CRratio*Rpool[plant])  - (CRratio*PartP[plant]*Rpool[plant])  +
                     (PartC[plant]*Cpool[plant]) ) / ( (CRratio*Rpool[plant])+Cpool[plant] )
      end {Both C & N available}
     else
      begin {No C or N therefore allocate to shoot}
       {*** allocate equally ***}
       ROOTallocate := 0.0 ;
       SHOOTallocate := 1.0
      end ;

    {*** Check ALLOCATION values ***}
    if ROOTallocate < 0 then
     begin {*** Plant Death! ***}
      deadPLANT[plant] := 1 ;
      PlantDeath( plant, ROOTbiomass, SHOOTbiomass, ROOTcell, SHOOTcell, SoilOrgMat )
     end ; {*** Plant Death! ***}
    if SHOOTallocate < 0 then
     begin {*** Plant Death! ***}
      deadPLANT[plant] := 1 ;
      PlantDeath( plant, ROOTbiomass, SHOOTbiomass, ROOTcell, SHOOTcell, SoilOrgMat )
     end ; {*** Plant Death! ***}
```

```
    {*** check again if plant is alive ***}
    if deadPLANT[plant] = 0 then
     begin {plant still alive}
      {*** ROOT and SHOOT growth ***}
      ROOTincrease[plant] := ROOTallocate * Assimilates[plant] ;
      SHOOTincrease[plant] := SHOOTallocate * Assimilates[plant] ;
      Assimilates[plant] := 0
     end {plant still alive}
   end {plant alive}
 end {plant}

end ; {Partition}

{&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*}

procedure determinevacantROOTcell(   LAYER, x, y, plant : integer ;
                                     var newCELLx, newCELLy : integer ) ;

var
 eachX, eachY, bestx, besty, cellx, celly, CELLtype, VACANTnumber : integer ;
 highestR : real ;

begin {determinevacantROOTcell}

 VACANTnumber := 0 ; highestR := 0 ;
 for eachX := -1 to 1 do
 begin {eachX}
  for eachY := -1 to 1 do
  begin {eachY}
   cellx := (x+eachX) ;
   celly := (y+eachY) ;
   if cellx < 1 then cellx := MAXx ;
   if cellx > MAXx then cellx := 1 ;
   if celly < 1 then celly := MAXy ;
   if celly > MAXy then celly := 1 ;
   CELLtype := ROOTcell[LAYER,cellx,celly] ;
   if CELLtype = 0 then
    begin {cell unoccupied}
     VACANTnumber := VACANTnumber + 1 ;
     if SoilR[LAYER,cellx,celly] > highestR then
      begin {'best' cell so far...}
       highestR := SoilR[LAYER,cellx,celly] ;
       bestx := cellx ;
       besty := celly
      end
    end
  end {eachY}
 end ; {eachX}
 if VACANTnumber > 0 then
  begin {unoccupied neighbours exist}
```

```
   newCELLx := bestx ;
   newCELLy := besty
  end
end ; {determinevacantROOTcell}

{&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*}

procedure ROOTcellgrowth(     plant : integer ;  var PlantTooDeep : integer ;
                              var ROOTcell : SOILcellINT ;
                              var CELLgrowthNUMBER, Depth : eachPLANTint ) ;

var
 OUTCOME, eachLAYER, LAYER, x, y, growth, timeoutCOUNT, rndx, rndy, NEXTx, NEXTy,
       newCELLx, newCELLy : integer ;


begin {ROOTcellgrowth}

 {*** determine which position to start the growth Template at ***}
 LAYER := 1 ; x := PlantX[plant] ; y := PlantY[plant] ;
 growth := 0 ;
 timeoutCOUNT := 0 ;

 repeat

     {*** Read in Rnd data from file ***}
     if eof(ROOTrnd) = TRUE then
      begin
       reset(ROOTrnd) ;
       writeln(' Warning: resetting ROOTrnd file ')
      end ;
     readln(ROOTrnd,rndx,rndy) ;
     {*** Check if NEXT(x/y) cell is outside array envelope ***}
     {*** and if so then wrap-round... ***}
     NEXTx := x+rndx ; NEXTy := y+rndy ;
     if NEXTx < 1 then NEXTx := MAXx ;
     if NEXTx > MAXx then NEXTx := 1 ;
     if NEXTy < 1 then NEXTy := MAXy ;
     if NEXTy > MAXy then NEXTy := 1 ;

