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ON COEXISTENCE: a causal approach to diversity and stability in grassland vegetation



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W.G. Braakhekke

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**ON COEXISTENCE:
a causal approach to diversity and stability
in grassland vegetation**

Proefschrift

ter verkrijging van de graad van
doctor in de landbouwwetenschappen,
op gezag van de rector magnificus,
dr. H.C. van der Plas,
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Abstract

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Ways of explaining coexistence of plant species in grassland are discussed. By adapting the competition model of De Wit (1960) it is shown that in various more complicated situations competition may lead to stable equilibria. Conditions for stable equilibrium between species in a homogeneous environment are derived from a model of multiple resource competition with complementary resources. This simple model explains complex patterns and processes in vegetation in terms of physiological differences and interactions between species.

Competition experiments in the field show that *Plantago lanceolata* and *Chrysanthemum leucanthemum* occupy partly different niches in time. The yield of *P. lanceolata* decreased after two years, probably by senescence and auto-inhibition. The reaction of *C. leucanthemum* to this caused high Relative Yield Total (RYT), but there was no equilibrium.

Attempts to prove experimentally the existence of a stable equilibrium point under the equilibrium conditions derived from the model of multiple resource competition were not successful, because none of the combinations of species and nutrients investigated met the equilibrium conditions. However, the results of experiments in which *P. lanceolata* and *Sanguisorba minor* were competing for potassium and magnesium show that competitive ability depends on the composition of the nutrient solution, and that equilibrium is likely to be attained with other, more suitable combinations of species and nutrients.

Free descriptors: cation requirement, cation uptake, *Chrysanthemum leucanthemum*, competition model, niche differentiation, *Plantago lanceolata*, Relative Yield Total, *Sanguisorba minor*.

The investigations were carried out at the Centre for Agrobiological Research (CABO) at Wageningen.

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Stellingen

1. Het bestuderen van concurrentieverschijnselen is van groot belang voor een goed inzicht in het functioneren van stabiele plantengemeenschappen, omdat hun structuur grotendeels wordt bepaald door de mogelijkheden die de soorten hebben om de interspecifieke concurrentie te vermijden.

2. In de synoecologie is onderzoek naar de invloed van een plant op zijn omgeving even belangrijk als onderzoek naar de invloed van de omgeving op een plant.

3. Omdat de meeste autoecologen nauw verwante soorten op verschillende groeiplaatsen vergelijken en niet verschillende soorten op een zelfde groeiplaats, bestaat er nog steeds een brede kloof tussen de autoecologie en de synoecologie.

4. Een oecologische nis is geen "hol" maar een "rol".

Westhoff, V. (1965) Plantengemeenschappen. In: Uit de plantenwereld. De Haan, Zeist; Van Loghum Slaterus, Arnhem, p. 293.
Dobben, W.H. van (1974) Oecologische nis en oecologische isolatie. Inaugurele rede. LR Wageningen, p. 2.
Dit proefschrift, p. 69.

5. De verklaring van diversiteit vereist een diversiteit van verklaringen.

Dit proefschrift, p. 21.

6. In tegenstelling tot de mening van Titman (1976) is een constante aantalsverhouding van soorten in een mengcultuur onvoldoende bewijs voor stabiele coexistentie.

Titman, D. (1976) Science 192: 463-465.

7. De opvatting van Grime (1977) dat de concurrentiekracht van een plantesoort onafhankelijk is van de omstandigheden is onhoudbaar.

Grime, J.P. (1977) Am. Nat. 111: 1169-1194.
Dit proefschrift, p. 144.

8. Redacteurs van wetenschappelijke tijdschriften moeten zich steeds bewust zijn van het wezenlijke verschil tussen significant en interessant.

9. Het herhaaldelijk wijzigen van wetenschappelijke en Nederlandse plantennamen in opeenvolgende flora's schaadt de belangrijkste functie van een naam. Veranderende taxonomische en historische inzichten dienen anders dan in de naamgeving te worden gedemonstreerd.

10. Het equivalent, zijnde de hoeveelheid stof die in een ionreactie equivalent is met een mol waterstofionen, dient te worden toegelaten naast het internationale stelsel van eenheden.

11. Het biologieonderwijs op scholen voor AVO en WVO moet meer gericht zijn op de belevingswereld van de leerlingen dan op de belangstelling van biologen. Zo zou minder aandacht besteed moeten worden aan de citroenzuurcyclus en meer aan de menstruatiecyclus.

12. Niet alleen de oecologische maar ook de ethische aspecten van de rol die de mens speelt in de natuur moeten aan de orde komen in het biologieonderwijs.

13. Omdat het kwellen en verminken van dieren voor sport en vermaak ethisch onaanvaardbaar is, verdient de sportvisserij geen overheidssteun en dient de Landbouwhogeschool geen medewerking te verlenen aan onderzoek ten behoeve van de sportvisserij.

14. Omdat verwachtingen van de onderzoeker omtrent de resultaten van zijn experimenten kunnen leiden tot foutieve weergave van die resultaten, is het beter de punten in een grafiek te laten intekenen door iemand die niet bij het onderzoek is betrokken.

Vergelijk: J.P. van den Bergh en W.G. Braakhekke, 1978. In: A.H.J. Freysen & J.W. Woldendorp (Eds.), Structure and functioning of plant populations. North-Holland Publ. Comp., Amsterdam, p. 134, Fig. 5.
Dit proefschrift, Fig. 37a.

Stellingen behorend bij het proefschrift van W.G. Braakhekke,
On coexistence: a causal approach to diversity and stability in grassland vegetation.
Wageningen, 31 oktober 1980.

Woord vooraf

Met dit proefschrift heb ik mij begeven op drie vakgebieden: de theoretische oecologie, de experimentele vegetatiekunde en de oecofysiologie. Dit is gevaarlijk, want het verdrievoudigt het potentiële aantal opponenten en het vergroot bovendien de kans dat zij terecht opponeren. Ik heb echter de hoop dat ook het aantal geïnteresseerden evenredig is toegenomen en heb daarom geprobeerd de tekst begrijpelijk te houden voor lezers zonder specialistische kennis op de betreden vakgebieden.

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Curriculum vitae

Wim Braakhekke werd geboren op 21 juli 1948 te Deventer. Na de lagere school bezocht hij het Nijmeegs Lyceum waar hij in 1967 het eindexamen HBS-b aflegde. Na de vervulling van de dienstplicht begon hij in 1969 met de studie in de biologie aan de Katholieke Universiteit te Nijmegen waar in 1972 het kandidaats- en in 1975 het doctoraalexamen werd afgelegd. Voor dit laatste examen werd onderzoek verricht op de volgende gebieden: beschrijvend vegetatiekundig onderzoek bij prof.dr. V. Westhoff; experimenteel vegetatiekundig onderzoek bij prof.dr. V. Westhoff, uitgevoerd op het voormalig IBS, thans CABO, o.l.v. drs. M.J.M. Oomes; bodemkundig onderzoek bij dr. D. Teunissen, o.l.v. drs. L. Kempers; aquatisch-oecologisch onderzoek bij prof.dr. C. den Hartog, o.l.v. mw.dr. J.F.M. Geelen.

Na het doctoraalexamen werd hij aangesteld bij de Nederlandse organisatie voor Zuiver Wetenschappelijk Onderzoek en gedetacheerd bij het Centrum voor Agrobiologisch Onderzoek te Wageningen, waar hij onderzoek verrichtte in het kader van het BION-project (14-75-02) 'Evenwichten in korte begroeiingen', en het CABO-project (423) 'Onderzoek naar de floristische stabiliteit van begroeiingen', welk onderzoek resulteerde in dit proefschrift.

Momenteel is hij werkzaam als wetenschappelijk medewerker bij de Vakgroep Bodemkunde en Bemestingsleer van de Landbouwhogeschool te Wageningen.

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List of abbreviations

A	= relative area
DM	= dry matter
E	= total amount of a nutrient present
e	= use efficiency, $e = O/R$
g	= relative amount of biomass invested in generative reproduction
k_{ab}^n	= relative crowding coefficient of species a with respect to species b in competition for nutrient n
M	= yield in monoculture, M_s^n is the potential yield of species s if nutrient n were limiting
m_s^n	= minimum concentration of nutrient n in species s, $m = U/O$
meq	= milliequivalent (see below)
N	= population density
O	= yield in mixed culture, O_s^n is the potential yield of species s if nutrient n were limiting
Q	= $(k_{ab}^2 z_a + z_b) / (k_{ab}^1 z_a + z_b)$
r	= relative yield, $r = O/M$
R	= total amount of a resource present
RRR	= Relative Replacement Rate, $RRR_{ab} = (N_a/N_b)_{t+1} / (N_a/N_b)_t$
RYT	= Relative Yield Total, $RYT = r_a + r_b$
s	= contribution of immigrated seeds to the initial plant frequency
U	= amount of a nutrient taken up
v	= relative amount of biomass invested in vegetative reproduction
Y	= yield at which the allelopathic effect of a species completely suppresses its competitor
Z	= initial seed or plant frequency
z	= relative seed or plant frequency

Greek symbols

α	= relative reproductive rate, $\alpha_{ab} = (O_a/O_b)_{t+1} / (O_a/O_b)_t$
β	= space occupied by one plant standing alone
ρ	= relative replacement rate, $\rho_{ab} = (r_a/r_b)_{t+1} / (r_a/r_b)_t$
Ω	= theoretical yield at infinite plant density

Indices

1, 2, ...n	= resources or nutrients
a, b, ...s	= species
x, y	= uptake mechanisms
t	= time
*	= indicates equilibrium

Ionic species are represented by their chemical symbols, omitting charge signs, e.g. Ca instead of Ca^{2+} .

In defining a quantity of ions it is often desirable to use the number of elementary charges rather than the number of particles. To this end one may use the ionic equivalent. This is that entity which, in an ionic reaction, would combine with or substitute for one entity of hydrogen ions (IUPAC, 1978). When, according to the SI, only the mole is used to indicate the amount of substance (i.e. a number of entities) it should be specified each time what kind of entity is referred to, e.g. molecules or ionic equivalents. This is cumbersome. Therefore the familiar milliequivalent (meq) is used in this report to designate the amount of substance which, in an ionic reaction, would combine with or substitute for or be in any other appropriate way equivalent to one mmol of hydrogen ions.

Once defined, plant species are named by their genus names:

<i>Anthoxanthum</i>	= <i>A. odoratum</i> L.
<i>Anthyllis</i>	= <i>A. vulneraria</i> L.
<i>Cerastium</i>	= <i>C. holosteoides</i> Fr.
<i>Chrysanthemum</i>	= <i>C. leucanthemum</i> L.
<i>Plantago</i>	= <i>P. lanceolata</i> L.
<i>Rumex</i>	= <i>R. acetosa</i> L.
<i>Sanguisorba</i>	= <i>S. minor</i> Scop.

(nomenclature according to Heukels & Van Ooststroom (1975))

1 Introduction

In the past decennia, a considerable amount of literature has been published on the balance of nature and the relation supposed between diversity and stability of ecosystems. The 22nd Brookhaven Symposium in Biology (Woodwell & Smith, 1969) and the First International Congress of Ecology (see Van Dobben & Lowe-McConnel, 1975) gave a good picture of the developments, which took place mainly at the theoretical level and in the ecosystem research. The belief that the diversity of an ecosystem enhances its stability seems to have lost ground. Instead it is thought now that the stability or better constancy of the environment offers the opportunity for a diverse ecosystem to develop. The work of May (1974) has contributed much to this change. Recently Harrison (1979) pointed out that the advocates of these seemingly conflicting hypotheses are talking about different components of ecosystem stability and that both viewpoints are supported by mathematical evidence.

As yet, little is known of the processes for the individual and population that determine diversity. Especially in plant ecology, a big gap exists between research at the individual level and at the community level. Only in the last years has activity been growing in this field (see the proceedings of the Symposium 'Plant Relations in Pastures' (Wilson, 1978) and the congress 'Structure and functioning of plant populations' (Freysen & Woldendorp, 1978)), forcefully stimulated by the work of Harper and his colleagues, culminating in his book 'Population Biology of Plants' (Harper, 1977).

With the research described in this report, I hope to help bridging the gap in knowledge between the individual and the community. It is devoted to the competition between populations and to the mechanisms that allow populations of different species to coexist in a stable equilibrium. These mechanisms determine the diversity and stability of a community.

The immediate occasion to this research was an experiment of Van den Bergh & Elberse (1975), (see also Van den Bergh and Braakhekke, 1978) with mixtures of grasses and grassland herbs. The results of this experiment indicated niche differentiation between some of the species. Although niche differentiation is expected to be important in plant communities it had rarely been demonstrated in experiments before. This justified further inquiries into its causes. The results of such fundamental research could also be of agricultural interest, e.g. for vegetation management, mixed cropping and weed research. In addition the opportunity could be used to exploit the potentialities of the competition theory of De Wit (1960) in studying equilibria.

The report is divided into two parts. In the theoretical part a simple frame work of conceptions and terms is presented (Chapter 2). As a starting point for further investigations various mechanisms that may promote species richness are discussed. (Chap-

ter 3). Some mechanisms are illustrated with the help of models based on De Wit's competition theory, which is briefly introduced (Chapter 4). The conditions for equilibria based on differential nutrient limitation are derived from a model of multiple nutrient competition (Chapter 5). These conditions show that stable coexistence between plant species is theoretically possible in homogeneous environments.

In Part II of this report two field trials are described that have been carried out to find an explanation for the results of the experiment of Van den Bergh & Elberse (1975). In a number of experiments under controlled conditions attempts were made to obtain experimental evidence for the equilibrium possibilities resulting from differential nutrient limitation. The aim was finding a suitable species combination and demonstrating the existence of a stable equilibrium ratio between plant species growing on water culture in a climate room.

Reading this report it is good to know that we did not attain our aim. This does not repudiate the equilibrium possibilities resulting from differential nutrient limitation. While our investigations were still running, Titman (1976) published results of competition experiments with fresh water algae demonstrating this possibility. The knowledge and time were lacking to improve our model to such an extent that it predicts the results of a competition experiment with terrestrial plants accurately enough, and to look further for a species combination meeting the equilibrium conditions amply enough.

Part I Theory

2 Terms and concepts

2.1 THE BALANCE OF NATURE

The concepts and terms given in this chapter have been adopted from general ecological literature, notably from Lewontin (1969) and Orians (1975).

Referring to plant communities the 'balance of nature' is defined as the permanent existence or the regular return of a particular structure of the vegetation. By structure is meant the species composition, number of individuals, age distribution and spatial arrangement of the populations in the community. Strictly speaking, such a balance cannot exist. Because of continual environmental fluctuations, disturbances and shifting of the balance brought about by gradual changes in the environment, the vegetation never returns exactly to a previous state. Therefore 'balance of nature' and related terms like equilibrium and homeostasis refer to the presence of mechanisms resisting and reducing changes in community structure rather than to the absence of changes. Disturbance of the balance implies that these mechanisms are put out of action, or are not strong enough to prevent extinction of a population.

2.2 EQUILIBRIA IN MODELS

To gain insight into the functioning of a community; it is useful to present the relations between the species in a model. In a deterministic model equilibrium can be formulated as a situation in which the population densities (N) do not change and are not zero:

$$N_t = N_{t+1} \neq 0$$

A more general case is the 'limit cycle' in which the densities are subjected to periodic changes but each time return to the same level. Because plant populations often exhibit such cyclic changes it will be more suitable to use their ratios, preferably at similar points in successive growth cycles, instead of using absolute densities in defining equilibria:

$$(N_a/N_b)_t = (N_a/N_b)_{t+1} \text{ or}$$

$$RRR_{ab} = (N_a/N_b)_{t+1} / (N_a/N_b)_t = 1$$

This double quotient is called the Relative Replacement Rate (De Wit, 1960; De Wit & Van den Bergh, 1965; see Section 4.4). It is comparable to the relative fitness used in population genetics.

2.3 DIVERSITY AND COEXISTENCE

The terms diversity, species density and species richness refer to the floristical richness of a vegetation. Species richness is the broadest of these terms. It refers to the number of species living together in a vegetation stand. Species density refers to the number of species per unit area. In grasslands an area of one to four square meters is usually taken for this. According to Grime (1973) herbaceous vegetation may be considered 'species rich' when the species density exceeds 20 species in one square meter; densities of more than 40 species per m² occur rarely. The term diversity is used when the species are weighted according to their importance. Equilibria between interacting populations contribute to all three kinds of floristical richness. Therefore the distinction between them is immaterial to the investigations presented here, so that the terms diversity, species richness and species density may be used interchangeably.

This report deals with the floristical richness of more or less homogeneous vegetation stands in which the species may be coexisting. Species are considered coexisting when their populations are truly living together in the sense of occurring within each others sphere of influence. Thus, when species are living in different habitats, whether or not because of competitive exclusion, they are not coexisting, except perhaps along the border of their habitats. This is not a matter of scale. It is also applied to micro-habitats within a vegetation stand that may look homogeneous on a superficial view.

2.4 STABILITY

The term stability can be used with respect to an equilibrium state or to a system that is in equilibrium. It refers broadly to a tendency to remain near an equilibrium point or to return to it after a disturbance. This statement reveals two aspects of stability: the ability to remain constant under environmental stress or disturbance, which is called inertia or resistance, and the ability to return to normal after a departure of the equilibrium state. The latter aspect corresponds to Lyapunov's definition of stability which is used by mathematicians. It is also termed resilience or elasticity.

The stability of a system finds expression in constancy and persistence. Persistence (survival time, or the ability to remain within an acceptable range) is brought about by both aspects of stability. Constancy (lack of variation) results only from the aspect called resistance. The constancy and persistence of an ecosystem may also be based on the stability of another system that is connected with the first and screens it from or buffers external disturbances.

In judging the stability of a system the level of observation and the sort of parameter one considers is decisive. An ecosystem may be highly variable on the level of individuals and genotypes and at the same time constant at the level of species composition; it may be variable in the species composition but constant in biomass or energy flow.

When we use the word stability in this report we refer only to the aspect of resilience, since our methods give no information about resistance. When the ability of

a population to return to its equilibrium density is independent of the size of the departure there is global stability. The rate of return is called the elasticity of the equilibrium. The return may be monotonous or with damped oscillations. When return is possible only after small departures there is local or neighbourhood stability. We will deal only with global stability (see Section 4.3, Equation 4.4, for a definition).

If a small departure causes a population density to move further and further from its equilibrium level the equilibrium is unstable. The boundary case between stable and unstable is called neutral equilibrium. In this case a departure is maintained without increasing or decreasing. Figure 1 illustrates these cases.

Besides departures of the population densities from their equilibrium states, environmental disturbances can also cause changes in other parameters and even in the fundamental structure of a system, so that it passes into a different system. If gradual changes in the parameters of a system cause a gradual shifting of the equilibrium state, the system is said to have structural stability. If this stability is great, i.e. when important external disturbances bring about only small changes in the equilibrium state, the system is robust. With structural unstable systems a change in the parameters has a qualitatively discontinuous effect on the equilibrium state. This is the case in systems with a neutral equilibrium: each change in an environmental or a system parameter makes the equilibrium disappear or changes it in a stable or unstable equilibrium. Equilibria based on such infinitely delicate weighing of parameters cannot exist in nature, because they would be disturbed by environmental fluctuations.

If for example the competitive relation between two species depends only on the temperature, one gaining at low and the other at high temperatures, with a neutral equilibrium at 20°C, one of them will be ousted when the temperature deviates only a fraction from 20°C. When the temperature fluctuates frequently below and above 20°C, now one species gains and then the other and it may take a long time before one species will suppress the other completely. However, we do not speak of an equilibrium in such a case.

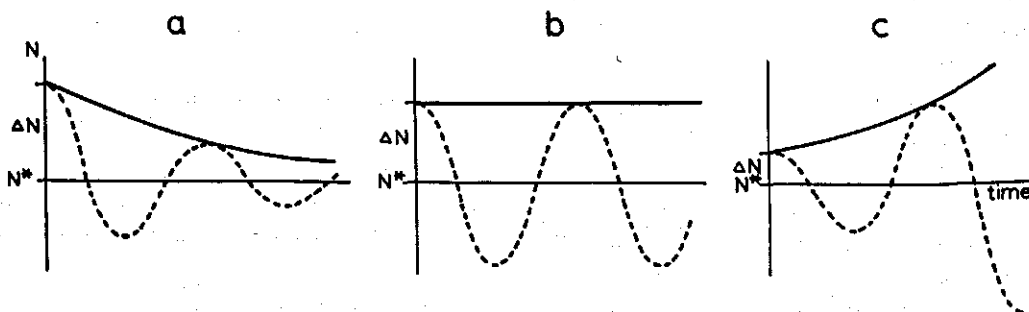


Fig. 1. Monotonous (continuous line) and oscillating course (interrupted line) of the population density (N), after a departure (ΔN) from the equilibrium density (N^*), when the equilibrium point is stable (a), neutral (b), or unstable (c). (After May, 1974)

2.5 COMPETITION

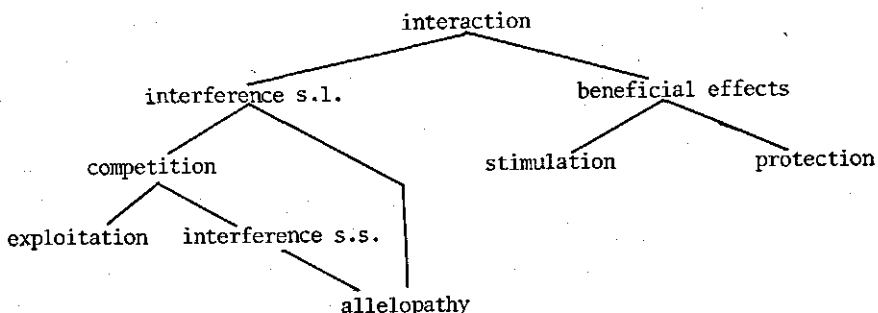
Since there is some discussion about the use of the term 'competition' (Birch, 1957; Harper, 1961; 1977: p. 727; Miller, 1967; Tinnin, 1972; Hall, 1977; Grime, 1977; 1978: discussion) I want to make clear how it is used in this report.

Competition is defined as a process of partition of environmental resources that are in short supply, brought about by the simultaneous demand of individuals, by which they mutually reduce their growth or reproductive capacity. This definition keeps close to the etymological meaning which is 'seek together' and to the general accepted use as proposed by Clements et al. (1929) and Donald (1963), which always involves 'combined demands' and 'mutual limitation' (Miller, 1967). Phrases like 'competition for different spaces' are incorrect unless it is meant that the individuals of one species are competing among themselves for another resource than the individuals of another species do. Strictly speaking species are not limited by competition, but by the availability of a resource that is reduced by the activity of competitors as well as the species itself. One should speak of 'severe competition induced stress' instead of 'severe competition', but there is little harm in a somewhat loosely use of the word. I reject however definitions that are derived from measurements or mathematics or such blunt statements like competition is anything which eliminates one of two sympatric species occupying the same niche (Kaplan & Yorke, 1977), because these lead to tautologies and semantics (Peters, 1976).

The word 'interaction' is preferred for all influences that individuals have on each other, regardless whether these are positive or negative, directly or intermediated by an influence on the environment. The word 'interference' is preferred for negative interactions or as Harper (1961) formulated it: 'those hardships which are caused by the proximity of neighbours', and not in the wider sense used by Hall (1974a). Competition is one form of interference.

Some problems may arise when it is tried to measure the partition of resources and to classify the mechanisms by which it is accomplished. The partition of a resource is commonly measured by the use that is made of it (growth, yield). In some cases it is possible to measure the partition directly (amounts taken up). Terms that are related to mechanisms of competition are exploitation and interference s.s. (Elton & Miller, 1954) and priority (Yapp, 1925). With exploitation it is indicated that the partition of the resource is accomplished merely by using it: 'Who eats fastest gets most'. With interference s.s. some more highly evolved strategy is indicated in which some form of space is substituted for a resource and is the proximate object of competition. The effect of interference s.s. is, therefore, to prevent the access of a competitor to a required resource. Territorial behaviour and possibly allelopathy are examples of this strategy. The partition is completed before the resources are actually used up in these cases (see Tinnin (1972) for a discussion of the ambiguous use of "interference"). Priority can be considered an extreme form of competition whereby one individual or species can take possession of all or more that it needs before another can get anything, either because it comes first in time or because it comes first in place (in the case of tall plants overshadowing smaller plants).

The relations between various terms are presented in the following scheme.



2.6 NICHE DIFFERENTIATION

The central question in studying the origin and maintenance of the balance of nature is: 'What qualities of species enable them to live next to each other without ousting each other?'. If we confine ourselves to species on the same trophic level, we are dealing with the principle of competitive exclusion or the 'Gause principle', which follows from theoretical considerations and can be formulated as: 'Species cannot live permanently in the same habitat unless they have different niches'. Because all species are per definition different the question is: What difference between species leads to niche differentiation in such a manner that they can coexist in the same habitat?

The often very loosely used term 'niche' deserves a further explanation. It is used in an ambiguous meaning as a 'distributional unit' and as a 'functional relationship', which leads to much confusion. (For a description of the history of the niche concept and the attempts at explaining the meaning we refer to Whittaker et al. (1973; 1975), Van Dobben (1974), Rejmanek & Jenik (1975), Grubb (1977) and Kroes (1977)). It seems that a uniform interpretation is unattainable for the present. This is not necessarily a problem when the meaning is indicated wherever the term is used. In the present report it is used as a functional relationship of a species to its environment. The term habitat is used with reference to a spatial relationship. Niche differentiation refers to a functional difference between species that leads not to spatial separation but instead to coexistence in one homogeneous environment. The formulation of the competitive exclusion principle given above illustrates this meaning.

From theoretical considerations it follows that a necessary condition for a stable coexistence is that the species populations are regulated in different ways. These considerations were developed and extended by Williams (1957), MacArthur & Levin (1964), Rescigno & Richardson (1965), Levin (1970), Maynard Smith (1974), Kaplan & Yorke (1977). Moreover Deakin (1975) showed that an ecosystem in stable equilibrium must contain at least one self-regulating species. Since regulation involves limitation the way of limitation is the crucial aspect of the niche. Therefore it is preferred to speak of different niches only, when species living in the same habitat are limited in different ways.

Ecologically, species differences can have two effects. In the first place, they

may separate the species because they are adaptations to different environments or at least cause different competitive abilities in different environments (habitat differentiation). Secondly, they may enable species to coexist in the same environment (niche differentiation). The same difference may cause both effects as will be shown later on. Both effects may play a part in the survival of the species. The consequences for the structure and functioning of the ecosystem are, however, profoundly different. It is therefore useful to distinguish between niche and habitat differentiation, because this will allow a better understanding of the pattern and diversity of vegetation.

It took long before the functional meaning of the niche was accepted in plant ecology. It was difficult to see how plant species could function differently enough to prevent competitive exclusion (Harper, 1967; Van Dobben, 1974). In contrast to animals plants have few possibilities to specialize on different resources in one habitat; they all have the same basic needs: light, CO₂, water and mineral nutrients. Although the existence of vegetation layers and synusiae and the presence of species with different life forms points to functional differentiation within a plant community, it was not clear how this differentiation could prevent competitive exclusion. Harper (1967) draw the attention to this. He referred to several experiments with species mixtures in which a tendency was observed to a stable equilibrium. In one case only it was clear what species difference was responsible, namely the difference in nitrogen source between legumes and grasses (Ennik, 1960; see also De Wit et al., 1966).

In the last decade the understanding of the equilibrium mechanisms has considerably increased. Levin's (1970) extension of the competitive exclusion principle showed that it is not necessary for species to use different resources; if only they are limited by different factors. Bradshaw (1969) already remarked: 'we need only to propose that plant species require different proportions of nutrients for stable cohabitation to ensue'. But he was not the first who came to this conclusion. He was foreshadowed more than a century ago by Justus Liebig (1843, p. 74) who wrote in his essay on alternate husbandry:

Die verschiedenen Pflanzengattungen bedürfen zu ihrem Wachstum und vollommen Ausbildung entweder die nämlichen anorganischen Nahrungstoffe, aber in ungleicher Menge, oder in ungleichen Zeiten, oder sie bedürfen verschiedener Mineralsubstanzen. Auf der Verschiedenheit der zu ihrer Entwicklung nöthigen Nahrungstoffe, welche der Boden darbieten muss, beruht es, dass manche Pflanzengattungen nebeneinander wachsend sich gegenseitig in ihrer Entwicklung hemmen, dass andere hingegen üppig nebeneinander gedeihen.

As far as I know there are no references on this subject of the period between Liebig (1843) and Bradshaw (1969).

Other density dependent factors such as predators and pathogens may also limit the growth of a population. Thus a large number of possible combinations of limiting factors is presented to explain stable equilibria between plant species. The next chapter reviews these possibilities.

3 Mechanisms maintaining species richness in grasslands

In studying the 'balance of nature' it is useful to have an overall picture of the mechanisms that are known to or may be expected to lead to stable equilibria between species, and thereby contribute to stability and diversity of the community as a whole. Since Harper (1977) attended for a great deal to this need, I will confine myself to a classification and a brief description of the mechanisms; for this I have also used the reviews of Trenbath (1974, 1976), Whittaker (1975) and Grubb (1977).

In the previous section it was mentioned that the fundamental condition for stable coexistence is that species are regulated in a different way. All mechanisms can therefore essentially be reduced to differences between species which under special conditions may lead to differences in place, time, factor or way of limitation, which may in turn lead to stabilization of the species mixture. To put it differently: for an equilibrium to ensue each species must be best in something, sometimes, some place or some way and the conditions must allow them to express this quality, which means that their growth must be determined mainly by the things they are good in.

Mechanisms can be grouped according to several criteria like working type, the environmental factors that are involved or the effects on community structure and dynamics. I chose the first criterion and start the list with some mechanisms that, strictly speaking, do not lead to coexistence but yet may contribute to the species richness of a vegetation.

3.1 MECHANISMS DEPENDING ON ENVIRONMENTAL HETEROGENEITY

Many plant ecologists explain the presence of different species within what is considered to be a homogeneous stand, by assuming horizontal micro-environmental heterogeneity, combined with differences between the preferences of species for the various micro-environments, each species growing in the microhabitat in which it is the best competitor (Thomas & Dale, 1976; Hickman, 1977; Platt & Weis, 1977). Several theoretical studies have been published on the effect of environmental heterogeneity on population biology. We will only refer to Horn & MacArthur (1972), Smith (1972), Roff (1975) and Levin (1976). Essentially this mechanism does not lead to real coexistence between species, but only to micro-monocultures ('non-coexistence equilibrium'). Harper et al. (1961) called this 'spurious cohabitation'. The small scale does not alter the fact that the species are excluding each other from their microhabitats; whereby the interactions are reduced to 'boundary disputes'.

Several investigations show that the occurring 'together' of species can indeed be explained in this way (Harper & Sagar, 1953; Sharitz & McCormick, 1973; Werner & Platt, 1976). Particularly seeds and seedlings may utilize the micro-environmental heterogeneity

to a very small scale. Grubb (1977) stressed the possibility that species may coexist because they differ in their 'regeneration niche', i.e. have different requirements during the replacement of old plants by young ones. This possibility, however, is severely restricted by the condition that the stabilization resulting from regeneration-niche differences should not be undone by competition in the later phases of life, which requires either approximately equal competitive ability or niche differentiation between the adult individuals.

The micro-environmental heterogeneity may result from many causes. Two main aspects are worth notifying:

- heterogeneity may be permanent or transient;
- heterogeneity may be allogenic or autogenic with respect to the vegetation.

These categories differ in their effect on species strategies and community structure. Species that are adapted to microhabitats of a transient nature must be able to jump over to other microhabitats by means of efficient vegetative or generative dispersion ('fugitive species in a harlequin environment', Horn & MacArthur, 1972) or to consolidate the conquered place. The vegetation will show a continuously changing mosaic pattern. Examples of transient heterogeneity are abundant, most are due to animal or human activities or plant influences (autogenic heterogeneity). Most of the permanent heterogeneity is due to edaphic and topographic differences.

Table 1. Causes of species richness in grasslands.

-
1. *Spatial differentiation between species* (spurious cohabitation or 'non-coexistence equilibrium').
Depends on micro-environmental heterogeneity combined with habitat differentiation.
Types of heterogeneity: permanent + transient; allogenic + autogenic.
 2. *Continuous immigration and extinction of species in each others habitat* ('non-equilibrium coexistence').
Depends on environmental heterogeneity and habitat differentiation.
 3. *Temporal differentiation between species* ('non-equilibrium coexistence' or 'Pendelsuccession').
Depends on environmental fluctuations and habitat differentiation.
 4. *Functional differentiation between species* ('stable equilibrium coexistence').
 - 4.a Differential resource use.
 - 4.a.1. Different limiting resources; depends on qualitative or quantitative differences in resource use (air and soil nitrogen).
 - 4.a.2. Different place of resource use; depends on different abilities to reach a resource (rooting depths).
 - 4.a.3. Different time of resource use; depends on different growth periodicity, endogeneously or imposed (early and late species).
 - 4.a.4. Different efficiencies of resource use; depends on spatial or temporal differences in availability of a resource, caused by activities of competitors (light and shadow plants).
 - 4.b Differentiation with respect to other regulating factors (predators, parasites, pathogens).
 - 4.c. Other mechanisms
 - 4.c.1. Allelopathy and autotoxicity.
 - 4.c.2. Beneficial effects between species (protection, commensalism).
 - 4.c.3. Genetic feed-back (in combination with differential resource use).
 - 4.c.4. Different responses of resource allocation to competition.
-

Autogenic heterogeneity is worth special attention when we are interested in species richness. By influences on microclimate, root activities and litter effects the plants produce heterogeneity themselves. This may affect species density in two ways. Firstly, the conditions for other species may be relatively improved, thus leading to coexistence, a shifting mosaic pattern or succession. This subject is discussed in considerable detail by Fox (1977) and Connell & Slatyer (1977). Secondly, the conditions for other species may be relatively deteriorated, thus leading to species poorness and course patterns. It is known that dominating species may create or leave possibilities for subordinate species to live in their neighbourhood. It should not be forgotten, however, to solve the question how the dominant species is prevented from excluding the subordinate species and vice versa.

Another result of environmental heterogeneity is that there may be 'non-equilibrium coexistence' within microhabitats, resulting from a continuous immigration and extinction of species in each others microhabitats (May, 1974). When this immigration is by means of seed propagation, large distances may be bridged and the underlying heterogeneity may not be very obvious.

From the above it will be clear that micro-environmental heterogeneity may play an important role in determining species density, also in grasslands where animal and human influences are often very pronounced. However, heterogeneity on a scale smaller than the size of the individual spheres of influence may not be very important. In most grassland vegetations the individuals of different species are in such intense contact and intermingled above and particularly below the ground, that horizontal micro-environmental heterogeneity certainly cannot be the only factor that is responsible for the high species densities observed.

3.2 MECHANISMS DEPENDING ON ENVIRONMENTAL FLUCTUATIONS

Many ecologists, probably intuitively, feel that in continuously changing environments species may continue living together if they are alternately the strongest competitor (Grubb, 1977; Grime, 1978). Hutchinson (1971), dealing with the 'paradox of the plankton', argued that environmental fluctuations may prevent that an equilibrium is achieved, thereby promoting 'non-equilibrium coexistence' between species that otherwise would exclude each other. This can be considered as an analog in time to the effect of environmental heterogeneity, which promotes instead a 'non-coexistence equilibrium'. Recently, an interesting contribution to this field was made by Huston (1979), who showed that this component of species diversity (non-equilibrium coexistence through continual interruption of competitive exclusion by environmental variability) has an optimum which is determined by a balance between environmental variability and favourability.

Environmental fluctuations alone, however, cannot prevent extinction in the long run, except when the fluctuations are exactly around a mean value where the species match each other. As mentioned before, exact equalities are infinite improbable in nature (which has been called the 'axiom of inequality' (Hardin, 1960)). This possibility can therefore be repudiated with the same right as in the non-fluctuating environment.

The situation is different when the fluctuations are accompanied with some density

or frequency-dependent mechanism that reduces the chance of total extinction. Environmental heterogeneity may provide such a mechanism. In fact the transient microhabitats discussed before are an example of combined environmental heterogeneity and variability that promotes non-equilibrium coexistence. Another example is the instable 'now and then' type of border region, between different environments, where species live together in a 'pendelsuccession' (Van Leeuwen, 1966). Exogenous perturbations causing periodic, proportional reductions of the species populations may lead to dynamic equilibria in model ecosystems (Tuljapurka & Semura, 1977). According to these authors, self-regulation of the species is an important factor in making such equilibria possible. It is also possible that resources are delivered in a discontinuous way or that species create fluctuations by removing resources in a discontinuous way. This will be discussed in Section 3.3.1. In most combinations of environmental variability with stabilizing mechanisms the variability itself plays no essential role. Several theoretical studies show that the main effect of variability is a decrease in the species density rather than an increase (Smith, 1972; May, 1974).

3.3 MECHANISMS DEPENDING ON FUNCTIONAL DIFFERENTIATION BETWEEN SPECIES

From the previous sections it is clear that spatial heterogeneity and to a less extent variability of the environment contributes to the maintenance of species density, but that they cannot explain all of it. In addition to habitat differentiation, which is the common ground of the above effects, functional differentiation is likely to contribute to the reduction of competitive interactions. In Section 2.5 it was mentioned that this functional differentiation should lead to a difference in the way of population regulation in order to do so.

There are many factors that influence plant growth and population density. It was argued by Hairston et al. (1960), see also Slobodkin et al. (1967), that the trophic level of primary producers in general will be resource limited. Differentiation with respect to resource use may therefore be expected to be important in reducing competition between plants. This is niche differentiation in the familiar Eltonian sense. Besides resource limitation other factors may play an important role in the regulation of population density of the separate species, e.g. predators, pests, parasites and abiotic factors. Differentiation with respect to these factors is also considered as niche differentiation, in a more extended but still functional sense. First differential resource use will be discussed.

3.3.1 . *Differential use of resources*

For plants the most obvious possibility of differential resource use: the use of different resources, is rather restricted, because all plants need basically the same elements and these are presented to them in a rather undifferentiated way. This is unlike the resources of animals, in which most of the basically required elements are presented neatly packaged together in a very differentiated way.

Among the few possibilities the differentiation in the forms in which nitrogen can

be taken up is the most conspicuous. Nitrogen may be taken up as NO_3 , NH_4 , urea, N_2 (with the help of root-nodule bacteria), from dead organic substances (with the help of mycorrhiza) and even from living animals (by insect eating plants). Species differences in the amounts of mycorrhizal roots result also in differentiation in the uptake of other elements, notably phosphorus. Differences in substrate type used by the fungi involved, combined with host specificity, might also contribute to reducing resource competition between host plants. It is suggested that mycorrhiza are very important in natural ecosystems, not only for their role in the nutrient recycling, but also for their influence on plant species composition and density (Mosse, 1978; Fitter, 1977).

Quantitative rather than qualitative differences in resource use offer the better possibilities of competition avoidance between plants. The fact that plant species differ in their relative nutrient requirements and uptake abilities is well established (see for example Chapman (1966) and Collander (1941)). Much literature is reviewed by Andrew & Johansen (1978) and Robson & Loneragan (1978). Species that grow closely together in the same vegetation often show different mineral compositions (Thomas et al., 1952; Vengris et al., 1953; Van der Kley, 1957; De Vries & Dijkshoorn, 1961; Gerloff et al., 1966; Horak & Kinzel, 1971). Strangely enough, these differences have been considered mainly as adaptations to different habitats and their possible role in reducing competition was hardly recognized (see however Liebig (1843), Bradshaw (1969) and Woodwell et al. (1975). Only recently this last possibility has been proposed for phytoplankton communities as an alternative to Hutchinson's (1961; 1965) solution of the 'paradox of the plankton' (Philips, 1974; Stewart & Levin, 1973; Petersen, 1975; Tilman, 1977). An important objective of the research presented in this report is to investigate the potential role of this mechanism in terrestrial plant communities; details will be discussed hereafter.

Apart from the above mentioned differences in resource use, leading to limitation by different resources, coexistence of plant species in homogeneous environments may also be allowed by differences in the use of one and the same resource, viz. by differences in place, time and efficiency of use. These mechanisms are closely related to, often accompanied by, but not necessarily dependent on the heterogeneity and variability of the environment discussed in Sections 3.1 and 3.2.

With differentiation in the place of resource use, we think of different rooting depths or soil-pore diameters (Sheikh & Rutter, 1969). Especially the differences in rooting behaviour are very conspicuous and well known owing to the extensive work of Weaver (1958) and others (Coupland et al., 1965). When two species limited by the same nutrient obtain this nutrient from different soil layers, coexistence is possible (Parrish & Bazzaz, 1976; Ernst, 1978; Yeaton et al., 1977). For this it is not necessary that the soil layers are chemically or physically different. Such differences may accentuate as well as reduce the differences in root distribution when the species have different or equal preferences for soil properties respectively. The equilibrium possibilities resulting from differential rooting patterns have been investigated theoretically and experimentally by Berendse (1979, 1980). One important condition is that the species with the shallowest roots is the best competitor in the upper soil layer.

Differences in the time of resource use may also lead to coexistence between species

that are limited by the same resource. Phenological spread is a well-known phenomenon in many vegetations ranging from arable land to grassland and deciduous woodland. Much attention has been paid to the distinct differences in flowering time. How this has to be translated into terms of differential resource use is uncertain. One might think of a reduction in the competition for pollinators (Parrish & Bazzaz, 1979). It is however hard to imagine that pollination is such an important limiting factor in our grasslands that differentiation with respect to this factor can contribute to the stability of the community (Harper, 1977, p. 719). Probably the flowering patterns are mainly a reflection of the phenological spread of vegetative activities which will overlap much more, because they cover much longer periods.

The reasoning that differences in the timing of the vegetative activities can contribute to the coexistence of species is mostly intuitive. There is little experimental evidence. The most conclusive experiments are those of Schepers & Sibma (1976) with early and late potatoes. Many other experiments give only indications (Van den Bergh & De Wit, 1961; Putwain & Harper, 1972; Khan et al., 1975; Al-Mufti et al., 1977). To permit this kind of coexistence one obvious condition has to be met: the early species must not be able to consume all of the limiting resource. This means that the resource must be delivered continuously (not the 'stock' but the 'flow' is limited) and that the early species ceases growth for some other reason than food shortage (e.g. adverse conditions or some endogenous rhythm).