     if ROOTcell[LAYER,NEXTx,NEXTy] = 0 then
       begin {cell unoccupied and available}
        {*** determine how many cells surrounding x,y are
        unoccupied/vacant and, based on probability from
        respective SoilR values, choose one to grow into ***}
        determinevacantROOTcell( LAYER, x, y, plant, newCELLx, newCELLy ) ;
        {*** grow into this cell ***}
        ROOTcell[ LAYER, newCELLx, newCELLy ] := plant ;
        growth := 1
       end {cell unoccupied and available}
```

```
        else if ROOTcell[LAYER,NEXTx,NEXTy] = plant then
         begin {cell belongs to ownplant}
          {*** move template to that cell. This follows the root out ***}
          x := NEXTx ;
          y := NEXTy
         end {cell belongs to ownplant}
        else
         begin {cell belongs to otherplant}
          {*** reset x and y back to plant centre ***}
          { these have been taken out so routine searches around rather
          than resetting back at plant origin }
          {x := PlantX[plant] ;}
          {y := PlantY[plant] }
         end ; {cell belongs to otherplant}

       timeoutCOUNT := timeoutCOUNT + 1 ;
       if timeoutCOUNT > ROOTtimeout[plant] then
         begin {plant growth limits reached at present level}
         {*** shift growth search position down to next layer ***}
         LAYER := LAYER + 1 ;
         {check if modelled space is exceeded...}
         if LAYER > MAXdepth then
          begin
           writeln(           ' Warning: MaxROOT depth reached by plant ', plant:3,
                              ' at TIME=',TIME:3, ' repl=',repl:2, ' soilR=',InitialResource) ;
           PlantTooDeep := 1 ;
           growth := 1 ;
           LAYER := MAXdepth
          end ;
         {check if this is a NEW layer for the plant...}
         if LAYER > Depth[plant] then Depth[plant] := Depth[plant] + 1 ;
         {*** reset x and y to centre of plant ***}
         x := PlantX[plant] ;
         y := PlantY[plant] ;
         timeoutCOUNT := 0
        end ; {plant growth limits reached at present level}

 until growth = 1 ;

 {now account for this growth...}
 CELLgrowthNUMBER[plant] := CELLgrowthNUMBER[plant] - 1

end ; {ROOTcellgrowth}

{&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*}
```

```
procedure ROOTgrowth(      ROOTincrease : eachPLANTreal ;  var PlantTooDeep : integer ;
                           var ROOTbiomass : eachPLANTreal ;  var ROOTcell : SOILcellINT ;
                           var Depth : eachPLANTint ) ;
var
 CELLgrowthNUMBER : eachPLANTint ;
 TOTALcellNUMBER, plant, LAYER, x, y, CELLtype, CELLdifference : integer ;

begin {ROOTgrowth}

 {determine the whole number of cells to growth for each plant and in total}
 TOTALcellNUMBER := 0 ;
 for plant := 1 to PLANTnumber do
 begin {plant}

  if deadPLANT[plant] = 0 then
    begin {plant is alive}
     CELLgrowthNUMBER[plant] :=
           round(((ROOTincrease[plant]+ROOTbiomass[plant])/ROOTCELLmass) - 0.5) -
           round((ROOTbiomass[plant]/ROOTCELLmass) - 0.5 ) ;
     {*** Increase ROOTbiomass by the growth implied by ROOTincrease ***}
     ROOTbiomass[plant] := ROOTbiomass[plant] + ROOTincrease[plant] ;
    end
   else
    CELLgrowthNUMBER[plant] := 0 ;
  TOTALcellNUMBER := TOTALcellNUMBER + CELLgrowthNUMBER[plant]

 end ; {plant}
 {*** go thru' plants in turn and grow 1 cell and repeat, until all growth completed ***}
 plant := 1 ;