When the limiting resource is delivered in a discontinuous way ('seasonable mode', Stewart & Levin, 1973) there is also a possibility of coexistence between species, viz. when they have different uptake efficiencies (not to be confused with use efficiencies). When one species takes up rapidly but only at high concentrations of the resource in the environment, and another species takes up slowly, but also at low concentrations, they can coexist when the limiting resource is discontinuously supplied at high concentrations and exhausted afterwards (exhaustion is implicit in the limitation when the 'stock' instead of the 'flow' is limited). Grenney et al. (1973) showed that temporal variations in flow rates and nutrient supply allow coexistence of phytoplankton species in chemostat conditions, where all species were nitrate limited.

Another possibility is that the resource is delivered continuously, but that the uptake is discontinuous because there is an unfavourable period for both species. This results in a temporary accumulation of the limiting resource of which the rapid but inefficient species may profit. After some time the combined uptake activities of the species will have lowered the concentration so much that the efficient species can only use the resources supplied, until the next unfavourable period begins.

Differences in uptake efficiency of one and the same resource may contribute to coexistence only if the resource is presented at different concentrations, which compels combination with differences in time or place of supply. When the resource is presented at one concentration only, either the inefficient species cannot survive or the efficient species is not limited by it.

In the above two cases differences in efficiency act in combination with temporal variations in resource supply or in other conditions. Coexistence is also possible when differences in efficiency are combined with differences in position with respect to a

resource e.g. the sun or ground water. Dominant species that are closest to the resource may be unable to absorb the limiting resources completely. This permits coexistence with subordinate species that are adapted to utilize 'the crumbs of the rich man's table' (Harper, 1977). Tree species will probably not produce leaves in the lower regions where the light intensity is below their compensation point, thus allowing some light to pass through that can be used by understorey species with a lower compensation point. It is however unlikely that comparable phenomena occur in grasslands, because most grassland species are 'sun plants' (Ludlow, 1978, p. 46).

Complementary to the approach followed above, dealing with differentiation of resource use by the way of differentiation, we can take the different limiting resources as a lead and investigate the possibilities of coexistence, when they are limiting one or more species. This requires, however, much more specific knowledge about the resources -how they are presented in space and time, their form and mobility and the way they are used and needed by the species- than the above, rather general, approach, and it is more useful in the context of a specific case.

3.3.2 *Differentiation for other regulating factors*

Factors, other than resources, that may limit plant population density are predators, pathogens, parasites and abiotic factors. Dealing with grasslands the predators, including man, deserve our special attention, because in many cases their continual activity is the main reason that further succession of the grass vegetation to a climax vegetation ceases. Apart from preventing the ingression of late successional species, predators may also modify the relation between the species present, in such a manner that their coexistence is possible. Species that are weak competitors for nutrients or light may persist, because the stronger competitors are controlled by predators or pathogens (Paine, 1966; Trenbath, 1977).

The importance of predators in the vegetation is increasingly appreciated (Harper, 1969; 1977). It is realized that predation and competition are complementary (Menge & Sutherland, 1977), rather than mutually exclusive (Pianka, 1966). The combination of both may be essential in the stabilization of species-rich communities (May, 1973; Maynard Smith, 1974). It is however difficult to investigate the effect of predation on the structure and functioning of plant communities and to derive equilibrium conditions, because predation is not a simple constant factor. Stabilizing effects will be difficult to distinguish, because of the fluctuation in population densities that seems to be characteristic for predation, especially in simple ecosystems which are among the first to be investigated. Heterogeneity of the environment is often increased by predators, which makes it difficult to recognize the predation effect. Experiments with natural vegetations and their component species will therefore be hard to interpret and give only incomplete insight in the role of predation. However, in addition to theoretical considerations, experiments under controlled conditions with simple ecosystems like bacteria and phages (Levin et al., 1977; Chao et al., 1977) give strong indications of the importance of predation.

More or less the same remarks can be made with regard to the influence of pathogens and parasites. The abiotic factors, other than resources, e.g. climate, soil physical factors etc., have already been discussed as far as their spatial heterogeneity and variability are concerned. Apart from this they are supposed to have only a modifying, but not a stabilizing effect on the relation between species, because they act independently of the density or frequency of the species. Whenever it is observed that changes in abiotic factors affect the coexistence of species it must be because they modify the extent to which stabilizing mechanisms can work.

3.4 OTHER MECHANISMS

3.4.1 *Allelopathy*

It is known that, besides removing resources from the environment, plants may have still other detrimental influences on each other by adding harmful substances to the environment. These substances, called allelochemicals (Whittaker & Feeny, 1971), may affect organisms of the same or other species; they may be excreted by living plants or released from dead parts, actively, passively or intermediated by the activity of other organisms like bacteria. Many reviews have been published dealing with this subject, recently by Rice (1974, 1977) and Eussen (1978). A plea for the widespread occurrence and importance of allelopathy in natural communities was made by Whittaker (1970). A more sceptical and critical comment was given by Harper (1977).

The adaptive value, if any, of released substances toxic to the releasing plant and its congeners (auto-inhibitors), is rather paradoxical. They may be defense mechanisms against predation. Perhaps they prevent overcrowded populations and their negative effects as territorial behaviour does with animals. The supra-optimal density effects discussed in Section 4.9.7. could be reduced in this way. On the other hand it may be that auto-inhibitors cause these very effects, namely, when they are released later in the season and reach toxic concentrations only in dense populations. Perhaps auto-inhibitors are released only, because they are wastes that do more harm within the plant than outside.

It is not intended to review this controversial matter nor to shed a new light on it. We only suggest that auto-inhibitors may affect the species equilibrium, because they gradually vitiate the environment of a plant and reduce its competitive ability. When this plant dies, of self-intoxification, of competition-induced starvation, or of other causes, it leaves a site where no individual of its own species can thrive for some time ahead. When this species is able to exploit new sites frequently, because it is a strong competitor initially, or because other species are also self-inhibiting, or for other reasons, a continuous alteration of species will be observed (Fox, 1977). This was already referred to in Section 3.1 as a form of autogenic transient micro-environmental heterogeneity leading to spurious cohabitation.

The adaptive value of substances that reduce the growth of other species is easier to understand, because together with growth the competitive ability of the other species will be reduced. This can be considered as a form of interference s.s. (see Section 2.5) in which a competitor's access to a resource is impeded otherwise than by taking it up.

The term ' α -selection' was introduced by Gill (1974) as a supplement to the concepts of r- and k-selection, to denote selection for the ability of interference competition.

As this mechanism intensifies the competitive interactions it seems improbable that it might contribute to the realization of species equilibria. However, one possibility was mentioned by Newman & Rovira (1975), namely that 'allelopathy provides a form of self-balancing negative feedback in the community'. They argue that 'nutrient deficiency can increase the amount of toxic substances in a plant. If the amount exuded is also increased, and if the substances are more toxic to the other species than to the species producing them, then a species doing poorly in direct competition for nutrients would automatically increase its ability to suppress its competitors by allelopathy'. This mechanism may lead to equilibria between species because the gross competitive ability (allelopathic plus competitive ability) increases with the negative impact of competitors on the nutritional status of a species, which will be greatest at low frequencies of that species when it is losing.

3.4.2 *Mutualism*

Plant species may exercise on each other one-sided or reciprocal beneficial effects. The well-known, commercially exploited example is that grasses may profit from rhizobially fixed air nitrogen, released by legume roots. Perhaps more common in natural vegetation is that plants protect each other from the harshness of the environment, e.g. against heat, desiccation, wind, cold, predation, heavy rain and hail damage. More direct beneficial effects from other plants are experienced by parasites, epiphytes and liana's. Interesting possibilities needing further investigation are that species cure nutrient deficiencies (Trenbath, 1976, p. 154) or prevent salt damage (Progrebniak, 1962; De Ridder, 1976) to neighbouring plants of other species.

Because of anthropocentric habits of thought the possibility that plants might coexist because they benefit from the presence of each other, appeals much to the imagination, which carries a risk of overvaluing it. In general, however, beneficial effects do not enhance the stability of a community (May, 1974). Mathematical analysis of Lotka-Volterra models suggests that in nature mutualism is less common than competition and predation (Goh, 1979). Rather specific conditions have to be met. Beneficial effects promote coexistence only, if they compensate for the negative influences of the 'benefactor' on the 'beneficiary' and if of the other hand the beneficiary is not able to exclude his benefactor. Therefore the effect must depend on the continuous presence and frequency of the benefactor, on the understanding that it is stronger as there are more benefactors per beneficiary. At high frequencies of the benefactor its positive influence has to predominate, otherwise there is no benefit at all; at low frequencies its negative effect has to predominate, otherwise it would be excluded and succession would be the result.

Beneficial effects are not easily recognized. A close positive correlation of the occurrence of two species is certainly not enough, because this may be simply a result of equal habitat preference in combination with niche differentiation. When woodland herbs occur only together with tree species, this may be because they are niche differentiated with respect to the tree species and experience too much competition from free

land herbs outside the wood. That the negative influence of the tree species is greater on the free land species than on the woodland species can hardly be considered as a beneficial effect. Experiments are needed to assess the occurrence and the size of beneficial effects and their necessity for coexistence.

3.4.3 *Genetic feedback*

According to Pimentel (1968) a genetic feedback mechanism may enable species to coexist and utilize the same thing in the ecosystem, when they are fairly evenly balanced in their competitive ability. He argued that selection under intraspecific competitive pressure is not the same as under interspecific competitive pressure, and that their effects are in fact conflicting. Depending on its frequency a species in a species mixture is selected for intra- or interspecific competitive ability. When after several generations this selection becomes fruitful, the frequency of the species begins to change in favour of the minor species, which has improved its interspecific competitive ability as opposed to the major species which neglected it. Within some generations the minor species will become major and the process is reversed. This results in oscillations with period and amplitude depending on the time lag between, and the rates of the changes in genetic composition of the species composition of the mixture.

Pimentel provided also evidence supporting the concept of genetic feedback, but the nature of the genetic changes is still unknown. The simplest explanation would be that one (or both) of the species A and B consists of two genotypes: A_1 strong in intraspecific competition, and A_2 strong in interspecific competition ($A_1 > A_2$ and $A_2 > B$). For the genetic feedback to work it is necessary that B is stronger than A_1 , which results in a circular order of competitive ability ($A_1 > A_2 > B > A$). This demonstrates that Pimentel's suggestion that genetic feedback enables coexistence of species occupying the same niche, is not correct. There must be some form of niche differentiation involved. Competition between A_1 and A_2 has to be for another resource or in a different way than competition between A_1 and B or A_2 and B, the circular relationship not being possible otherwise. This follows in fact directly from the assumption that intraspecific competition is not the same as interspecific competition, and that an individual can be good in one and bad in the other.

3.4.4 *Differences in resource allocation*

Trenbath (1976) suggested an ecologically interesting mechanism that may lead to equilibria. He argues that the relative proportion of dry matter allocated to seeds may vary with the degree to which a plant is suppressed by competition with neighbours, and that species may show different responses: one increasing and another decreasing its relative investment in seeds with increasing weight per plant. Trenbath shows that when a strong competitor having the first response, is combined with a weak competitor having the second response the total seed production of a mixture may exceed the seed production of the monocultures which, as we will show, indicates a possibility for an equilibrium. Species reproducing mainly by seeds might thus coexist, when they have contrasting stra-

tegies of resource allocation to seeds. The same mechanism might work with respect to other organs responsible for reproduction, like rhizomes or storage roots.

3.5 DISCUSSION

The preceding survey of mechanisms that may contribute to the species richness of plant communities is not meant to be an exhausting review of the literature. Perhaps more categories of mechanisms can be distinguished; certainly more examples can be given of each category. It is anyhow clear that we are not at a loss for possible explanations of species coexistence. The division in categories is to facilitate thinking about this complex matter. There may be doubts whether a specific case belongs to one or another category, especially with the mechanisms discussed at the end of Section 3.3.1. However, because the possibilities and limitations of every mechanism should be investigated separately and not as a member of a category, no time should be wasted in meditating on its place in the scheme.

All mechanisms resolve into the principle that the qualities of the species are played off against each other, in such a manner that each species profits from its specific abilities. This requires that at least two pairs of things are different. Firstly, the species must be different in two aspects, which is obvious because each must be better in something. Secondly, some difference in external conditions is involved, e.g. different conditions in space or in time, two different resources or predators. In many mathematical models of species interactions the roles of species characteristics and environmental conditions are merged in some interaction coefficient. It is however important to distinguish between these roles when we are interested in the question why some species combinations can coexist in one place and not in another, or why in some place one species combination can coexist and another cannot.

The environmental conditions in some site can meet the conditions for coexistence of more or less species combinations simultaneously. This explains why the species density is higher at one place than at another. The number of potentially limiting factors is of great importance in this matter. The following line of thoughts illustrates this point.

When in some hypothetical place a resource is abundant and not limiting any of the species coexisting in that place, differentiation with respect to the use of that resource cannot contribute to species richness. If one could reduce the availability of that resource it would become limiting; at first to a species that is inefficient in the uptake or the use of it. As a result the resource that was limiting this species before, will be used less efficiently. Possibly some is left unused, since the other species present can neither use it, because they are limited by other factors. A species excluded before may enter the community, if it is able to manage on the left-overs. A further reduction in the availability of the resource first mentioned will induce a second species to be limited by it. When there is an appropriate difference between the two species limited by this resource, with respect to its use, they can continue coexisting.

The possibilities of coexistence of species limited by the same resource are however not endless. The conditions for coexistence will be increasingly hard to meet,

when more species are limited by it and at further reduction of the ability species will begin to exclude each other. When availability becomes extremely low and unbalanced with respect to the other resources, taking into account the requirements of the species at hand, only one limiting factor will predominate and the species richness will be determined by the conditions that set the number of species coexisting on one resource, e.g. environmental variability.

Since nutrient shortages can be regarded as a form of stress, we have just explained the relationship between environmental stress and species richness proposed by Grime (1978), namely an increase of richness at moderate stress and a decrease at extreme intensities of stress. At the same time it is evident that the intensity of stress in general is inappropriate to characterize the influence of the environment on species coexistence. It is not so much the severity of the shortages that determines the influence on coexistence, but their balance or imbalance which in turn determines the number of potentially limiting factors. When we reduce the availability of all resources simultaneously instead of that of only one resource, we interpret this as more stress; expectations are, however, that richness decreases to a less extent or not at all. When we increase the availability of all resources except for one, we interpret this as a greater relief of stress than increasing only one resource; we expect, however, richness to decrease to a much greater extent (the latter is seen in highly manured grasslands where light is the predominant limiting resource).

In this view species poorness will often be determined by a single cause, whereas species richness has no simple explanation (if it is not accepted as an explanation to say that there are no reasons for richness to be low). Each species present has its own way of surviving and deserves its own explanation. Thus, explaining diversity requires a diversity of explanations. Speaking in general terms of stress, disturbance and competition does not help much. It is necessary to specify different types of stress and disturbance, and competition for different resources. The differences and similarities of species in their response to these matters determine whether they can coexist or not.

The above illustrates a way of thinking. It is simplistic in so far as it is suggested that population density is regulated by one master factor only. In natural populations resource limitation as well as predators and pathogens will play a role. Equilibrium mechanisms may complete or reinforce each other. For example, different rooting depths combined with different habitat preferences permit a calcifuge and a calcicole species to coexist, where acid soil lays on top of a calcareous underground (Lotschert, 1952). Different growth periods will often be combined with or imposed upon by different efficiencies. Nutrient shortages may reinforce or counteract each other: sodium supplied to grasses may reduce their potassium requirement (Smith, 1974); magnesium may interfere with calcium uptake (Section 7.4).

Nitrogen is known as an almost universal limiting factor. Disregarding competitive effects, one would expect most species in a species rich grassland to react positively on a moderate nitrogen dressing. At first sight this would be in conflict with the fact that only few species can coexist on one limiting resource. It is however conceivable that other resources and conditions interact with the nitrogen requirement, which makes niche differentiation with respect to the use of one master factor feasible.

Two-species interactions are only a first step in the analysis of coexistence mechanisms. Addition of a third species may destroy or create equilibrium possibilities or reverse the dominance between two species. Diffuse competition (Pianka, 1974) and indirect interaction (Levine, 1977) may be important. Mechanisms will change and disappear from time to time because of the fluctuating environmental conditions.

The complexity of population regulation as expressed above, will generally hamper the determination of which mechanisms contribute to the diversity in an actual vegetation. The first thing to do is to investigate theoretically and experimentally the separate mechanisms and the conditions under which they can effect coexistence. Attempts to do so for one mechanism are described hereafter.

Then a comparative study should be made of the factors that regulate the population densities of species in one and the same actual vegetation to see whether there is some differentiation and whether this suffices to explain the coexistence. We suggest a combination of descriptive and experimental approaches. Close observations may reveal much about the regulating factors, e.g. observations on phenology, rooting pattern, deficiency symptoms, pathogen and predator damage, chemical composition. With selective experimental treatments to reinforce or reduce the separate regulating factors, preceded and followed by detailed observations, the importance may be tested of the possible regulating factors revealed by the observations, e.g. addition of nutrients, watering, shadowing, clipping, fencing, fungicide and insecticide treatments, sowing, transplantations, species removals, root cutting, etc.

With regard to resource limitations in the field, these are considered to operate mostly without distinct and recognizable symptoms ('hidden hunger') and one has to resort to chemical analysis for diagnosis. This requires much insight in the relation between chemical composition and growth rate of a plant. We therefore urgently need more quantitative and comparative research on growth under suboptimal conditions of many kinds and especially in many combinations.

4 The competition model of De Wit

Since competition is considered the most important means of interaction between plant species, a good description of the competition process and its results is indispensable in understanding equilibria between plant species. After comparing the different methods to analyse competition experiments, Trenbath (1978) concluded that the model of De Wit is most suitable for ecological purposes. This model describes the results of competition rather than the process itself.

A description of the model will be given emphasizing equilibria. (For a more comprehensive description we refer to De Wit (1960) and Van den Bergh (1968)). After this, we will explore the possibilities of the model for the description of some more complicated ways of competition.

4.1 THE REPLACEMENT DIAGRAM: RYT

Competition between plant species can be studied best in experiments based on the replacement principle. The growth of two species (a and b), measured by their yields per area (O_a and O_b) in a series of mixtures with different initial plant frequencies (Z_a and Z_b) but the same total plant density ($Z_a + Z_b = \text{constant}$, or $Z_a + cZ_b = \text{constant}$, when one plant of b replaces c plants of a) is compared to the growth in monocultures, measured by the monoculture yields, M_a and M_b . Except for the competitive situation all the conditions are kept equal. The relative plant frequencies are defined by:

$$z_a = Z_a / (Z_a + Z_b) \text{ and } z_b = Z_b / (Z_a + Z_b)$$

The relative yields are defined by:

$$r_a = O_a / M_a \text{ and } r_b = O_b / M_b$$

The absolute or relative yields can be plotted in replacement diagrams (Fig. 2) against the relative plant frequencies that are plotted in opposite directions. When two species are competing equally strong an individual does not sense a difference between the presence of an individual of its own species and one of the other species (interspecific competition equals intraspecific competition). We expect in this case a linear relationship between the relative frequency of a species in a mixture and its share of the resources ('space' in De Wit's terms). It may, however, be that they have different efficiencies in using the resources obtained for growth. Therefore, the monoculture yields may differ. This difference is eliminated by plotting relative yields in the replacement diagram (Fig. 2b). A linear relationship is also obtained, when the

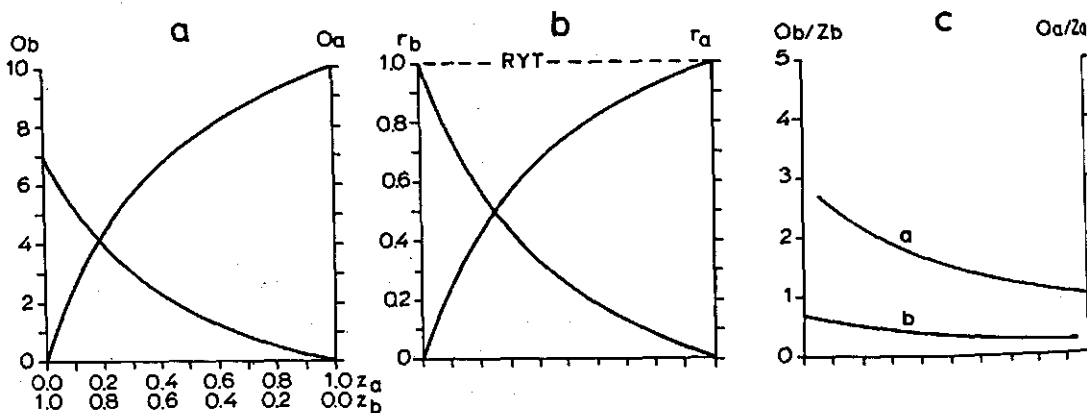


Fig. 2. Replacement diagrams of two competing species (a and b): (a) absolute yields; (b) relative yields; (c) per plant yields. The curves are calculated according to the Equations 4.3 with $k_{ab} = 3$; $M_a = 10$; $M_b = 7$ and $Z_a + Z_b = 10$. Explanation and symbols in text.

total plant density was so low that individuals did not yet interact at the time of observation.

If an individual is less depressed by the presence of an individual of the other species than by one of its own species, it profits from the replacement of its equals by individuals of the other species, which is seen from the per plant yields (Fig. 2c). The relative yield of this species in a mixture will be greater than its relative plant frequency. Since both values run from zero to one, this will give a convex curve in the replacement diagram.

In most experiments a convex curve of one species is accompanied by a concave curve of the other species, in such a way that the sum of the relative yields (Relative Yield Total: RYT) equals one (Trenbath, 1974).

$$RYT = O_a/M_a + O_b/M_b = 1 \quad (4.1)$$

The gain of one species goes together with a loss for the other species; apparently they are dependent upon the same resources. From $RYT = 1$ we can conclude that the species in the present experiment have the same niche.

4.2 THE RELATIVE CROWDING COEFFICIENT: $k_{ab} \cdot k_{ba} = 1$

De Wit (1960) derived equations for the yields in the competition experiments just described. He assumed the ratio of the yields of the species to be proportional to the ratio of the initial plant frequencies and the ratio of the monoculture yields with a proportionality coefficient, k_{ab} , which he called the relative crowding coefficient of species a with respect to species b:

$$O_a/O_b = (Z_a/Z_b) (M_a/M_b) k_{ab} \quad (4.2)$$

Assuming that the species crowd for the same space the following equations can be derived from Equations 4.1 and 4.2:

$$O_a = k_{ab} z_a (k_{ab} z_a + z_b)^{-1} M_a \quad (4.3a)$$

$$O_b = z_b (k_{ab} z_a + z_b)^{-1} M_b \quad (4.3b)$$

Equation (4.3b) may also be written as:

$$O_b = k_{ba} z_b (k_{ba} z_b + z_a)^{-1} M_b \quad (4.3c)$$

with

$$k_{ab} k_{ba} = 1$$

The relative crowding coefficients determine the curvature of the curves in the replacement diagram. It has been shown that the results of many competition experiments may be described by Equations 4.3. The k -values depend on the experimental conditions and the harvesting time and, if the species have different growth rhythms, also on the total plant density (De Wit, 1960). Sometimes, it is found in experiments that the k -value depends on the plant frequency, which results in sigmoid replacement curves. These interesting cases are discussed in Section 4.10. In the rest of Chapter 4 it is assumed that k -values are frequency independent.

In some experiments the RYT turned out to be greater than one (Trenbath (1974) gives a review of these cases). A gain in relative yield of one species in a mixture is in these cases not completely compensated by a loss in relative yield of the other species. In agricultural terms this means that, to obtain the same yields of two species, a greater area is needed sowing them separately than sowing them in a mixture: a mixture makes better use of the environmental resources.

In ecological terms this means that the species do not crowd for exactly the same 'space': growing in the same field they use somewhat different resources. So an RYT > 1 indicates some form of niche differentiation. When the curves of the two species are convex it implies for both species that intraspecific competition is greater than interspecific competition. This is a well-known condition for the existence of a stable equilibrium between competing species. We will first examine how a stable equilibrium can be defined in terms of De Wit's model and then show that in most cases RYT > 1 is indeed one of the conditions.

4.3 THE RATIO DIAGRAM

The long term course of the competitive exclusion can be deduced from short term experiments using a ratio diagram (Fig. 3). A ratio diagram shows on logarithmic scales the relation between population ratios of two species at two moments in a series of mixtures with different initial ratios in accordance with the replacement principle.

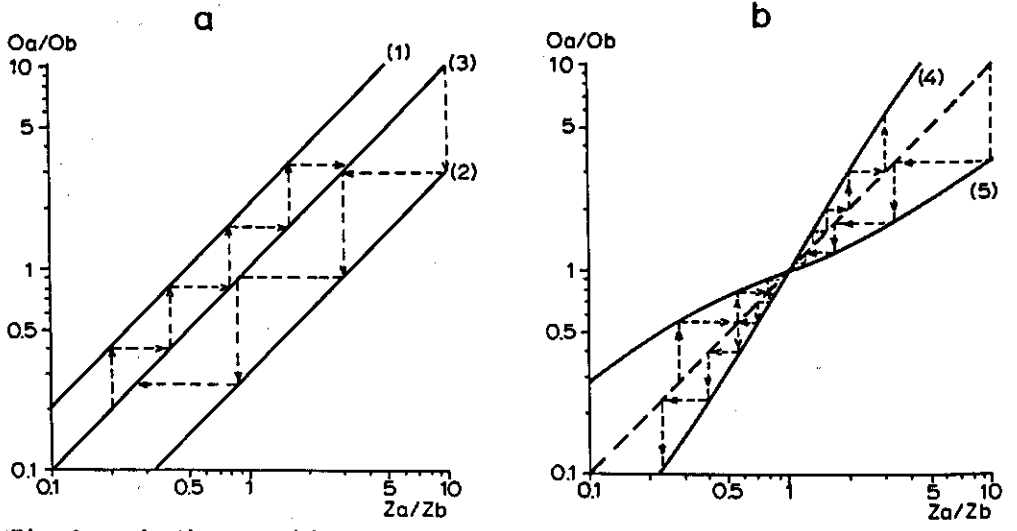


Fig. 3. Ratio diagrams. (a) Frequency independent RRR: (1) species a wins; (2) species b wins; (3) neutral equilibrium. (b) Frequency dependent RRR with an unstable equilibrium point (4) and a stable equilibrium point (5). The ratio of initial plant frequencies (Z_a/Z_b) and the yield ratio O_a/O_b are plotted as the population ratios $(N_a/N_b)_t$ and $(N_a/N_b)_{t+1}$, respectively.

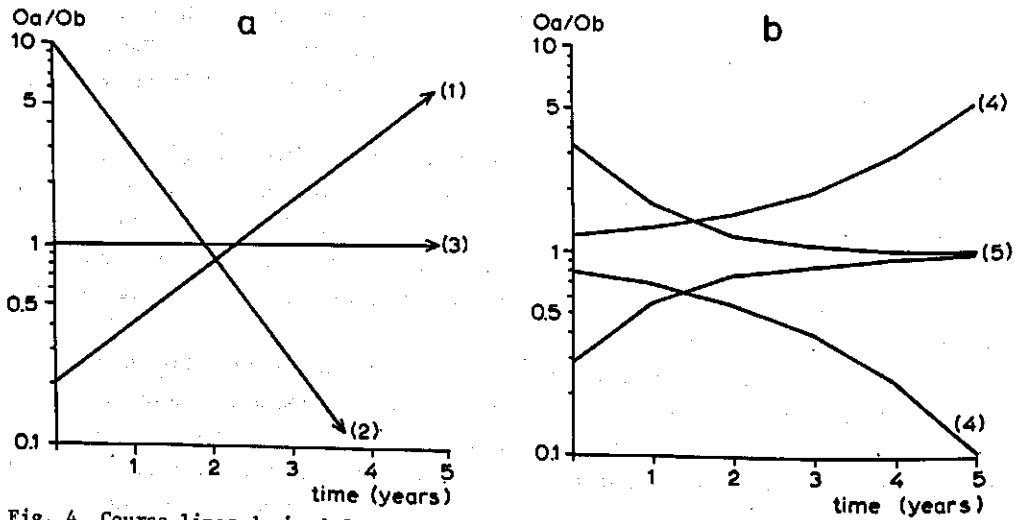


Fig. 4. Course lines derived from the ratio lines 1 to 5 of Figure 3 by stepwise reading the yield ratio of one year from the yield ratio in the previous year, along the dashed lines in Figure 3. With ratio lines 4 and 5 this is done starting from two initial ratios on either side of the equilibrium point.

From the definition of the relative replacement rate (Eqn 2.1) follows:

$$\log (N_a/N_b)_{t+1} = \log RRR_{ab} + \log (N_a/N_b)_t$$

So the RRR can be read from the ratio diagram as the vertical distance from what is called the ratio line to the diagonal of the diagram, which is indicated by an auxiliary line.

If the RRR is independent of the plant frequency the ratio line is parallel to the diagonal. If species a wins RRR_{ab} is greater than one and the position of the ratio line is above the diagonal. If b wins the ratio line is below the diagonal. Because equilibrium was defined as $RRR_{ab} = 1$, the diagonal is the set of all equilibrium ratios $(N_a/N_b)^*$. For an equilibrium to be stable it is necessary for a departure of the equilibrium ratio e.g. an increase in species a, to be followed by a shift in the opposition direction. Species b must increase relative to species a at population ratios greater than the equilibrium ratio and vice versa at population ratios smaller than the equilibrium ratio. This means that the ratio line must intersect the diagonal from left-above to right-below and the RRR must therefore be frequency dependent. Global stability can be defined as:

$$\lim_{N_a/N_b \rightarrow 0} RRR_{ab} > 1 > \lim_{N_a/N_b \rightarrow \infty} RRR_{ab} \quad (4.4)$$

provided there is only one intersection. It will be shown that this is possible when $k_{ab} k_{ba} > 1$.

The great advantage in using ratio diagrams in studying equilibria, is that it is not necessary to wait until a mixture has settled on an equilibrium ratio. From a short experiment with a range of initial ratios it is possible to obtain information about the existence and stability of equilibrium points. The disturbing influence of the ever-changing environment is largely eliminated, because all the mixtures are grown at the same time. This advantage cannot be appreciated enough, although there are some problems in estimating the RRR as we will see in Section 4.4.

The expected course of the population ratio in subsequent years can be read step-wise from the ratio diagram by taking the final ratio of one year as the initial ratio of the next year (dotted lines in Fig. 3). In doing so it is assumed that the conditions are the same in all the years. The successive population ratios can be plotted on logarithmic scale against time, to obtain so-called course lines (Fig. 4).

4.4 ESTIMATING RELATIVE REPLACEMENT RATES (RRR)

In comparing population ratios it is important that the population densities of the species are measured in the same way each time (e.g. as number of individuals or biomass per area) and that the units in the different years are comparable. By comparable is meant that they must have the same relation to the reproductive capacity of the population. Units such as individuals or shoots or grams may be different each year, because individuals and shoots may have different weights, and grams of biomass may be composed of different amounts of materials important to the performance of the plant in the next year, like reserves and meristems. If population units are not comparable a correction has to be applied.

With plants the population densities are usually measured by harvesting. Of annual species the whole population is measured this way (provided there is no seed bank in the soil) and resown directly or in the next year. If we assume that the seeds are exact

replicas of those in the previous year, the RRR may be estimated by α which is called the relative reproductive rate.

$$\alpha_{ab} = (O_a/O_b)_{t+1}/(O_a/O_b)_t = (N_a/N_b)_{t+1}/(N_a/N_b)_t = RRR_{ab}$$

Using Equations 4.3.a,b with $z_a = (O_a/(O_a + O_b))_t$ and $z_b = (O_b/(O_a + O_b))_t$

it is found that

$$\alpha = k_{ab} (M_a/M_b)_{t+1}$$

With perennial species in most cases only a part of the population is recovered by harvesting. The parts remaining (roots and stubbles) are difficult to recover and cannot be measured without destroying them. They are, however, the very parts that determine the yield in the next year. In this case the ratio between yields cannot be used as an estimate of the population ratio, because we do not know how the harvest is related to the parts remaining. Probably this relation varies for the two species and in different years.

These differences can be eliminated largely by considering the mixture yields in relation to monoculture yields (De Wit & Van den Bergh, 1965). Instead of the yields we use relative yields ($r = O/M$) to estimate RRR. In doing so one assumes that the yields in monoculture and mixture have the same relation to the total population in monoculture and mixture:

$$N_a(\text{mixt}) = O_a x_a \text{ and } N_a(\text{mono}) = M_a x_a$$

in which x_a is a proportionality constant. Now the following relation holds:

$$RRR_{ab} = (O_a x_a / O_b x_b)_{t+1} / (O_a x_a / O_b x_b)_t \quad (4.5)$$

Next it is assumed that the populations in the monocultures are stable, which means that they do not change in the subsequent years, or at least that the ratio between the two monoculture populations does not change, so

$$(M_a x_a / M_b x_b)_{t+1} / (M_a x_a / M_b x_b)_t = 1 \quad (4.6)$$

$(M_a/M_b)_{t+1} / (M_a/M_b)_t$ may be different from one, because the x 's are probably not the same each year; otherwise the correction would not be necessary and α would equal ρ , see below). Then we may divide Equation 4.5 by the left-hand side of Equation 4.6 thus eliminating the unknown x 's and obtain:

$$\rho_{ab} = (r_a/r_b)_{t+1} / (r_a/r_b)_t = RRR_{ab}$$

ρ was originally defined by De Wit & Van den Bergh (1965) as the relative replacement

rate. Both α and ρ are estimates of the RRR defined our way, using population densities. Calculating ρ with Equation 4.3a,b with $z_a = (0_a / (0_a + 0_b))_t$ and $z_b = (0_b / (0_a + 0_b))_t$, it is found that

$$\rho_{ab} = k_{ab} (M_a / M_b)_t$$

so that

$$\alpha_{ab} = \rho_{ab} (M_a / M_b)_{t+1} / (M_a / M_b)_t$$

With the annual species, of which the yield units are exact replicas and the whole population is harvested ($x = 1$) α equals ρ . In the case of perennials only ρ is a good estimate of RRR (provided the two assumptions made above are correct), because the x 's are not unity and may differ between species and years.

In some cases it is not correct to assume that the yields in monoculture and mixture are in the same relation to the population density, namely when the proportion harvested of a population decreases when the population decreases due to competition. This is the case when a decrease of the population not only means a decrease of the density of individuals but also of the size of the individuals, and the yield is obtained by mowing. In such a case a species may eventually disappear from the harvest, but still be present in the mixture. The act of harvesting may even change the competitive relationship in favour of an equilibrium, while the yields suggest complete exclusion. No correction is possible in these cases. Observations on the remaining parts of the populations have to reveal whether a different way of harvesting is necessary.

As was mentioned before, the advantage of using ratio diagrams is that it permits us to investigate the equilibrium possibilities in one single year. In many experiments the ratio of the planting or sowing densities (Z_a / Z_b) is used as an estimate of the initial population ratio. This may however give some problems with the determination of a possible equilibrium population ratio, because it is possible that the assumption of the population units being replicas or of the monocultures being stable is not allowed.

In most experiments with annuals the yields are much greater than the quantities sown. When the entire yield is resown, like in natural vegetations, the sowing density in the second year will be much higher and the reproductive rate ($a = M/Z$) much lower. In the monocultures this will proceed until they are stable ($a = 1$) (in the mixtures the changes in population densities may continue as a result of competition). In the first year one population unit has a much higher yield expectancy than in the next years. Yield units are therefore not comparable and α may not used as an estimate of RRR. The monocultures are not stable and it is not sure that they stabilize at the same rate, so it is not certain that the double quotient of the monoculture populations (Eqn 4.6) is unity, therefore ρ may neither be used. This makes it necessary to use sowing densities conforming to those in stabilized monocultures. In the agricultural practice the monoculture densities are artificially stabilized by resowing only a limited and fixed quantity and withholding the rest of the yield. An extra, anthropogenous mortality is introduced this way.

With perennial species there are also some problems in using Z_a/Z_b as an estimate of the initial population ratio. The seeds or the young plants are of course incomparable to the yield units or the remaining parts. The monocultures are not stable in the first year and can neither be stabilized by enlarging the plant density as with the annual species. There may be differences in the rate of stabilizing. It is therefore unlikely that Equation 4.6 holds, which means that ρ may not be used as an estimate of RRR in the first year. It is necessary to wait until the monocultures are stabilized. Several course lines presented by Van den Bergh (1968) show that completely erroneous conclusions may be drawn about the competitive ability of the species, when only the first growing period is observed.

We will show later on that the problems discussed above chiefly concern the level of the ratio line and not its slope. It is advisable not to attach too much value to the existence and the position of an intersection of the ratio line with the diagonal in the results of short term experiments, because this depends on the comparability of the yield and seed units. Even in long term experiments one must be careful in drawing conclusions from equilibrium ratios, because the position of the ratio line is easily influenced by factors that are independent of the competition process (e.g. temperature). More important is the establishment that the RRR is frequency dependent.

4.5 NICHE DIFFERENTIATION: $k_{ab} k_{ba} > 1$

It was mentioned in Section 4.2 that in some experiments the RYT was greater than one. In these cases Equations 4.3a and 4.3b do not describe the yield curves in the replacement diagram, because they were derived assuming $RYT = 1$. With $RYT > 1$ the curves in the replacement diagram do not compensate each other, so k_{ba} will not be the inverse of k_{ab} . With increasing RYT, the yield of one or both species is less depressed by the presence of the other, the limit being total independence of the yields in the mixtures. In this case the yield curve will be the same as in a spacing experiment (Fig. 5), which can be looked upon as a 'degenerate form' of a replacement series (in which one species does not grow).

De Wit (1960) showed that the results of a spacing experiment can be described by Equation 4.3 by substituting Z_a/Z_m and $(Z_m - Z_a)/Z_m$ for z_a and z_b , in which Z_a is one of the plant densities from the spacing series and Z_m is the highest density of the series. O_a and M_a are the yields at densities Z_a and Z_m .

$$O_a = k_{ab} (Z_a/Z_m) \{k_{ab} (Z_a/Z_m) + (Z_m - Z_a)/Z_m\}^{-1} M_a$$

After some rearrangements the following convenient hyperbolic function is arrived at:

$$O_a = \beta Z_a (\beta Z_a + 1)^{-1} \Omega_a \quad (4.7)$$

$$\text{with } \Omega_a = k_{ab} M_a (k_{ab} - 1)^{-1}$$

$$\text{and } \beta_a = (k_{ab} - 1) Z_m \text{ or } k_{ab} = \beta_a Z_m + 1$$

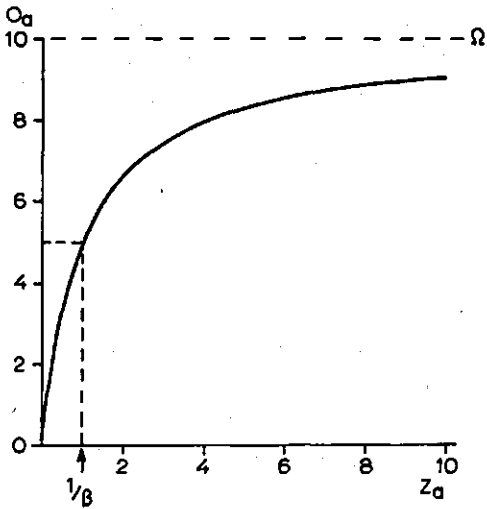


Fig. 5. Yield-density relationship or 'spacing curve' according to the spacing formula of De Wit (Eqn. 4.7.). Explanation in text.

For species b a similar function can be derived. Ω is the theoretical yield at infinite plant density and β can be considered as the space that is occupied by one plant growing alone. Both are dependent on the conditions and increase in time. It has been proved that this function gives a satisfactory description of yield-density relationships in practice (De Wit, 1960; Willey & Heath, 1969), however deviations are sometimes observed at very low and very high densities.

When species do not interfere with each other (have entirely different niches) the yields in a replacement series are described by Equation 4.7 and the product $k_{ab} k_{ba}$

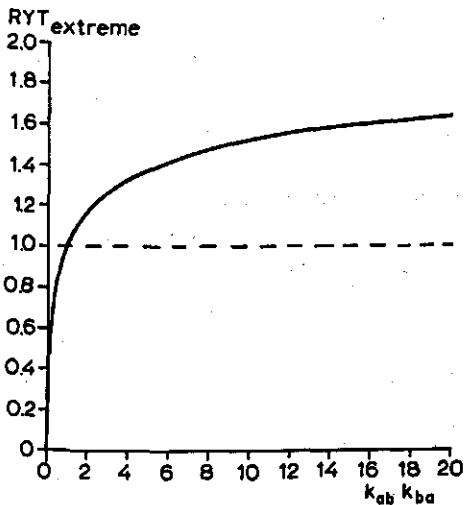


Fig. 6. Relation between the extreme value of the Relative Yield Total and the product of the relative crowding coefficients ($k_{ab} k_{ba}$).

equals $(\beta_a Z_m + 1) (\beta_b Z_m + 1)$ in which Z_m is the total plant density. Assuming that the relative crowding coefficients are independent of the plant ratio, it can be shown (by substituting Equations 4.3a and 4.3c in $O_a/M_a + O_b/M_b > 1$) that $RYT > 1$ means $k_{ab} k_{ba} > 1$ and $RYT < 1$ means $k_{ab} k_{ba} < 1$.

The RYT is frequency dependent. The frequency with the highest RYT depends on k_{ab}/k_{ba} ; the highest value itself is a function of $k_{ab} k_{ba}$:

$$RYT \text{ extreme} = 2(k_{ab} k_{ba} - \sqrt{k_{ab} k_{ba}}) / (k_{ab} k_{ba} - 1)$$

(Fig. 6; Van den Bergh, 1968). Of course like the k-values, RYT depends on conditions, harvest time and in some cases on total plant density. The assumption of frequency independent k-values is allowed in many but by no means in all experiments with plants. Frequency dependent k-values will be discussed in Section 4.10.