 repeat

    {check if plant has any cells left to grow...}
    if CELLgrowthNUMBER[plant]>0 then
     begin  {...and if so, call routine for 1 cell growth}
      ROOTcellgrowth(plant, PlantTooDeep, ROOTcell, CELLgrowthNUMBER, Depth) ;
      {account for growth from TOTALcellNUMBER}
      TOTALcellNUMBER := TOTALcellNUMBER - 1
     end ;
    {increment plant and reset if neccessary}
    plant := plant + 1 ; if plant > PLANTnumber then plant := 1 ;
    {check if plants have outgrown modelled space...}
    if PlantTooDeep=1 then
     {...and if so, exit from repeat..until loop NOW!}
     TOTALcellNUMBER:=0 ;

 until TOTALcellNUMBER = 0 ;

end ; {ROOTgrowth}
```

```
{&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*}

procedure determinevacantSHOOTcell(        LAYER, x, y, plant : integer ;
                                           var newCELLx, newCELLy : integer ) ;

var
 eachX, eachY, besty, bestx, cellx, celly, CELLtype, VACANTnumber : integer ;
 highestLIGHT : real ;

begin {determinevacantSHOOTcell}

 VACANTnumber := 0 ; highestLIGHT := 0 ;
 for eachX := -1 to 1 do
 begin {eachX}
  for eachY := -1 to 1 do
  begin {eachY}
   cellx := x + eachX ;
   celly := y + eachY ;
   if cellx < 1 then cellx := MAXx ;
   if cellx > MAXx then cellx := 1 ;
   if celly < 1 then celly := MAXy ;
   if celly > MAXy then celly := 1 ;
   CELLtype := SHOOTcell[LAYER,cellx,celly] ;
   if CELLtype = 0 then
    begin {cell unoccupied}
     VACANTnumber := VACANTnumber + 1 ;
     if Light[LAYER,cellx,celly] > highestLIGHT then
      begin {'best' cell so far...}
       highestLIGHT := Light[LAYER,cellx,celly] ;
       bestx := cellx ;
       besty := celly
      end
    end
  end {eachY}
 end ; {eachX}

 if VACANTnumber > 0 then
  begin {unoccupied neighbours exist}
   newCELLx := bestx ;
   newCELLy := besty
  end

end ; {determinevacantSHOOTcell}

{&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*}
```

```
procedure SHOOTcellgrowth(   plant : integer ; var PlantTooHigh : integer ;
                             var SHOOTcell : ABOVEGROUNDcellINT ;
                             var CELLgrowthNUMBER, Height : eachPLANTint ) ;

var
 eachLAYER, OUTCOME, LAYER, x, y, growth, timeoutCOUNT, rndx, rndy, NEXTx, NEXTy,
        newCELLx, newCELLy : integer ;

begin {SHOOTcellgrowth}

 {*** determine which position to start growth Template at ***}
 LAYER := 1 ; x := PlantX[plant] ; y := PlantY[plant] ;
 growth := 0 ;
 timeoutCOUNT := 0 ;

 repeat

      {*** Read in Rnd data from file ***}
      if eof(SHOOTrnd) = TRUE then
       begin
        reset(SHOOTrnd) ;
        writeln(' Warning: SHOOTrnd reset ')
       end ;
      readln(SHOOTrnd,rndx,rndy) ;
      {*** Check if NEXT? cell is outside array envelope ***}
      NEXTx := x+rndx ; NEXTy := y+rndy ;
      if NEXTx < 1 then NEXTx := MAXx ;
      if NEXTx > MAXx then NEXTx := 1 ;
      if NEXTy < 1 then NEXTy := MAXy ;
      if NEXTy > MAXy then NEXTy := 1 ;

      if SHOOTcell[LAYER,NEXTx,NEXTy] = 0 then
        begin {cell unoccupied and available}
         {*** determine how many cells surrounding x,y are
         unoccupied/vacant and, based on respective LIGHTlevel values,
         choose best one to grow into ***}
         determinevacantSHOOTcell( LAYER, x, y, plant, newCELLx, newCELLy ) ;
         {*** grow into this cell ***}
         SHOOTcell[ LAYER, newCELLx, newCELLy ] := plant ;
         growth := 1
        end {cell unoccupied and available}

       else if SHOOTcell[LAYER,NEXTx,NEXTy] = plant then
        begin {cell belongs to ownplant}
         {move template to that cell. This follows the root out?}
         x := NEXTx ;
         y := NEXTy
        end
```