4.6 RELATION BETWEEN $RYT > 1$ AND EQUILIBRIA

Equilibrium with global stability was defined as:

$$RRR_{ab} = 1 \text{ with } \lim_{N_a/N_b \rightarrow 0} RRR_{ab} > 1 > \lim_{N_a/N_b \rightarrow \infty} RRR_{ab} \quad (4.4)$$

In the following we will use α as an estimate of RRR. Using Equations 4.3 and 4.3c α can be written as:

$$\begin{aligned} \alpha_{ab} &= (O_a/O_b)_{t+1} / (O_a/O_b)_t = (O_a/O_b) / (z_a/z_b) \\ &= (k_{ab}/k_{ba}) (M_a/M_b) (k_{ba} z_b + z_a) / (k_{ab} z_a + z_b) \end{aligned} \quad (4.8)$$

An equilibrium point exists if $\alpha = 1$ or:

$$(k_{ab}/k_{ba}) (M_a/M_b) = (k_{ab} z_a + z_b) / (k_{ba} z_b + z_a) \quad (4.9)$$

The right-hand side of Equation 4.9 is frequency dependent, running from k_{ab} to k_{ba}^{-1} when z_a/z_b runs from zero to infinity. An equilibrium is possible only if the left-hand side is between these limits or M_a/M_b is between k_{ab}^{-1} and k_{ba} . From Equation 4.9 we find the equilibrium ratio:

$$(z_a/z_b)^* = (M_a/M_b - 1/k_{ab}) / \{1 - (1/k_{ba}) (M_a/M_b)\}$$

Using Equation 4.4 it is found that the equilibrium is stable when:

$$1/k_{ab} < M_a/M_b < k_{ba} \quad (4.10a)$$

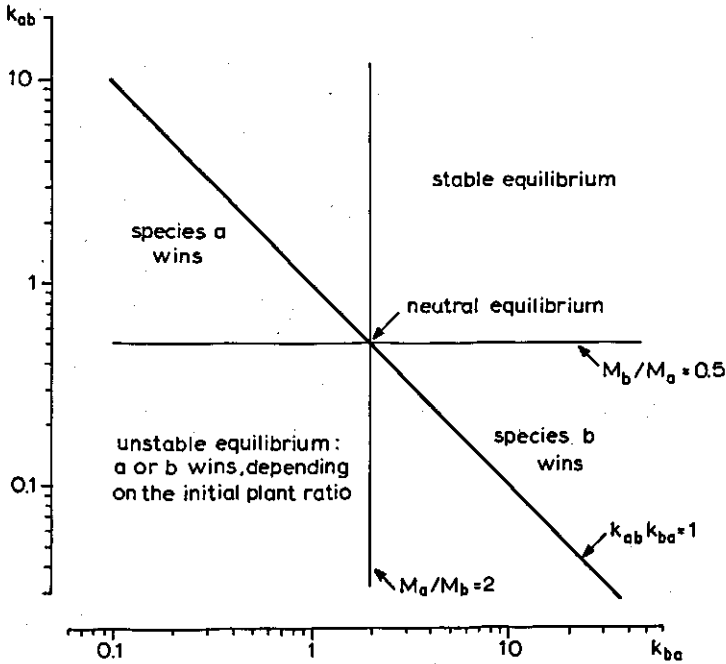


Fig. 7. Graphical representation of the equilibrium conditions of the De Wit model when $M_a/M_b = 2$. The combinations of k_{ab} and k_{ba} values that result in stable equilibria are situated in the top right-hand quadrant.

This condition is graphically represented in Figure 7. An unstable equilibrium point exists when

$$1/k_{ab} = M_a/M_b = k_{ba} \quad (4.11c)$$

These conditions resemble the equilibrium conditions of the Lotka-Volterra equations for competing species (see for example Harper, 1977, p. 13). In fact De Wit (1960) has shown that his Equations 4.3 are a particular solution of the Lotka Volterra equations. Because α varies monotonously with z_a/z_b , stability is always global in De Wit's model. A measure of stability is the elasticity, i.e. the rate at which the population moves towards the equilibrium point. This rate depends on the extent to which α deviates from one, the limits being:

$$\lim_{z_a/z_b \rightarrow 0} \alpha_{ab} = k_{ab} (M_a/M_b) \quad \text{and} \quad \lim_{z_a/z_b \rightarrow \infty} \alpha_{ab} = (1/k_{ba}) (M_a/M_b)$$

These limits give an impression of the elasticity of the equilibrium at population ratios lower or higher than the equilibrium ratio. They determine the maximum size of the yearly changes in the population ratio, indicated by the dotted lines in Figure 3.

If Equation 4.10a is written as $1 < (M_a/M_b)k_{ab} < k_{ab} k_{ba}$, it is seen that a

necessary, though insufficient condition for the existence of a stable equilibrium point is $k_{ab} k_{ba} > 1$, which also means $RYT > 1$. In principle all the information necessary in assessing the equilibrium possibilities of a species combination in a certain environment is given by the two k -values and the two M -values or by a ratio diagram. However, the RYT already gives the vital information whether there is niche differentiation. The advantages in using RYT -values are that it is easy to measure, independent of assumptions about the applicability of equations and independent of possible variations in M -values. It will be clear that RYT is an important parameter, not only in agricultural research, but also in ecological, population dynamic and population genetic research.

It should be restated here that it is assumed that k -values are frequency independent. When k -values are frequency dependent there are equilibrium possibilities also with $RYT = 1$ (see Section 4.9).

4.7 INTERPRETATION OF RYT

In Figure 8 possible RYT -values and their interpretations are summarized. $RYT = 1$ indicates exactly overlapping niches (a common limiting factor) (f, g and h), or the absence of any inter- or intraspecific interaction (g).

An RYT of two will be approached in due time, when the species have entirely different niches (use different resources). The curves are the same as those of density series (c). Intermediate values reflect partly different niches (d, e): the environment is used more efficiently by a mixture than by monocultures. The total yield in the mixture may, however, be lower than in the highest yielding monoculture when the species with the highest yielding monoculture has a relative crowding coefficient smaller than one (e).

RYT -values smaller than one (i) indicate that the environment is used less efficiently by a mixture than by monocultures. This happens when one or both species claim parts of the environment without actually using them, e.g. when there are allelopathic effects, but also when there is increased overconsumption in mixtures as compared to monocultures, because each species takes up faster the resources that limit the other (see Section 5.3.3).

Equations 4.3 may not be used when other forms of interaction are involved, e.g. when one species grows better or only grows in the presence of the other species ($RYT > 2$ is possible: (a and b)), when the k -values are frequency dependent, or when monoculture density is supra-optimal. These cases will be discussed in the Section 4.9.

Finally, it should be realized that intermediate RYT -values may be result of a combination of positive and negative effects.

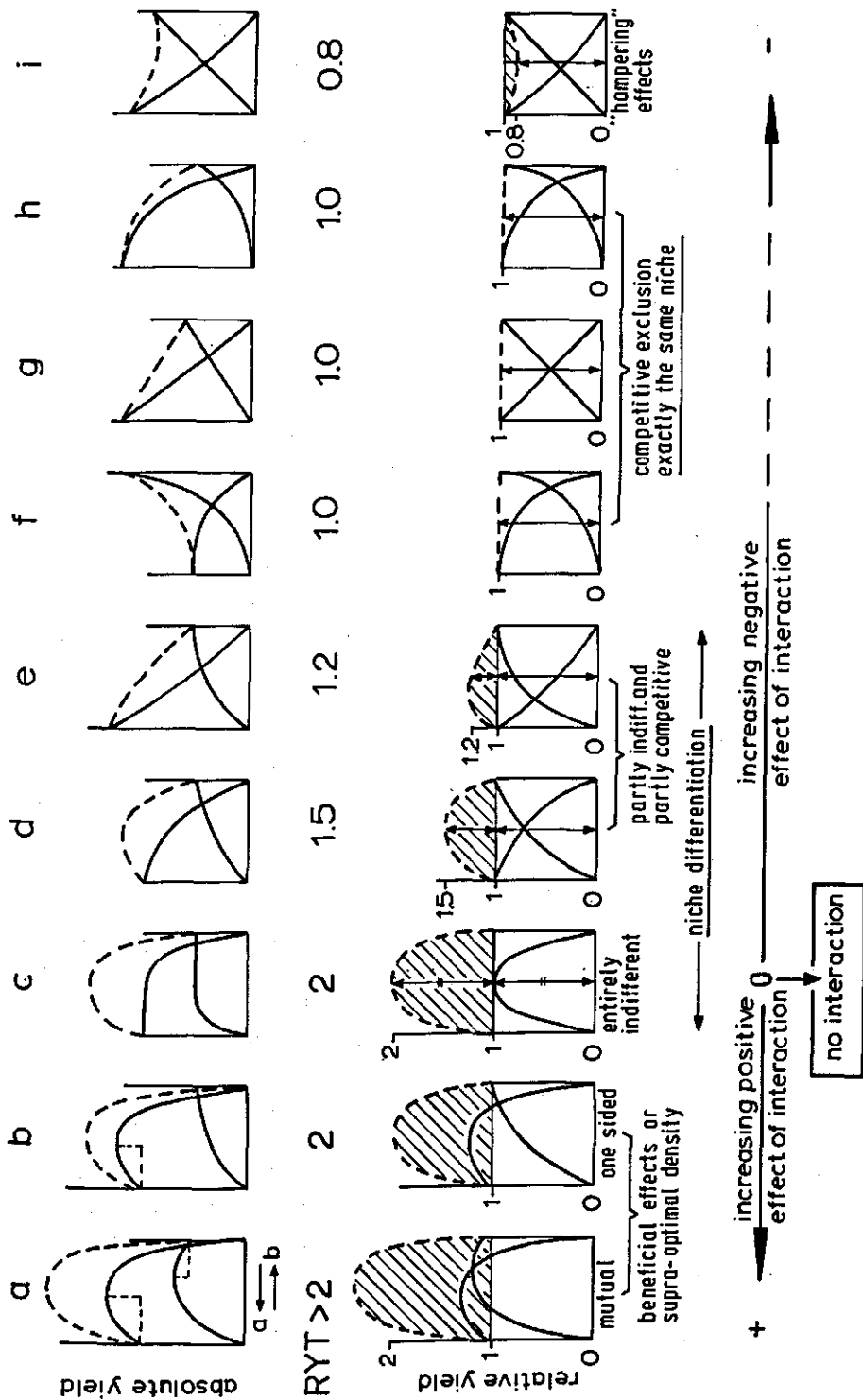


Fig. 8. RYT-values and their interpretation. Explanation in text. (After Van den Bergh & Braakhekke, 1978, changed).

4.8 SEARCHING FOR RYT > 1

In the past decennia ecologists as well as agriculturalists have been searching for mixtures of species with a more efficient utilization of the environment. Taking into account the high species density in natural vegetations especially in grasslands, suggesting a considerable amount of niche differentiation, one would expect to find RYT-values exceeding unity in many cases. The experimental results are however disappointing. Trenbath (1974) collected a large number of published results and found RYT-values close to unity in most of the experiments, excluding mixtures of legume and non-legume species. There was, however, a slight asymmetry in the distribution of the RYT-values: 13.6% was smaller than 0.9 and 20.3% was greater than 1.1. The 20.3% may, however, be an overestimation of the chance to find RYT > 1.1 because some of the investigators may have been aiming at overyielding mixtures, choosing species mixtures that they expected to have for some reason an advantage over the monocultures and negative results are less likely to be published.

This should not lead ecologists to the conclusion that niche differentiation is a rare event in nature. These data provide at best an estimation of the chance that randomly chosen species show niche differentiation under experimental conditions. In natural vegetations however the species are far from randomly chosen; they are selected in a long period from a large number of species for their ability to coexist and especially in species-rich communities the conditions are very different from those in most of the experiments.

On closer examination it becomes evident that the traditionally used experimental conditions strongly reduce the chance for possible niche differentiation to come to expression (Whittington & O'Brien, 1968). Compare some common features of experiments with the conditions necessary to permit the mechanisms discussed in Chapter 3. Pot experiments do not allow for different rooting depths. Constant conditions and short-term experiments reduce possible differences in growth rhythm. Fertilizers and water are often amply supplied, reducing the possibility of differential resource limitation. Diseases and predators are exterminated. Field plots are made homogeneous. Species are chosen arbitrary and seeds are from different places, which does not allow for adaptation of the species populations to each other.

It is obvious that we must pay much attention to the experimental conditions when we are investigating niche differentiation. Negative results are common but cannot nullify the possibility of niche differentiation in general. On the other hand it is difficult to create experimental conditions appropriate for the expression of small niche differences, which may yet contribute to species richness in natural vegetation wherever the conditions are favourable.

4.9 SUGGESTION FOR ANALYSIS OF COMPLICATED WAYS OF COMPETITION

In a study on the mechanisms underlying equilibria it is useful to describe in more detail the cases in which competition is reduced by differential use of the environmental resources or in which exclusion is counteracted otherwise. The simplest way of doing

so is by formulating the different processes involved in the interaction separately and investigating the effect of their simultaneous operation. This deductive approach will be applied with the help of simple mathematic formulation or graphical analysis in the following cases:

- competition in a heterogeneous environment;
- combination of generative and vegetative reproduction;
- multi-resource competition with complementary resources;
- multi-resource competition with substitutable resources;
- competition between species with a resource refuge;
- inversion of competitive dominance within one season;
- seed immigration;
- supra-optimal density effects;
- allelopathy;
- mutualism.

The intention is not to give conclusive evidence of cases observed, but only to indicate more or less intuitively what observations could be expected from more complicated ways of competition and what possible explanations there are for patterns observed in replacement diagrams. Exact mathematical treatment will be difficult, if not impossible in most cases, because the different processes involved in the interaction are not so independent as supposed here. A thorough knowledge of the influence of combinations of the species on their environment, combined with the use of simulation techniques will be necessary to obtain a more precise insight into these cases. The examples of phytoplankton competition discussed in Section 5.4 show the possibilities of this approach. With terrestrial plants, however, the situation is more complex and knowledge is still too limited to use the simulation approach with success in the more complicated cases of competition. There is no use in making models more and more complicated to include alle possible effects so long as no specific information from actual situations is available.

4.9.1 *Competition in a heterogeneous environment*

As was argued in Section 3.1 micro-environmental heterogeneity may contribute considerably to the species richness of grassland vegetations. Of the cases that will be discussed here competition in a heterogeneous environment is the simplest. A mathematical treatment is possible. We consider a field composed of patches of different soil conditions, e.g. high and low pH, with a relative area A^1 for one condition and A^2 for the other ($A^1 + A^2 = 1$). (The numbers are raised indices and do not indicate a power, except when accompanied by a negative sign.). When two species a and b have different growing and competitive abilities on these patches and on each patch competition proceeds according to De Wit's model with $RYT = 1$, we can write down the Equations 4.3 a,b for the different patches:

$$O_a^1 = k_{ab}^1 z_a^1 (k_{ab}^1 z_a^1 + z_b^1)^{-1} M_a^1 A^1 \quad (4.11)$$

$$\begin{aligned}
O_b^1 &= z_b^1 (k_{ab}^1 z_a^1 + z_b^1)^{-1} M_b^1 A^1 \\
O_a^2 &= k_{ab}^2 z_a^2 (k_{ab}^2 z_a^2 + z_b^2)^{-1} M_a^2 A^2 \\
O_b^2 &= z_b^2 (k_{ab}^2 z_a^2 + z_b^2)^{-1} M_b^2 A^2
\end{aligned}
\tag{4.11}$$

The total yields of the heterogeneous field will be

$$O_a = O_a^1 + O_a^2 \text{ and } O_b = O_b^1 + O_b^2
\tag{4.12}$$

In Figure 9 the outcome of this model is shown for various combinations of k , M and A values, assuming that the seeds are homogeneously dispersed on the whole field each year ($z_a^1 = z_a^2$ and $z_b^1 = z_b^2$). The summation of a convex and a concave curve results in a sigmoid curve; a frequency dependent relative crowding coefficient is obtained

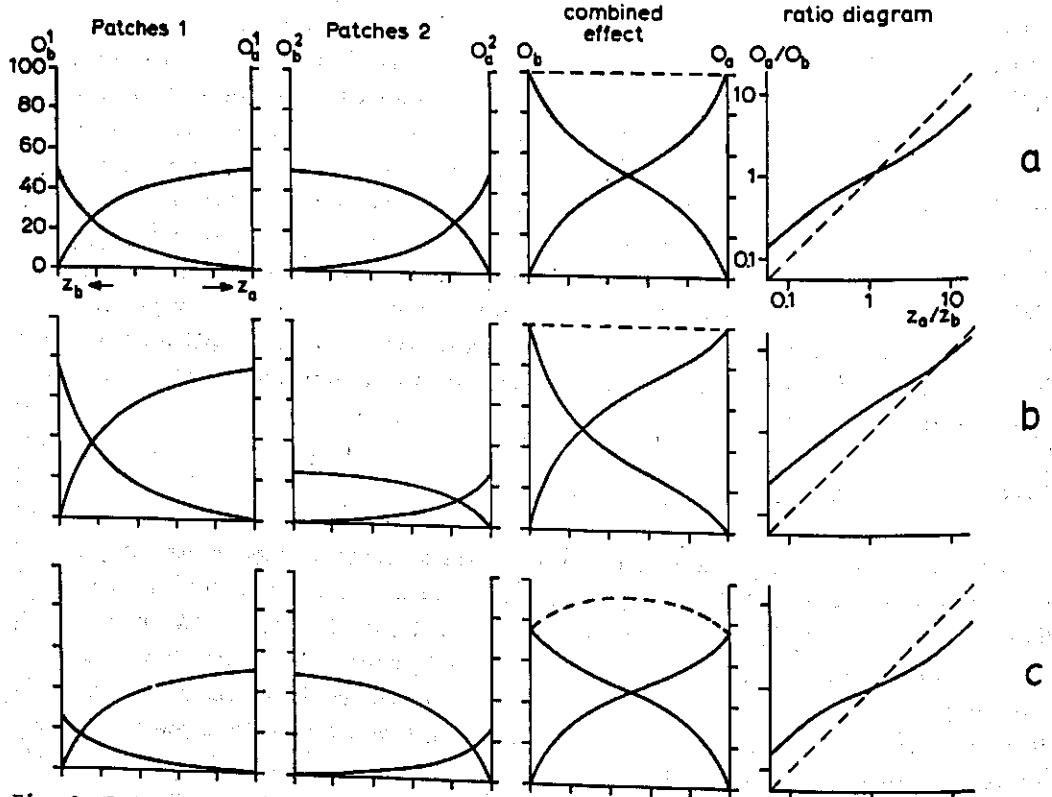


Fig. 9. Competition in heterogeneous environments. The competition processes on two different patches and their combined effect are shown separately for three different cases: (a) The species having opposite competitive abilities on the two kinds of patches that are in total equally large. $k_{ab}^1 = 5.0$; $k_{ab}^2 = 0.5$; $A^1 = A^2 = 0.5$; $M_a^1 = M_a^2 = M_b^1 = M_b^2 = 100$. (b) As (a), but one kind of patches is more abundant than the other. $A^1 = 0.75$; $A^2 = 0.25$. (c) As (a), but with a positive correlation between the competitive ability and the monoculture yield of a species on a patch. $M_a^1 = M_b^2 = 100$; $M_a^2 = M_b^1 = 50$. Explanation in text.

by summation of curves with frequency independent relative crowding coefficients. This phenomenon was noted before by R.L. Hall (pers. comm.) and Berendse (1979). It offers a relatively simple explanation for the existence of frequency dependent competitive ability. The two curves added may represent various processes. Some of these are discussed in the following sections.

With frequency dependent relative crowding coefficients stable equilibria may exist even when $RYT = 1$, as can be seen in Figure 9a and b. The equilibrium conditions can be obtained using α :

$$\alpha_{ab} = (O_a/O_b)/(z_a/z_b) = (k_{ab}^1 M_a^1 A^1 Q + k_{ab}^2 M_a^2 A^2)/(M_b^1 A^1 Q + M_b^2 A^2)$$

in which

$$Q = (k_{ab}^2 z_a + z_b)/(k_{ab}^1 z_a + z_b)$$

The presence of Q makes α frequency dependent, except of course when $k_{ab}^1 = k_{ab}^2$. A stable equilibrium point exists when Equation 4.4 holds or:

$$(M_a^1 A^1 + M_a^2 A^2)/(M_b^1 A^1 (k_{ab}^1)^{-1} + M_b^2 A^2 (k_{ab}^2)^{-1}) < 1 <$$

$$(k_{ab}^1 M_a^1 A^1 + k_{ab}^2 M_a^2 A^2)/(M_b^1 A^1 + M_b^2 A^2)$$

This condition indicates that the equilibrium depends on all the parameters: M , A and k values.

It can be seen from Figure 9c that yield advantages are to be expected from mixtures in a heterogeneous environment, when yielding capacity and competitive ability are positively correlated, i.e. when the species that yields best in monoculture on a patch is winning in the mixture on that patch. In these cases the yields may approach the maximum yields which are possible when combining knowledge of the environmental pattern with careful placement of seeds on the right places. Trenbath (1974) has shown the existence of a weak positive correlation between aggressiveness in mixtures and biomass production in pure stands. According to De Waal (1951), cited by De Wit (1960), this kind of advantage was the main reason for mixed cultivation of barley and oats in Denmark.