```
       else
        begin {cell belongs to otherplant}
         {*** reset x and y back to plant centre ***}
         {these have been taken out so routine search around rather than resetting back at plant origin }
         { x := PlantX[plant] ; }
         { y := PlantY[plant] }
        end ;

      timeoutCOUNT := timeoutCOUNT + 1 ;
      if timeoutCOUNT > SHOOTtimeout[plant] then
       begin {plant growth limits reached at present level}
        {shift growth search to next layer up}
        LAYER := LAYER + 1 ;
        {check if modelled space is exceeded...}
        if LAYER > MAXheight then
         begin
          write(' Warning!!! PlantTooHigh reached by plant ', plant:3,' at TIME=',TIME:3 ) ;
          PlantTooHigh := 1 ;
          growth := 1 ;
          LAYER := MAXheight
         end ;
        {check if this is a NEW layer for the plant...}
        if LAYER > Height[plant] then Height[plant] := Height[plant] + 1 ;
        {*** reset x and y to centre of plant ***}
        x := PlantX[plant] ;
        y := PlantY[plant] ;
        timeoutCOUNT := 0
       end ; {plant growth limits reached at present level}

 until growth = 1 ;

 {now account for this growth...}
 CELLgrowthNUMBER[plant] := CELLgrowthNUMBER[plant] - 1

end ; {SHOOTcellgrowth}

{&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*}
```

```
procedure SHOOTgrowth(       SHOOTincrease : eachPLANTreal ; var PlantTooHigh : integer ;
                             var SHOOTbiomass : eachPLANTreal ;
                             var SHOOTcell : ABOVEGROUNDcellINT ;
                             var Height : eachPLANTint ) ;

var
 CELLgrowthNUMBER : eachPLANTint ;
 TOTALcellNUMBER, plant, LAYER, x, y, CELLtype, CELLdifference : integer ;

begin {SHOOTgrowth}

 {determine the whole number of cells to growth for each plant and in total}
 TOTALcellNUMBER := 0 ;
 for plant := 1 to PLANTnumber do
 begin {plant}
  if deadPLANT[plant] = 0 then
    begin {plant is alive}

     CELLgrowthNUMBER[plant] :=
           round( ((SHOOTincrease[plant]+SHOOTbiomass[plant])/SHOOTCELLmass) - 0.5)
           - round( (SHOOTbiomass[plant]/SHOOTCELLmass) - 0.5 ) ;
     {*** Increase SHOOTbiomass by the growth implied by SHOOTincrease ***}
     SHOOTbiomass[plant] := SHOOTbiomass[plant] + SHOOTincrease[plant] ;
    end
   else
    CELLgrowthNUMBER[plant] := 0 ;
  TOTALcellNUMBER := TOTALcellNUMBER + CELLgrowthNUMBER[plant]
 end ; {plant}
 {go thruough plants in turn and grow 1 cell and repeat, until all growth completed}
 plant := 1 ;

 repeat

      {check if plant has any cells left to grow...}
      if CELLgrowthNUMBER[plant]>0 then
       begin {...and if so, call routine for 1 cell growth}
        SHOOTcellgrowth(plant, PlantTooHigh, SHOOTcell, CELLgrowthNUMBER, Height) ;
        {account for growth from TOTALcellNUMBER}
        TOTALcellNUMBER := TOTALcellNUMBER - 1
       end ;
      {increment plant and reset if neccessary}
      plant := plant + 1 ; if plant > PLANTnumber then plant := 1 ;
      {check if plants have outgrown modelled space...}
      if PlantTooHigh=1 then  {...and if so, exit from repeat..until loop NOW}
       TOTALcellNUMBER := 0 ;

 until TOTALcellNUMBER = 0 ;

end ; {SHOOTgrowth}
```

```
{&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*}

procedure Decompose( var SoilOrgMat, SoilR : SoilcellREAL ) ;