When the seeds or other reproductive organs are not dispersed, but concentrated on the patches where the parental plants grow, the equilibrium condition is simply that RRR on one type of patch is greater than one and on the other type smaller than one and the only condition for the areas A^1 and A^2 is that they are not zero. The pattern of the species will become more and more distinct in this case. In intermediate cases the influence of A^1 and A^2 depends on the dispersal abilities and the size of the environmental grain and the sharpness of the borders depends on the steepness of the environmental gradient between the patches and the dispersal abilities of the species.

4.9.2 Combination of vegetative and generative reproduction

The combination of species with different reproductive strategies, often referred to as *r* and *k* species, can be considered as a special case of competition in a heterogeneous environment.

Two species are considered investing different proportions of their biomass in seeds and vegetative reproduction (g and v , $g + v \leq 1$). It is supposed that generative and vegetative reproduction prevail on different patches in the field, e.g. disturbed and undisturbed patches occurring in the proportions A^1 and A^2 in the field, respectively. The results of competition on the disturbed and undisturbed patches can be described by Equations 4.11. The relative plant frequencies on the patches are calculated from the harvest of the previous year and the relative proportions of seeds and organs for vegetative reproduction, assuming that these are homogeneously dispersed in the field or that disturbance is effective only for one year and occurs at random:

$$z_a^1 = 0_a g_a (0_a g_a + 0_b g_b)^{-1} \text{ and } z_b^1 = 0_b g_b (0_a g_a + 0_b g_b)^{-1}$$

Analogous equations can be derived for z_a^2 and z_b^2 , with v_a and v_b .

This definition of plant frequencies complicates the situation, but the results are essentially the same as in the previous case (Section 4.9.1), the important resemblance, being the summation of the results of separate patches. Calculations show that equilibrium can exist and that the conditions involve all parameters M , k , A , v and g . Equilibrium can exist even when k_{ab}^1 and k_{ab}^2 are unity, if only g and v differ in an appropriate way, since the quotients g_a/g_b and v_a/v_b have the same effect in the formulas as k_{ab}^1 and k_{ab}^2 (see Fig. 10).

Of course, the actual situation in the field and even in experiments will be more complicated in most cases. For instance, one would expect that vegetative organs will spread laterally into the disturbed patches and compete with the seedlings. Much information is needed before the model can be made predictive for actual situations.

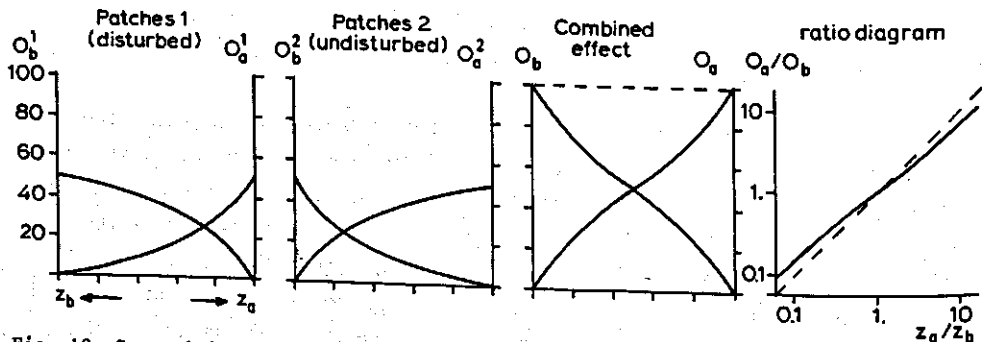


Fig. 10. Competition between two species *a* and *b* with high generative and high vegetative reproductive capacity, respectively, in a heterogeneous environment with patches where one or the other way of reproduction prevails (disturbed and undisturbed patches: A^1 and A^2 , resp.). $k_{ab}^1 = k_{ab}^2 = 1$; $M_a^1 = M_a^2 = M_b^1 = M_b^2 = 100$; $A^1 = A^2 = 0.5$; $g_a = v_b = 0.75$; $v_a = g_b = 0.25$. Explanation in text.

4.9.3 Multiple resource competition

Multiple resource competition is the classical conception of niche differentiation. Using De Wit's model it can be treated as follows.

Two species, a and b, are considered competing for two homogeneously distributed resources, R^1 and R^2 . When two species have different use efficiencies ($e = 0/r$) and competitive abilities for these resources, and assuming the competition processes are independent and proceed according to De Wit's model with $RYT = 1$, the equations for the two separate competition processes are:

$$0_a^1 = k_{ab}^1 z_a (k_{ab}^1 z_a + z_b)^{-1} e_a^1 R^1 \quad (4.11')$$

$$0_b^1 = z_b (k_{ab}^1 z_a + z_b)^{-1} e_b^1 R^1$$

$$0_a^2 = k_{ab}^2 z_a (k_{ab}^2 z_a + z_b)^{-1} e_a^2 R^2$$

$$0_b^2 = z_b (k_{ab}^2 z_a + z_b)^{-1} e_b^2 R^2$$

0_a^1 and 0_a^2 , and 0_b^1 and 0_b^2 are the potential yields the species can produce with the supplies of R^1 and R^2 that they have obtained.

How the potential yields combine and determine the actual yields, 0_a and 0_b , depends on the kind of resources. Taking the consumer needs as a criterion resources may be classified as complementary or substitutable or intermediate resources (Covich, 1972; Leon & Tumpson, 1975). Complementary resources have to be taken together, because they fulfil essential, qualitatively different functions and occur independently of each other in the environment. Most of the resources used by autotrophic organisms are of this type and resource limitation proceeds according to Liebig's Law of the Minimum: growth depends only on the limiting resource.

One of two substitutable resources, on the other hand, can be omitted, if there is enough of the other, because they fulfil qualitatively similar needs or they are composed of all the substances essential to the consumer. Most of the resources used by heterotrophs are of this type. It makes no difference to a predator whether he eats a hare or a rabbit. His growth depends on the sum of both. It makes however much difference to a plant whether it takes up nitrogen or potassium; its growth depends on the element that is limiting.

Some of the resources used by plants may also be of the substitutable or intermediate type. Consider only nitrogen from the soil and nitrogen from the air as used by legumes, or one element present in different places such as different soil layers or the patches in a heterogeneous environment, as already discussed. Different forms of soil nitrogen are also substitutable: NO_3 and NH_4 . Furthermore, it is known that some of the mineral elements have functions in common, like the osmotic function of the cations. Sodium or magnesium application can reduce the potassium requirement of plants (examples are cited by Black, 1968, p. 731-736 and Robson & Loneragan, 1978). Figure 11 gives a graphical representation of some possible relations between the yield and the consumed

quantities of two resources. From the three dimensional figures so-called 'indifference curves' (Leon & Tumpson, 1975) or 'isoquants' (Dumenil, 1961) are obtained by joining points of equal yield or growth and projecting the resulting lines on the resource plane.

Returning now to our model, we can distinguish two ways of combining the potential yields of the separate competition processes. With complementary resources the actual yield is the least of the two potential yields:

$$O_a = \text{MIN} (O_a^1, O_a^2) \text{ and } O_b = \text{MIN} (O_b^1, O_b^2) \quad (4.13)$$

With substitutable resources the actual yields are:

$$O_a = O_a^1 + O_a^2 \text{ and } O_b = O_b^1 + O_b^2 \quad (4.12)$$

In Figure 12 the outcome of these models is shown for various combinations of parameter values. It is seen that with complementary resources RRR is frequency dependent when the species are limited by different resources. Equilibria can exist when each species is limited by an element of which it obtains a larger quantity than the other species. The applicability and equilibrium conditions of this model will be discussed in more detail in Chapter 5. With substitutable resources RRR is also frequency dependent and the addition of the potential yield curves results in a S-shaped total yield curve.

⇒

Fig. 11. Contrasting relations between the consumed amounts of two resources and the consequent production of a species, and the effects on the results of a resource replacement experiment.

The figures of the first column are three-dimensional representations of the uptake-yield relationships. The second column gives the so-called 'isoquants', obtained by joining points of equal yields and projecting the resulting line on the resource plane. The representation used in the last two columns will be applied to the results of our resource replacement experiments (Sections 7.2.2 and 7.6). Column three gives the 'minimum concentration curves', obtained by dividing the indifference curves by their corresponding yield level. They represent the final internal concentrations of plants grown on a resource replacement series.

Column four gives diagonal sections along the dashed lines of the figures in the first column, representing the final yields of plants grown on a resource replacement series.

- (a) Complementary resources fulfilling two essential and specific functions.
- (b) Substitutable resources fulfilling one and the same essential function with equal efficiency.
- (c) Resources fulfilling two equally important essential but nonspecific functions with different efficiency.
- (d) Resources fulfilling each one essential and specific function. In addition they fulfil together a third essential but nonspecific function with equal efficiency. The three functions are equally important and the distribution of the consumed resources over the functions is optimal.
- (e) Resources fulfilling two specific interacting functions.

Yields are calculated with a reduced version of the formula of Homès & Van Schoor (1961):

$$O = U^1 U^2 (U^1 + U^2)^{-1}$$

uptake-yield relationship

maximum yield isoquants

minimum concentration curves

maximum yield in a resource replacement series

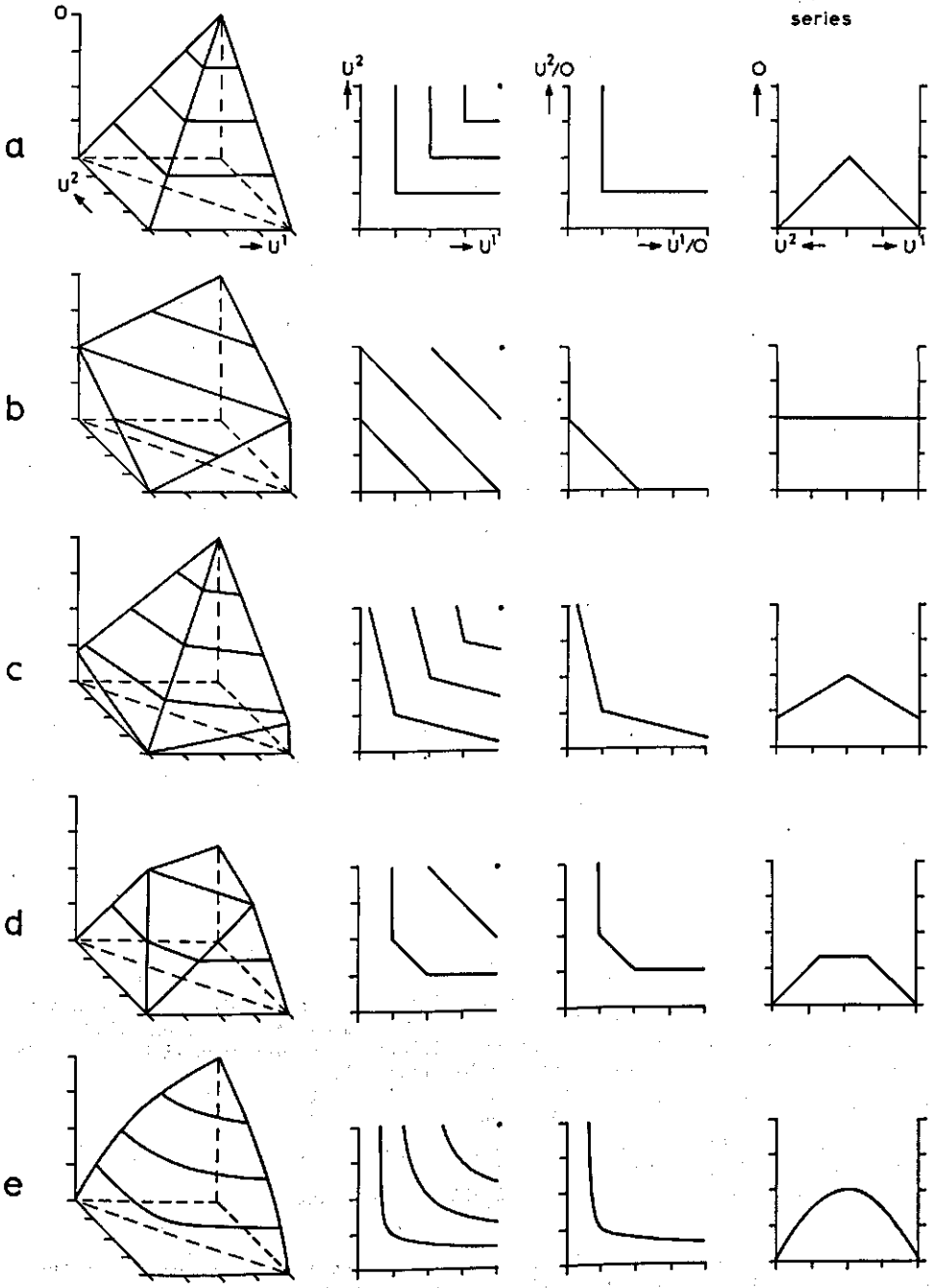
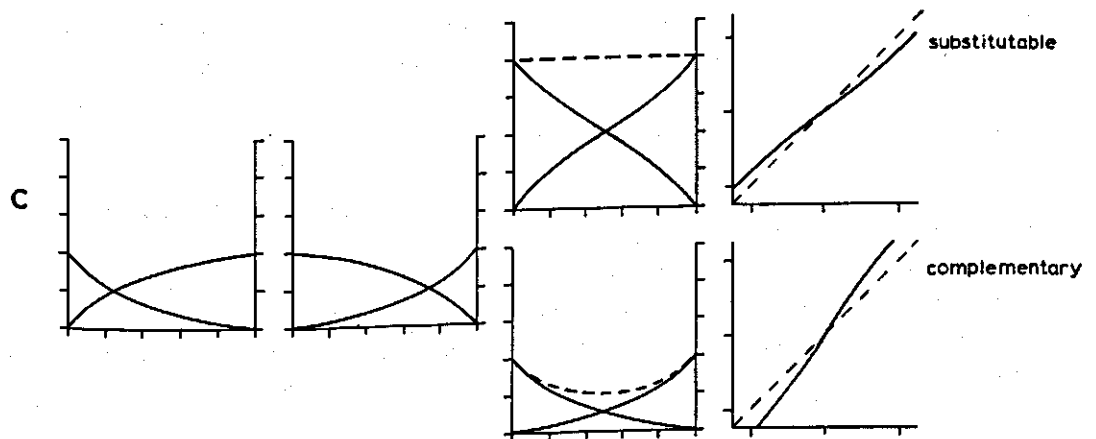
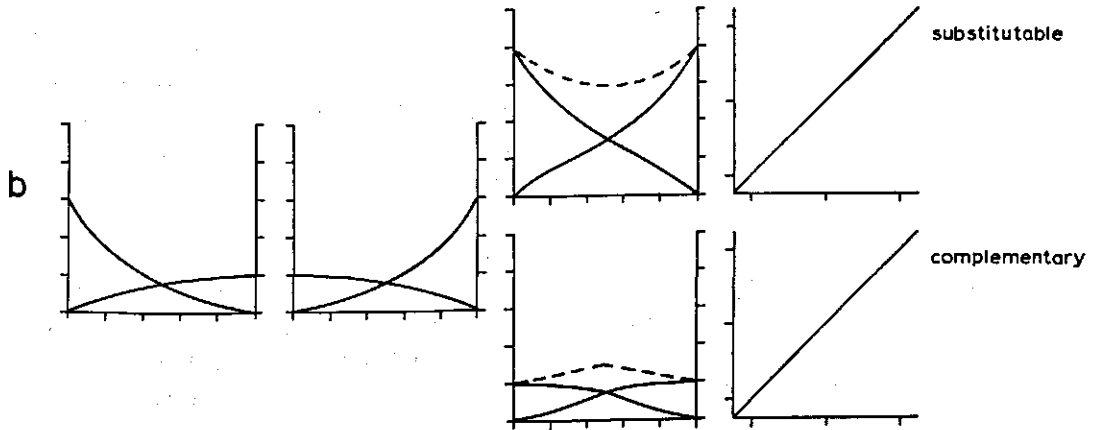
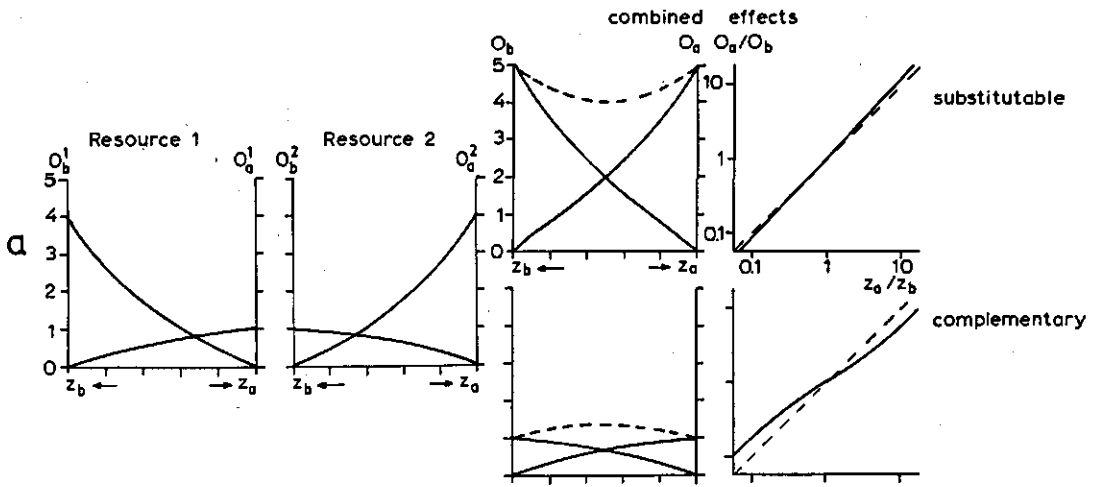




Fig. 12. The outcome of multiple resource competition for substitutable and for complementary resources as calculated according to the models discussed in Section 4.9.3, for three combinations of parameters, illustrating equilibrium possibilities with both kinds of resources (a and c) and one intermediate combination (b).

	e_a^1	e_a^2	e_b^1	e_b^2	k_{ab}^1	k_{ab}^2	R^1	R^2
(a)	0.01	0.04	0.04	0.01	2.	0.5	100	100
(b)	0.01	0.03	0.03	0.01	3.	0.333	100	100
(c)	0.02	0.02	0.02	0.02	3.	0.333	100	100

The two left-hand diagrams show the yields that might potentially be produced with the amounts absorbed of one resource, not taking the needs for the other resource into account. The actual yields displayed in the third column are obtained by adding the potential yields in case of substitutable resources, or by taking the least of the potential yields in case of complementary resources. The ratio diagrams in the fourth column are derived from the actual yield diagrams.



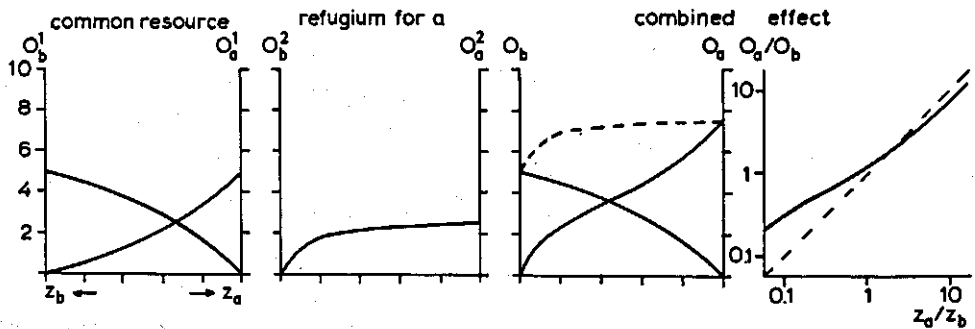


Fig. 13. The outcome of competition between two species when one of them has a resource refuge that is exploited according to a spacing curve. $e_a^1 = e_a^2 = e_b^1 = 0.1$; $e_b^2 = 0$; $k_{ab}^1 = 0.5$, $k_{ab}^2 = 10$; $R^1 = 50$; $R^2 = 25$.

4.9.4 Competition between species with resource refuges

A special case of multiple resource competition for substitutable resources occurs when the relative crowding coefficient of a species for one of the resources is zero. In this case the other species has a 'resource refuge' from which it cannot be excluded, provided it is able to reach this resource. The replacement diagram of competition in a resource refugium is degenerated to one yield-density curve (see Section 4.5). The replacement diagram in the common resource space may be of a normal shape (see Fig. 13).

Stable coexistence is possible when each species has a refuge or when the species without a refuge is the strongest competitor in the common resource space. As examples may serve the air nitrogen refuge of legumes in competition with grass and the combination of a deep and a shallow, but intensive, rooting species. The latter case is investigated in more detail by Berendse (1979). He also provides experimental evidence (Berendse, 1980). It may however be that the competition in the common space makes it impossible for the weakest species to use its refuge, or the reverse, that the possession of a refuge reinforces the position of a species in the common space.

4.9.5 Inversion of competitive dominance within one season

It was argued in Section 3.3.1 that differences in growth periodicity may lead to stable coexistence of species that use the same limiting resource, if this resource is continuously available. One can divide the season into periods (t_1, t_2, \dots, t_n) in which k or M values are different. The initial plant ratio of each period is the yield ratio at the end of the preceding period and yields of the subsequent periods are added. This results in the following simple model:

$$O_a^{t+1} = k_{ab}^t (k_{ab}^t + O_b^t/O_a^t)^{-1} M_a^t$$

$$O^{t+1} = (k_{ab}^t O_a^t / O_b^t + 1)^{-1} M_b^t$$

$$O_a = \sum_{t=0}^n O_a^t \text{ and } O_b = \sum_{t=0}^n O_b^t$$

In Figure 14 the results of some calculations, using this model are given. It is seen that equilibria are possible and that the overall k values at the end of the season are frequency dependent. We see here another simple possibility to explain S-shaped curves in the replacement diagram. The explanation is, however, not complete, when it is not made clear why the k values change in time, because they cannot be considered simply as a given species property.