 {***     Decompose porcedure takes each SOILcell in turn and if there is
          organic material present, transfers Resource from SoilOrgMat to
          SoilR. ***}

var
 LAYER, x, y : integer ;

begin {Decompose}

 for LAYER := 1 to MAXdepth do
 begin {LAYER}
  for x := 1 to MAXx do
  begin {x}
   for y := 1 to MAXy do
   begin {y}
    SoilR[LAYER,x,y] := SoilR[LAYER,x,y] + ( decayRATE * SoilOrgMat[LAYER,x,y] * Rcontent ) ;
    SoilOrgMat[LAYER,x,y] := (1-decayRATE) * SoilOrgMat[LAYER,x,y]
   end {y}
  end {x}
 end {LAYER}

end ; {Decompose}

{&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*}

procedure writePLANTdetails(           var PREVIOUSbiomass : eachPLANTreal ; deadPLANT :
                                       eachPLANTint ; ROOTbiomass, SHOOTbiomass :
                                       eachPLANTreal ) ;

var
 SPPbiomass, SPProotmass, SPPtotalR, SPPtotalC, SPPRpool,
          SPPCpool : array[1..SPECIESnumber] of real ;
 DEADnumber : array[1..SPECIESnumber] of integer ; s, plant : integer ;

begin

 {set SPPbiomass to zero}
 for s := 1 to SPECIESnumber do
 begin
 SPPbiomass[s] := 0 ;
 SPProotmass[s] := 0 ;
 DEADnumber[s] := 0 ;
 SPPRpool[s] := 0 ;
 SPPCpool[s] := 0
 end ;
```

```
 {go thru' plants and cummulate SPPbiomass & also find DEADnumber }
 for plant := 1 to PLANTnumber do
  begin
   SPPbiomass[Species[plant]] := SPPbiomass[Species[plant]] + ROOTbiomass[plant] +
          SHOOTbiomass[plant] ;
   SPProotmass[Species[plant]] := SPProotmass[Species[plant]] + ROOTbiomass[plant] ;
   DEADnumber[Species[plant]] := DEADnumber[Species[plant]] + deadPLANT[plant] ;
   {NB. this works because if plant is dead, then deadPLANT=1 else deadPLANT=0}
   SPPRpool[Species[plant]] := SPPRpool[Species[plant]] + Rpool[plant] ;
   SPPCpool[Species[plant]] := SPPCpool[Species[plant]] + Cpool[plant]
  end ;
 write(PLANTres, InitialResource:3:5,' ',TIME:4,' ',repl:2,' ') ;
 for s := 1 to SPECIESnumber do
  begin {s}
   SPPtotalR[s] := ( SPPbiomass[s] * Rcontent ) + SPPRpool[s] ;
   SPPtotalC[s] := ( SPPbiomass[s] * Ccontent ) + SPPCpool[s] ;
   SPPRpool[s] := SPPRpool[s] / SPPbiomass[s] ;
   SPPCpool[s] := SPPCpool[s] / SPPbiomass[s] ;
   write(PLANTres, SPPbiomass[s]:6:7,' ', SPProotmass[s]:6:7,' ', DEADnumber[s]:2 ,' ',
          SPPRpool[s]:6:7,' ', SPPCpool[s]:6:7,' ', SPPtotalR[s]:6:7,' ', SPPtotalC[s]:6:7,' ' )
  end ; {s}
 writeln(PLANTres,' ')

end ; {writePLANTdetails}

{&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*}

procedure writeGRADdetails ;

var
 SPPbiomass, SPProotmass, SPPtotalR, SPPtotalC, SPPRpool,
          SPPCpool : array[1..SPECIESnumber] of real ;
 DEADnumber : array[1..SPECIESnumber] of integer ;
 s, plant : integer ;

begin {writeGRADdetails}

 {set SPPbiomass to zero}
 for s := 1 to SPECIESnumber do
  begin
   SPPbiomass[s] := 0 ;
   SPProotmass[s] := 0 ;
   DEADnumber[s] := 0 ;
   SPPRpool[s] := 0 ;
   SPPCpool[s] := 0
  end ;
```

```
{go through plants and cummulate SPPbiomass & also find DEADnumber }
for plant := 1 to PLANTnumber do
 begin
  SPPbiomass[Species[plant]] := SPPbiomass[Species[plant]] + ROOTbiomass[plant]
        + SHOOTbiomass[plant] ;
  SPProotmass[Species[plant]] := SPProotmass[Species[plant]] + ROOTbiomass[plant] ;
  DEADnumber[Species[plant]] := DEADnumber[Species[plant]] + deadPLANT[plant] ;
  {NB. this works because if plant is dead, then deadPLANT=1 else deadPLANT=0}
  SPPRpool[Species[plant]] := SPPRpool[Species[plant]] + Rpool[plant] ;
  SPPCpool[Species[plant]] := SPPCpool[Species[plant]] + Cpool[plant]
 end ;
write(SPECIESres, InitialResource:3:5,' ',TIME:4,' ',repl:2,' ') ;
for s := 1 to SPECIESnumber do
 begin {s}
  SPPtotalR[s] := ( SPPbiomass[s] * Rcontent ) + SPPRpool[s] ;
  SPPtotalC[s] := ( SPPbiomass[s] * Ccontent ) + SPPCpool[s] ;
  write(SPECIESres, SPPbiomass[s]:6:7,' ', SPProotmass[s]:6:7,' ', DEADnumber[s]:2 ,' ',
        SPPRpool[s]:6:7,' ', SPPCpool[s]:6:7,' ', SPPtotalR[s]:6:7,' ', SPPtotalC[s]:6:7,' ' )
 end ; {s}
writeln(SPECIESres,' ')

end ; {writeGRADdetails}

{&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*}

procedure ResourcePictures ;

var
 relativeSoilR : real ;
 STRIPnumber, strip, dot1, dot2, LAYER, x, y : integer ;

begin {ResourcePictures}

 rewrite(SoilRres) ;
 rewrite(relSoilRres) ;
 rewrite(Lightres) ;
 STRIPnumber := round(MAXdepth/STRIPlength) ;
 for strip := 1 to STRIPnumber do
 begin {strip}
  for LAYER := (1+((strip-1)*STRIPlength)) to (strip*STRIPlength) do
  begin {LAYER}
   for x := 1 to MAXx do
   begin {x}
    for y := 1 to MAXy do
    begin {y}
     relativeSoilR := SoilR[LAYER,x,y]/InitialResource ;
     writeln(relSoilRres, x+((LAYER-(1+((strip-1)*STRIPlength)))*(MAXx+SPACEsize)),
          y+((strip-1)*(MAXy+SPACEsize)),' ', relativeSoilR:1:6 ) ;
     writeln(SoilRres, x+((LAYER-(1+((strip-1)*STRIPlength)))*(MAXx+SPACEsize)),
          y+((strip-1)*(MAXy+SPACEsize)),' ', SoilR[LAYER,x,y]:3:6 ) ;
```

```
     writeln(Lightres, x+((LAYER-(1+((strip-1)*STRIPlength)))*(MAXx+SPACEsize)),
           y+((strip-1)*(MAXy+SPACEsize)),' ', Light[(LAYER-1),x,y]:1:8 ) ;
    end {y}
   end {x}
  end {LAYER}
 end {strip}

end ; {ResourcePictures}

{&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*}

procedure PlantPictures ;

var
 relativeSoilR : real ;
 STRIPnumber, strip, dot1, dot2, LAYER, x, y : integer ;

begin {ResourcePictures}

 rewrite(ROOTres) ;
 rewrite(SHOOTres) ;
 STRIPnumber := round(MAXdepth/STRIPlength) ;
 for strip := 1 to STRIPnumber do
 begin {strip}
  for LAYER := (1+((strip-1)*STRIPlength)) to (strip*STRIPlength) do
  begin {LAYER}
   for x := 1 to MAXx do
   begin {x}
    for y := 1 to MAXy do
    begin {y}
     if ROOTcell[LAYER,x,y]>0 then
       begin
        dot1:=ROOTcell[LAYER,x,y] ;
        dot2:=Species[dot1]
       end
      else
       begin
        dot1:=0 ;
        dot2:=0
       end ;
     writeln(ROOTres, x+((LAYER-(1+((strip-1)*STRIPlength)))*(MAXx+SPACEsize)),
                      y+((strip-1)*(MAXy+SPACEsize)), dot1, dot2 )
    end {y}
   end {x}
  end {LAYER}
 end ; {strip}