A good explanation is available, when the species have nonsynchronous growth periods like in the experiments with early and late potatoes of Schepers & Sibma (1976) or *Phleum pratense* and *Anthoxanthum odoratum* of Van den Bergh & De Wit (1960). In these experiments one or both species had a 'time refuge': a period in which they

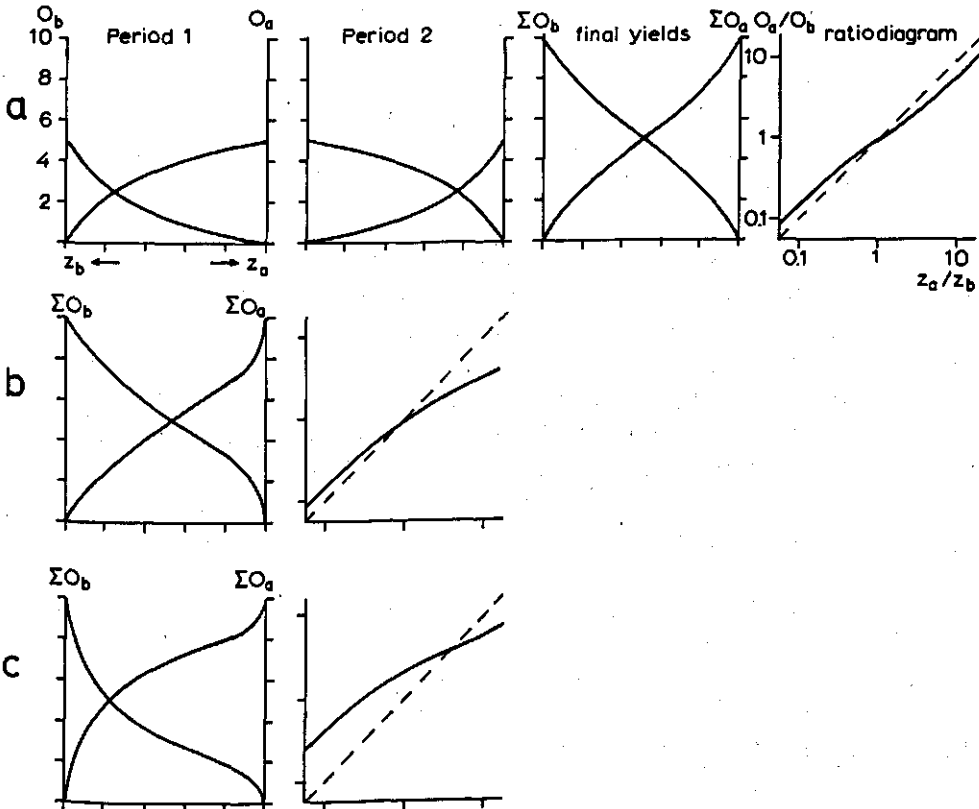


Fig. 14. Graphs illustrating the influence of changes in competitive dominance within one season on the outcome of competition.
 (a) The season is divided in two periods (1 and 2) with $k_{ab}^1 = 3$ and $k_{ab}^2 = 0.1$. $M_a^1 = M_a^2 = M_b^1 = M_b^2 = 5$.
 (b) The season divided in six periods (not shown) with k_{ab} changing from 2.0 via 1.5, 1.0, 0.5, 0.1 to 0.01, $M_a = M_b = 1.666$ in each period.
 (c) The season divided in five periods (not shown) with k_{ab} changing from 5.0 via 2.0, 1.0, 0.1 to 0.01. $M_a = M_b = 2.0$ in each period.

could use the continuously supplied limiting resource alone, because the k and M value of the other species were zero. This is a favourable situation in agriculture, because the resource exploitation is extended in time, which may result in larger yields in mixtures as compared to monocultures. In the extreme and self-evident case, when the two species are grown in different years, the curves in the ratio diagram are two convex spacing curves and the final RYT may approach two.

Equilibria are also possible when M values are equal in all the periods and only the k values change, as can be seen in Figure 14.

It is, however, difficult to imagine how this might happen in actual situations. The case which comes closest is the combination of species with the same start and end of the growing period, but with different growth habits, on the understanding that one is specialized in early closing of the canopy, without much investments in structural tissues and the other invests more in stems and roots and obtains dominance later in the season by shading the first. In this case there is no yield advantage of a mixture and RYT will be one. However the overall k values at the end of the season will be frequency dependent and equilibrium is possible.

4.9.6 Seed immigration

When seedling establishment takes place in autumn or spring, which is common in our region, the effect of seed immigration on the outcome of a replacement experiment is a change in the initial plant ratio of the following growth period, compared to the harvest ratio of the previous year. This is seen as follows.

We assume that the seeds come from outside the experimental field and that they are homogeneously dispersed over the whole field, each plot receiving the same amount of seeds of the two species (S_a and S_b) which have to be added to the populations already present. Since the new seedlings probably have different reproductive capacities compared to the plants present, the seedling amounts may have to be provided with a proportionality constant ($s_a = S_a p_a$). The changed initial relative plant frequencies are now:

$$z_a = (Z_a + s_a) / (Z_a + s_a + Z_b + s_b)$$

$$z_b = (Z_b + s_b) / (Z_a + s_a + Z_b + s_b)$$

The new plant ratio being:

$$Z_a/Z_b = (Z_a + s_a) / (Z_b + s_b)$$

Comparing this with the apparent initial ratio (Z_a/Z_b) as measured by the harvest ratio $0_a/0_b$, it is seen that the change of the plant ratio is frequency dependent; low ratios increase and high ratios decrease as a result of seed immigration, the amounts depending on the size of the immigrated seed populations compared to the populations present. When the apparent frequencies are plotted in the replacement diagram this results in the yields at low frequencies being higher and at high frequencies being lower

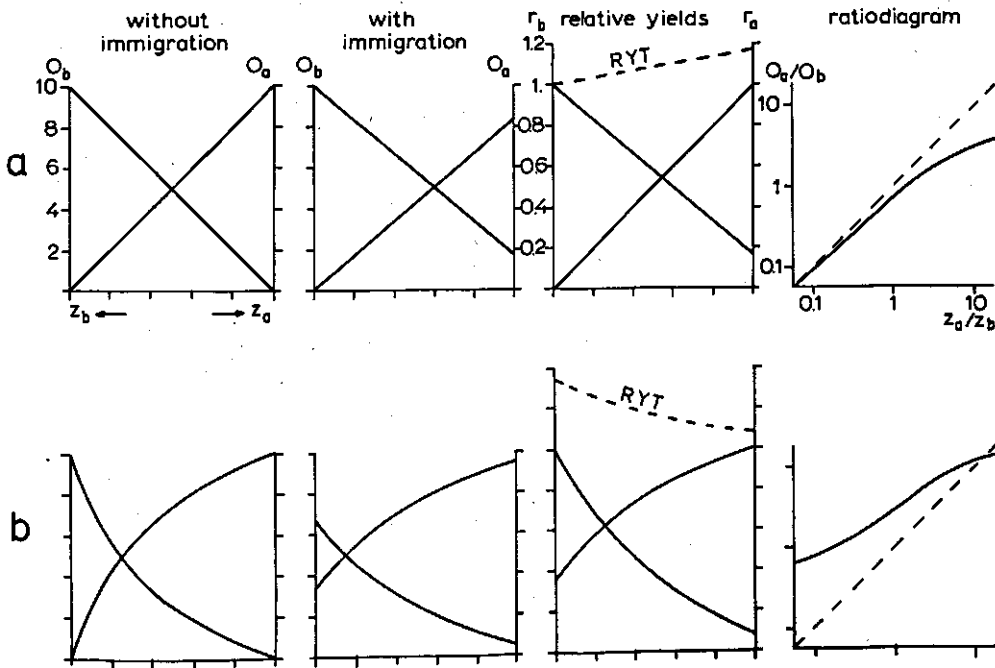


Fig. 15. Graphs illustrating the influence of seed immigration on the outcome of competition.

(a) immigration of one species. $k_{ab} = 1.0$; $s_a = 0$; $s_b = 0.2$; $M_a = M_b = 10$.

(b) immigration of both species. $k_{ab} = 3.0$; $s_a = s_b = 0.2$; $M_a = M_b = 10$.

than without seed immigration, the monocultures degenerating to mixtures (Fig. 15). It is as if the abscissa has shrunk and the replacement curves are cut off at one or both ends. The RYT in the monocultures is greater than unity due to this distortion of the replacement diagram. The ratio line has a peculiar shape, the asymptotes being horizontally instead of parallel to the diagonal. Evidently this makes seed immigration to a powerful stabilizing mechanism. Immigration of small amounts of seeds may already produce coexistence, where otherwise the species would exclude each other, provided of course that germination and establishment is possible.

Such coexistence depends on the presence of environmental heterogeneity, because the constancy of immigration must be guaranteed by the existence of a permanent seed source, i.e. a population near by, in a suitable habitat, where it cannot be excluded. In a homogeneous environment seed immigration will be proportional to plant frequency, in consequence of which the stabilizing effect disappears.

In a competition experiment mixtures with different frequencies are growing next to each other. When seeds are exchanged between plots, this may give the impression that immigration is independent of plant frequency, and a stabilizing effect may be observed in the first years.

However, when the experiment is continued long enough to let the plant frequencies converge, it will appear that the stabilizing effect disappears and one of the species is excluded. The stabilizing effect of seed immigration within competition experiments, consequently, has to be considered an artefact.

4.9.7 Effects of supra-optimal density

The possibility that yields for whatever reason are depressed at high densities is ignored by the theory of De Wit, because only competitive effects were considered. Agricultural practice has shown that this possibility is real, although not common (examples are given and mathematical treatments are reviewed by Willey & Heath, 1969.) and we must therefore take it into account, when interpreting the results of replacement experiments; especially because it includes possibilities for equilibria. Supra-optimal density effects may result in RYT-values that are greater than one. Even relative yields alone may be greater than one. Figure 16 shows how I suggest that these effects depress the upper part of the replacement curve and how this affects the ratio line.

Although it is known that supra-optimal density effects are possible in agricultural and experimental situations, the question remains whether they are important in natural situations. Most of the examples come from experiments in which only parts of the plants were included in the yield; especially, when some form of 'grading' was practiced, i.e. when only those plants or parts of plants are considered that fall within certain size limits. It is, however, not inconceivable that grading has a biological meaning when seeds are considered, because the success of a seedling will depend on the seed size. Another question is whether the yield depression in a mixture is confined to the species with the higher frequency or affects the minor party as well. Figure 16 shows that supra-optimal density effects may contribute to the realization of equilibria, when the minor party profits from the depression of the species with the higher frequency. Autotoxic activity, being one possible cause of supra-optimal density effects, might thus favour species density.

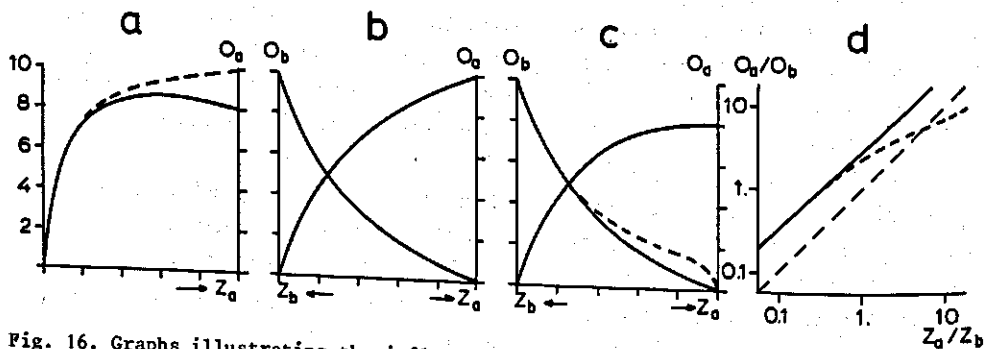


Fig. 16. Graphs illustrating the influence of supra-optimal density depression of one species on the outcome of competition.
 (a) Spacing curves of species a without (---) and with (—) supra-optimal density depression.
 (b) Replacement diagram without supra-optimal density depression ($k_{ab} = 3$; $M_a = M_b = 10$).
 (c) Replacement diagram with supra-optimal density depression of species a, not affecting species b (—) and favouring species b (---).
 (d) Ratio lines of the two cases of (c).

4.9.8 Allelopathy

As was mentioned in Section 3.4.1 allelopathy may be a part of the competitive strategy of a species, because it prevents a competitor's access to a resource. When the species releasing the allelopathic substances takes indeed full advantage of the reduced competition from its neighbours, the effect of allelopathy is not visible in a replacement series. The remaining question whether there was only exploitation competition or competition reinforced by allelopathy is however mainly academic. Only when the profit is delayed compared to the disadvantage to the other species, or when there is only a small profit or none at all, the allelopathic effect will be visible, because the RYT will be smaller than unity. The adaptive value becomes however doubtful in these last cases.

An $RYT < 1$ due to allelopathic effects and the impossibility of immediate utilization of the 'free space' by the releasing species was demonstrated in an experiment of Eussen (1978) with alang-alang (*Imperata cylindrica* (L.) Beauv.) and maize in replacement series (Fig. 17). As will be shown in Section 5.3.3 $RYT < 1$ in itself is not conclusive evidence for allelopathy, because it may also have been caused by luxury consumption.

To formulate allelopathic effects there are two possibilities. One can propose that the competitive ability of the receiving species is reduced and that the 'donor' only incompletely takes advantage of this, and represent this by k_{ab} , k_{ba} being smaller than one. Secondly, one can propose that the competitive abilities are not changed (at least initially), but that the receiving species is prevented from efficiently using the resources it seized and represent this by multiplying the potential yield of the receiving

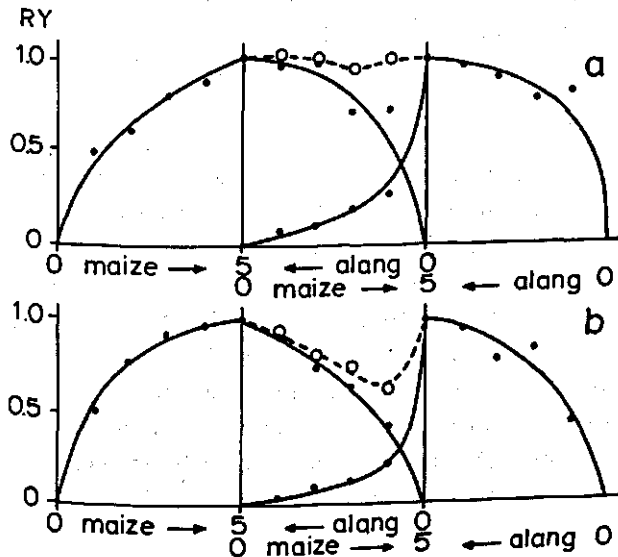


Fig. 17. The relative yields (RY) of alang-alang and maize in replacement experiments (middle part of the graphs) and spacing experiments (left and right parts), with alang-alang plant unit of 5 plants (a) and 10 plants (b).
 -o-: RYT. Absolute yields of monocultures: alang-alang: 10 g (a) and 21 g (b); maize: 15 g (a) and 32 g (b). (From Eussen, 1978)

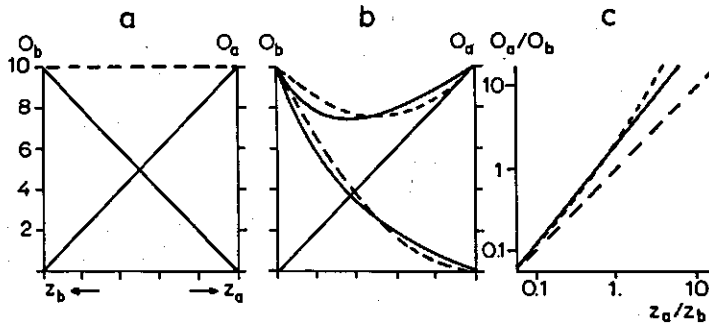


Fig. 18. Graphs illustrating the influence of allelopathic activity of one species on the outcome of competition.

(a) No allelopathic effect ($k_{ab} = 1$; $M_a = M_b = 10$).

(b) With allelopathic effect of species a on species b.

The effect is formulated in two ways:

(1) $k_{ab} k_{ba} < 1$ (—); $k_{ab} = 1$; $k_{ba} = 0.333$;

(2) O_b is multiplied with $1 - O_a/Y$ (---); $k_{ab} = 1$; $Y = 10$.

(c) Ratio lines of the two cases of (b).

species (b) with a reduction factor that is a decreasing function of yield or density of the releasing species (a) for example:

$$O_b = z_b (k_{ab} z_a + z_b)^{-1} M_b (1 - O_a/Y)$$

where Y is the yield of species a at which the concentration of the allelochemic is so high that growth of b is zero. The effects of these possible formulations are shown in Figure 18. The differences are small and probably undetectable in experiments. The actual situation will be an intermediate form of the two.

4.9.9 Mutualism

When beneficial or stimulating effects occur in the interaction between species the situation becomes very complicated and the limitations of our simple approach are felt. None the less, some points can be made. First we should distinguish between the donor and the acceptor of a stimulus. The stimulus may be providing access to a resource or alleviating a physical or biological stress. A stimulus becomes only available by the activity of the donor. It is not regarded as a stimulus when the donor first withholds a resource from the acceptor and later on places it at disposal again. A serious misinterpretation is sometimes found in the literature, when it is concluded from an $RYT > 1$ that the species benefit from the presence of each other. Without further information one can only conclude from $RYT > 1$ that the competition between the species is reduced some way or another.

The essential point for coexistence is that the stimulus reinforces the position of the acceptor more at low than at high frequencies of the acceptor, because the strength of the stimulus is positively correlated with the frequency of the donor. The donation may or may not be 'voluntarily' and may or may not be at the expense of the donor, but

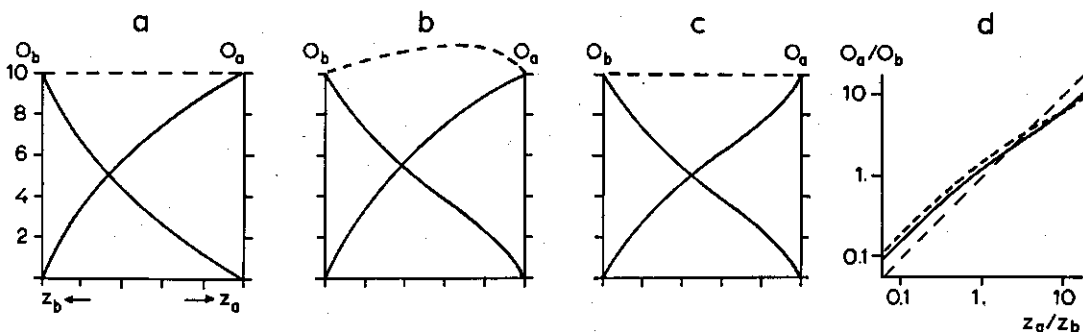


Fig. 19. Graphs illustrating the influence of a beneficial effect of one species on the other on the outcome of competition.

- (a) Replacement diagram without beneficial effect ($k_{ab} = 2$; $M_a = M_b = 10$).
 (b) With a beneficial effect of species a on species b.
 (c) The beneficial effect is compensated by a loss of the 'benefactor' species a.
 (d) Ratio lines derived from Figure b (—) and Figure c (---).

the size of the stimulus cannot be enlarged by 'extortion' at high acceptor frequencies. The effect of the stimulus depends on the density of the acceptor. At low densities it will not be able to take full advantage and its response will be like a yield-density relationship in a 'stimulus space' that decreases with increasing acceptor density. This is represented in Figure 19. This curve is added to the curve that represents the outcome of the competitive processes, resulting in a more or less S-shaped curve. The form of the competitive curves may be various. RYT may be one as well as greater than one in this part of the interaction. There may be a relation between the strength of the stimulus and the competitive ability of the acceptor, which results in a S-shaped curve for the donor also. When the donation of a stimulus goes fully at the expense of growth of the donor, the overall RYT will be one and the frequency dependency of the overall k -values alone has to account for the equilibrium possibilities.

4.10 Explaining frequency dependent competitive ability

In the previous sections we arrived at some possible explanations for the existence of frequency dependent competitive ability. This phenomenon has been observed in several experiments. It has drawn much attention and caused much speculation about its explanations. The experiments give however seldom enough information for a satisfactory explanation of the cause of the observed frequency dependency.