 STRIPnumber := round(MAXheight/STRIPlength) ;
```

```
 for strip := 1 to STRIPnumber do
 begin {strip}
  for LAYER := (1+((strip-1)*STRIPlength)) to (strip*STRIPlength) do
  begin {LAYER}
   for x := 1 to MAXx do
   begin {x}
    for y := 1 to MAXy do
    begin {y}

      if SHOOTcell[LAYER,x,y]>0 then
        begin
         dot1:=SHOOTcell[LAYER,x,y] ;
         dot2:=Species[dot1]
        end
       else
        begin
         dot1:=0 ;
         dot2:=0
        end ;
      writeln(SHOOTres, x+((LAYER-(1+((strip-1)*STRIPlength)))*(MAXx+SPACEsize)),
                   y+((strip-1)*(MAXy+SPACEsize)), dot1, dot2 )

    end {y}
   end {x}
  end {LAYER}
 end {strip}

end ; {PlantPictures}
```

```
{&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*}
                    { MAIN PROGRAM }
{&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*&*}


begin {*** MAIN PROGRAM ***}

 {*** SetUp Files ***}
 reset(PROBrnd) ;
 {*** open ROOTrnd and SHOOTrnd files ***}
 reset(ROOTrnd) ; reset(SHOOTrnd) ;
 rewrite(PLANTres) ; rewrite(GRADres) ; rewrite(SPECIESres) ;
 rewrite(Rres) ; rewrite(timeA) ; rewrite(timeB) ; rewrite(timeC) ;

 for P := 10 downto 0 do
 begin {P}

   InitialResource := 0.01 + ((P*P)/100) ;
   writeln(' ### Initial Resource = ',InitialResource:3:6 ) ;

   for repl := 1 to REPLICATIONS do
   begin {repl}

     writeln(' *** replication no. ',repl:2) ;

     {*** Initialization Routines ***}
     ROOTcellsetup( ROOTcell, Depth ) ;
     SHOOTcellsetup( Light, SHOOTcell, Height ) ;
     PLANTsetup( deadPLANT, PlantX, PlantY, ROOTtimeout, SHOOTtimeout, CaptGroCOUPLED,
          species,ROOTdensity, RootImax, RootKm, LAD, Assimilates, PREVIOUSbiomass, ROOTcell,
          SHOOTcell ) ;

     SOILsetup( SoilR, SoilWater, SoilOrgMat ) ;
     {*** Write Conditions --> DETAILS file ***}
     Conditions ;
```

```
      {*** Start simulation ***}
      STOP := 0 ;  TIME := 1 ;
      repeat

          writeln(' Time = ',TIME:4) ;
          {*** SOIL PROCESSES ***}
          calcWaterUptake( ROOTcellnumber, SHOOTcellnumber,  WaterUptake ) ;
          Decompose( SoilOrgMat, SoilR ) ;
          SoilRmovement( SoilR, SoilWater ) ;
          {*** CALCULATE LIGHT ***}
          shade( Light ) ;
          {Graphic output of resource distributions}
          ResourcePictures ;

          {*** RESOURCE CAPTURE ***}
          Uptake( SoilR, SoilWater, Ruptake ) ;
          Photosynthesis( Cproduction ) ;
          {*** PLANT PROCESSING OF RESOURCES ***}
          ResourcePooling( deadPLANT, Cproduction, Ruptake, Cpool, Rpool ) ;
          Maintenance( ROOTcellnumber, SHOOTcellnumber, Assimilates, deadPLANT ) ;
          Assimilation( deadPLANT, Rpool, Cpool, Assimilates ) ;
          Partition( Assimilates, deadPLANT,
          ROOTincrease, SHOOTincrease ) ;
          {*** PLANT GROWTH ***}
          ROOTgrowth( ROOTincrease, PlantTooDeep,ROOTbiomass, ROOTcell, Depth ) ;
          SHOOTgrowth( SHOOTincrease,PlantTooHigh,SHOOTbiomass,SHOOTcell,Height ) ;

          {*** OUTPUT of PARAMETERS ***}
          {Leave this in if you want pictures every  day...}
          {PlantPictures ;}

          TIME := TIME + 1 ;
          if TIME>TIMEEND then STOP:=1 ;
          {*** End simulation replication if end of space has been reached by growth ***}
          if PlantTooDeep=1 then STOP:=1 ;  if PlantTooHigh=1 then STOP:=1 ;
          {*** End simulation replication if all plants are dead ***}
          alive := 0 ;
          for plant:= 1 to PLANTnumber do
          if deadPLANT[plant]=0 then alive:=1 ;
          if alive=0 then STOP:=1 ;

      until STOP=1 ;
      writeGRADdetails ;  PlantPictures ;

    end {repl}

  end ; {P}
  writeln(' The End. ')

end. {*** MAIN PROGRAM ***}
```