With regard to competition between sexes of *Rumex acetosella* (Putwain & Harper, 1972) and varieties of *Linum usitatissimum* (Khan et al., 1975) differences in growth rhythm have been proposed, but simulation attempts could not provide support for this suggestion (Trenbath, 1978). Differences in growth rhythms and in 'alien' and 'self thinning' due to some unknown mechanism, were proposed as an explanation for frequency dependence in mixtures of *Papaver* species (Harper & McNaughton, 1962). With regard to *Drosophila* experiments preferential use of different parts of the substrate has been suggested (Ayala, 1971; Wallace, 1974), whether or not followed by a disadvantage of mixed populations at

a later stage (Antonovics & Ford, 1972). In legume-grass mixtures the transfer of nitrogen from the legume to the grass has been shown to cause increased yields and competitive ability of the grass and consequently decreased yields of the legume at high legume frequencies (Bakhuis & Kleter, 1965; De Wit et al., 1966). Simulation of competition between plankton species (presumably zooplankton) with different resource uptake and resource conversion functions resulted in S-shaped yield curves in a replacement diagram (Stewart & Levin, 1973). Recently Berendse (1980) obtained S-shaped replacement curves in experiments with the shallow rooting grass (*Anthoxanthum odoratum*) and the deep rooting herb *Plantago lanceolata* growing in long tubes. The curves were of normal shape when the species were forced to root in the same soil layer. Other experimental results showing frequency dependent curves in a replacement diagram are given by Seaton & Antonovics (1967), Chen (1973), Marshall & Jain (1969), Solbrig & Simpson (1974), Keder & Voskuilen (1978) and Rerkasem (1978).

The problem with S-shaped replacement curves is not a lack of possible explanations. With most of the analyses of more complicated ways of competition described in the nine previous sections we arrived at S-curves and possibly more explanations may be found. The problem is in the first place to decide when a deviation from the normal curve with frequency independent relative crowding coefficient is significant. Mostly the number of initial frequencies is too low and the scattering of the observations too high to be sure.

A bigger problem is to decide which explanation fits to an observed S-curve. This cannot be concluded from the shape of the curve since scattering of the observations will certainly make it impossible to detect the minor differences between the curves belonging to different explanations. Detailed information on the spatial, temporal and functional differences between the species and intelligent manipulating of the experimental conditions to eliminate the mechanisms one by one is needed to find a satisfactory explanation for actual cases of frequency dependent competitive ability.

Of all the explanations one could think of environmental heterogeneity, multiple resource competition and changing competitive ability within the season are surely the simplest. Only when these explanations fail should one look for other, increasingly complicated ones, like mutualism or supra-optimal density effects.

5 A model of competition for two nutrients

5.1 INTRODUCTION

Of the mechanisms contributing to coexistence discussed in Chapter 3, I want to examine the possible role of quantitative differences in resource use in more detail. This does not imply, however, that I consider this the most important mechanism. There are several other reasons:

-This mechanism was one of the few left to explain the results of the experiment of Van den Bergh & Elberse (1975) which was the direct motive for our research (see Chapter 6).

-Resource limitation is most probably of interest to plant growth, and differential limitation consequently has to be important in coexistence. The possible effect of quantitative differences in resource use in this is largely neglected and deserves more attention in my opinion.

-Resource limitation can relatively easy be manipulated experimentally, compared to other mechanisms of population regulation.

-Results of experiments on resource limitation are likely to be of interest in other fields of research, ecologically and agriculturally.

To examine the equilibrium possibilities emerging from limitation by different nutrients, I use the model suggested in Section 4.9.3 to describe multiple resource competition for complementary resources. I intend to keep things simple in this exploring phase and use as few parameters as possible in the model. It has the advantage that analytical treatment is possible and of a high degree of generality, which is, however, at the expense of realism.

Before the equilibrium conditions of the model are derived, the validity of its assumptions will be considered in the light of the literature. The conclusions drawn from the equilibrium conditions will be discussed and compared with the literature. The value of the model will be discussed in relation to the possibility to test it experimentally, and in relation to the field situation. Experiments to test the model are described in Part II of this report.

5.2 ASSUMPTIONS

The knowledge necessary to describe the competition for nutrients concerns the nutrient requirements and uptake abilities of plant species, and the influence of their activities on the environment and consequently on their neighbours. These complex characteristics have to be formulated as simple as possible, without violating reality to much.

The nutrient requirements can be expressed as the amount of one or more nutrients a plant needs to produce a certain quantity of biomass, i.e. some internal concentration. Although their nutrient concentrations are variable, plants have specific minimum concentrations of the essential elements ('functional requirements'; Loneragan & Snowball, 1969a), below which no growth is possible. At the minimum concentration growth depends completely on the amount taken up. The minimum content of potassium in dry matter of *Lolium perenne*, for example, is about 200 meq. kg⁻¹. A plant with this internal concentration does not grow. When a little potassium is supplied and taken up the plant grows until the minimum concentration is restored (Van Tuil, 1965).

Because nutrients are important determinants of plant growth primarily when they are limiting, the minimum concentration is a suitable measure for the nutrient requirement, when we are concerned with niche differentiation; better than the 'critical concentration' (above which an increase in concentration is not attended by an increment of growth; Ulrich, 1952) which is more suited to agricultural purposes. Although elements have roughly the same functions in various species, there are many indications that the minimum concentrations may differ (Chapman, 1966). We define the minimum concentration (m) as the quotient between the amount taken up (U) and the maximum yield (O) that is possible on this amount:

$$m = U/O \tag{5.1}$$

and as before we use a and b for the species and 1 and 2 for the resources. For practical reasons this 'minimum concentration' is defined differently from the 'functional requirement' of Loneragan & Snowball (1969a), which was determined on flowing culture solutions and defined as the minimum internal concentration at which growth is not (!) limited (not the internal concentration, but the uptake rate limits growth in this case). From the relation between concentration and relative yield it can be inferred that the numerical values will be about the same (Fig. 20). In accordance with the classical 'Law of the Minimum' of Liebig we suppose that the elements are complementary, which seems reasonable at least at their minimum concentrations, so that the yield of a species is limited by only one element at the time (except when $U^1/m^1 = U^2/m^2$). Consequently the maximum yield that a species can produce is equal to the least of the quotients U/m of all n nutrients involved:

$$O = \text{MIN} \{ U^1/m^1, \dots, U^n/m^n \} \tag{5.2}$$

Experiments show that plants can approach this sharp transition of one limiting factor to the other reasonably well (Boken, 1970; Van Keulen, 1977).

The uptake abilities of a species are often defined in relation to the concentration in the substrate as a hyperbolic saturation function. Dealing with intact higher plants this formulation is however highly complicated by the presence of cation-anion equilibria, competition between ions, possible feedback effects of the internal concentration of the plant, transport processes in the plant, concentration gradients around the roots, and the activities of micro-organisms and fungi. Models using this formulation will cer-

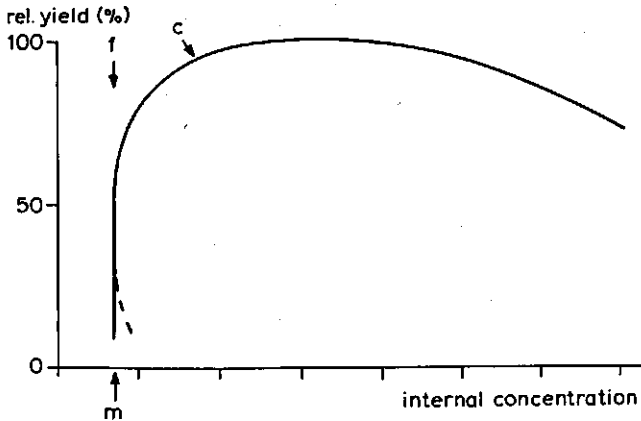


Fig. 20. Relation between the internal nutrient concentration of a plant and its growth rate or yield. (After Bates, 1971):

m = minimum concentration; f = functional requirement; c = critical concentration. The dashed line represents the 'Steenbjerg effect', which frequently occurs when whole plants are analysed (see Section 7.2.2.3.). It can, however, largely be avoided by careful selection of the tissue to be sampled for analysis.

tainly suffer from the problem of acquiring enough information, which makes experimental verification very difficult.

Since we use minimum concentrations as a measure for mineral requirements, we are for the present mainly interested in final yields, which enables us to eliminate the time aspect from the model. We are not interested in uptake rates, but only in the ultimate partition among the species of amounts of minerals supplied. We formulate this partition with the competition formula's of De Wit and evade thereby the complicated way in which it is accomplished.

$$U_a^n = k_{ab}^n z_a (k_{ab}^n z_a + z_b)^{-1} E_a^n$$

$$U_b^n = z_b (k_{ab}^n z_a + z_b)^{-1} E_b^n \quad (5.3)$$

($n = 1$ or 2)

in which U_a^n and E_a^n are the amounts of nutrient n taken up by species a in mixture and monoculture respectively.

The use of these formula's is illustrated by a competition experiment of Hall (1974b) with a *Setaria* and a *Desmodium* variety in which potassium was limiting (Fig. 21). Table 2 gives the relative crowding coefficients (k_{sd} and k_{ds}) of the two species and their products for the different elements and the dry matter production. It follows from the value of this product, calculated for potassium, that the species exclude each other in the potassium uptake, when this element is limiting. This is obvious when all of the potassium is taken up which was probably the case. Since the yield was determined by the uptake of potassium, the product of the dry matter k -values is about unity. Except for nitrogen the other products are about unity as well. It may however not be concluded

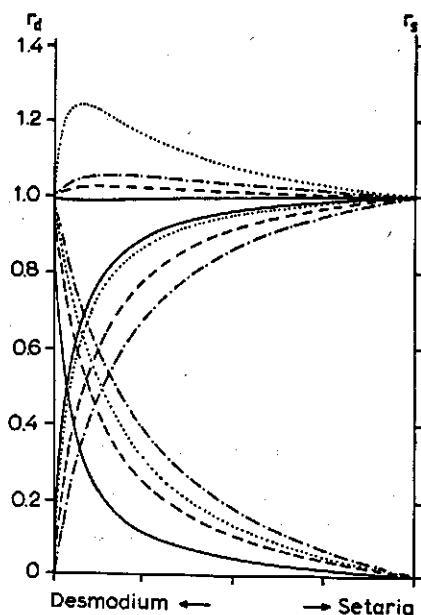


Fig. 21. The relative yield total and the relative yields of *Setaria anceps* and *Desmodium intortum* grown in a replacement series without added potassium (From Hall, 1974b). (---) dry matter, (—) potassium, (-.-.-) phosphorus, (....) nitrogen.

that the species exclude each other in the uptake of these elements too, because they were not limiting. There merely was no reason why the internal concentrations of these elements would be different in monoculture and mixture and, consequently, their k -values are about the same as the dry matter k -values. Nitrogen supply was not ample and since there was the possibility of using different nitrogen sources (*Desmodium* is a legume) the nitrogen nutrition in the mixtures could be improved compared to that in the monocultures, resulting in a nitrogen k -product being greater than unity. This could not influence the yields, because these were set by the potassium supply.

In another experiment this limitation was redressed by supplying extra potassium, and the dry matter k -product as well as the other products followed the nitrogen k -product up to values of about 5. It will be clear that the Equations 5.3 do not hold for

Table 2. Relative crowding coefficients, k_{sd} and k_{ds} , and their product for yield and nutrient uptake in a competition experiment with a *Desmodium* variety (d) and a *Setaria* variety (s) under potassium limitation. (From Hall, 1974 b).

	k_{sd}	k_{ds}	$k_{sd} k_{ds}$
Dry matter	10.08	0.11	1.11
Nitrogen	18.28	0.15	2.74
Phosphorus	5.98	0.21	1.26
Potassium	23.88	0.04	0.96
Magnesium	7.22	0.15	1.08
Calcium	6.45	0.17	1.10

nitrogen. We are certain they do so only for potassium, because the other elements were not limiting.

In spite of the fact that plant species are known to differ in the relative amounts in which nutrients are taken up (Collander, 1941; Horak & Kinzel, 1971; Loneragan & Snowball, 1969b) it was argued that the abilities of a species to compete for different resources will be strongly positively correlated (Grime, 1977). As a consequence equilibria resulting from a differentiation with respect to the limiting factor would be improbable. The experiments of Hall (1974) show indeed a strong positive correlation of the k-values of different nutrients. There are however also considerable differences between a species' k-values for different nutrients (compare the potassium and magnesium k-values in Table 2).

In the model we assume that the species exclude each other in the uptake of the separate nutrients and that the amounts supplied (E) are completely taken up:

$$E_a^n = E_b^n = U_a^n + U_b^n = E^n$$

The initial amounts in the plants are assumed to be negligible compared to the amounts taken up. It is important to realize that the k-values depend on conditions, e.g. substrate composition, and change in time until all nutrients are taken up.

The above assumptions lead to the model of competition for two complementary resources as represented schematically in Figure 22.

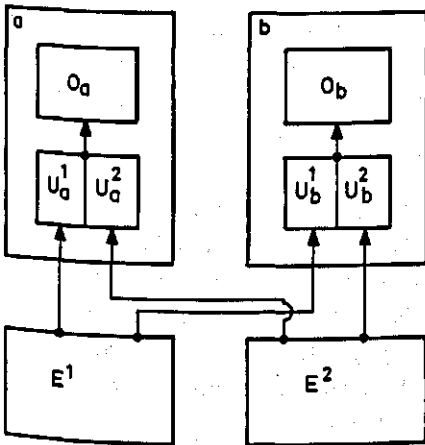


Fig. 22. Model of the competition for two complementary resources. Explanation in text.

$$O_a = \text{MIN} \{ (U_a^1/m_a^1), (U_a^2/m_a^2) \} \quad (5.2)$$

$$O_b = \text{MIN} \{ (U_b^1/m_b^1), (U_b^2/m_b^2) \} \quad (5.3a)$$

$$U_a^1 = k_{ab}^1 z_a (k_{ab}^1 z_a + z_b)^{-1} E^1 \quad (5.3b)$$

$$U_a^2 = k_{ab}^2 z_a (k_{ab}^2 z_a + z_b)^{-1} E^2$$

$$U_b^1 = z_b (k_{ab}^1 z_a + z_b)^{-1} E^1 \quad (5.3b)$$

$$U_b^2 = z_b (k_{ab}^2 z_a + z_b)^{-1} E^2$$

Symbols:

a and b are species

1 and 2 are resources

O = yield

U = amount taken up

E = amount present

m = minimum internal concentration

k = relative crowding coefficient

z = relative plant frequency

5.3 DERIVATION OF EQUILIBRIUM CONDITIONS

Hereafter equilibria will be defined as

$$RRR_{ab} = \alpha_{ab} = 1 \quad (2.1)$$

in which

$$\alpha_{ab} = (0_a/0_b)/(z_a/z_b) \quad (5.4)$$

This means that some conditions discussed in Section 4.4 are presupposed. The equilibrium point or equilibrium ratio is indicated as $(z_a/z_b)^*$. Global stability requires that

$$\lim_{z_a/z_b \rightarrow 0} \alpha_{ab} > 1 > \lim_{z_a/z_b \rightarrow \infty} \alpha_{ab} \quad (4.4)$$

Instability applies when the inequality signs in Equation 4.4 are reversed.

Neutral equilibria require equalities instead of inequalities in Equation 4.4.

In a species mixture two situations are possible:

- both species are limited by the same nutrient;
- the species are limited by different nutrients.

(The possibility that the species are limited by both nutrients at the same time is left out of consideration.) The conditions for stable equilibria require that α is frequency dependent at least near the equilibrium point. Since we assumed that the species exclude each other in the uptake of the separate nutrients, α is not frequency dependent in the first of the above situations which can be readily seen by substituting Equations 5.3 in Equation 5.4.

Therefore we will concentrate on the second situation and choose the case in which species a is limited by nutrient 1 and species b by nutrient 2. First we will derive the conditions to be met to realize this combination of limiting factors. Then we will combine these conditions with additional conditions for the realization of an equilibrium point, assuming that a is limited by 1 and b by 2. To facilitate understanding of these conditions we represent in Figure 23 the ratio lines of an imaginary species combination, meeting the conditions, at a number of substrate compositions.

5.3.1 Conditions for limitation by different nutrients

When species a is limited by nutrient 1 and species b by nutrient 2 the following applies:

$$U_a^1/m_a^1 < U_a^2/m_a^2 \text{ and } U_b^1/m_b^1 > U_b^2/m_b^2$$

$$\text{or } U_a^1/U_a^2 < m_a^1/m_a^2 \text{ and } U_b^1/U_b^2 > m_b^1/m_b^2$$

(5.5)

by substituting Equations 5.3 we obtain:

$$(k_{ab}^1/k_{ab}^2) (E^1/E^2) Q < (m_a^1/m_a^2) \text{ and } (E^1/E^2) Q > (m_b^1/m_b^2) \quad (5.6)$$

$$\text{in which } Q = (k_{ab}^2 z_a + z_b) (k_{ab}^1 z_a + z_b)^{-1} \quad (5.6')$$

Q is frequency dependent

$$\lim_{z_a/z_b \rightarrow 0} Q = 1 \text{ and } \lim_{z_a/z_b \rightarrow \infty} Q = k_{ab}^2/k_{ab}^1 \quad (5.7)$$

By combining the Equations 5.6 we obtain the condition to realize the situation in a species mixture in which a is limited by nutrient 1 and b by nutrient 2:

$$(m_b^1/m_b^2) < (E^1/E^2) Q < (k_{ab}^2/k_{ab}^1) (m_a^1/m_a^2) \quad (5.8)$$

The range described by Equation 5.8 is real only if the upper limit is greater than the lower limit. This imposes on the species characteristics k and m the condition that:

$$k_{ab}^1 (m_b^1/m_a^1) < k_{ab}^2 (m_b^2/m_a^2) \quad (5.9)$$

$$\text{or } k_{ab}^1/k_{ab}^2 < (m_a^1/m_a^2)/(m_b^1/m_b^2) \quad (5.10)$$

We recognize in the terms of Equation 5.9 the values of α , when both species are limited by nutrient 1 or 2 respectively.

By reversing the inequalities in Equation 5.8, 5.9 and 5.10 we obtain the conditions for limitation of species a by nutrient 2 and species b by nutrient 1. As the species meet the conditions of Equation 5.10 more liberally, which requires a great discrepancy between the uptake ratio U^1/U^2 and the requirement ratio m^1/m^2 of each species, more substrate compositions and initial plant frequencies are possible at which differential limitation can be realized.

5.3.2 Additional conditions for stable equilibrium

When species a is limited by nutrient 1 and species b by nutrient 2, i.e. when Equation 5.8 is met, α can be written as:

$$\alpha_{ab} = (0_a/0_b)/(z_a/z_b) = \{(U_a^1/m_a^1)/(U_b^2/m_b^2)\}/(z_a/z_b)$$

Substitution of Equations 5.3 yields:

$$\alpha_{ab} = k_{ab}^1 (m_b^2/m_a^1) (E^1/E^2) Q \quad (5.11)$$

Equilibrium being defined by $\alpha = 1$, the following equation holds in equilibrium:

$$Q^* = (1/k_{ab}^1) (m_a^1/m_b^2) (E^2/E^1) \quad (5.12)$$

From Equation 5.6' we arrive after some rearrangements at:

$$z_a/z_b = (1 - Q)/(k_{ab}^1 - k_{ab}^2) \quad (5.13)$$

Combination of Equation 5.13 with Equation 5.12 gives the equilibrium ratio:

$$(z_a/z_b)^* = \{1 - (1/k_{ab}^1) (m_a^1/m_b^2) (E^2/E^1)\} / \{(m_a^1/m_b^2) (E^2/E^1) - k_{ab}^2\} \quad (5.14)$$

It appears that the frequency of the species in equilibrium is determined by the substrate composition (E^1/E^2). The equilibrium disappears when the numerator or the denominator of Equation 5.14 runs to zero; this is when:

$$E^1/E^2 \rightarrow (1/k_{ab}^1) (m_a^1/m_b^2) \text{ or}$$

$$E^1/E^2 \rightarrow (1/k_{ab}^2) (m_a^1/m_b^2)$$

In deriving Equation 5.14 it was assumed that Equation 5.8 is met. This condition restricts the values that (E^1/E^2) and in most cases Q and consequently (z_a/z_b) may take, so that not all of the equilibrium ratios described by Equation 5.14 exist. At least around the equilibrium point itself the formulation of α used to calculate this point must be correct; i.e. Equation 5.8 has to be met when $\alpha = 1$. Since Equation 5.12 can be rewritten as:

$$Q^* (E^1/E^2) = (1/k_{ab}^1) (m_a^1/m_b^2)$$

Equation 5.8 requires that

$$(m_b^1/m_b^2) < (1/k_{ab}^1) (m_a^1/m_b^2) < (k_{ab}^2/k_{ab}^1) (m_a^1/m_a^2)$$

or

$$(k_{ab}^1/k_{ab}^2) < (1/k_{ab}^2) (m_a^1/m_b^1) < (m_a^1/m_a^2)/(m_b^1/m_b^2) \quad (5.15)$$

which is an extension of Equation 5.10. The equilibrium points described by Equation 5.14 exist only, when the species characteristics meet this extended condition.

The equilibrium point is stable when α decreases with increasing plant frequency. It is seen from Equation 5.11 that Q , which is the only frequency dependent term in α , has to decrease with decreasing z_a/z_b , for the equilibrium points to be stable. It follows from Equation 5.6' that this occurs, when k_{ab}^1 is greater than k_{ab}^2 or:

$$1 < k_{ab}^1/k_{ab}^2 \quad (5.16)$$

It appears that when an equilibrium point exists, it depends solely on the two k-values, whether it is stable or unstable.

The complete set of conditions that the species characteristics have to meet for the occurrence of a stable equilibrium point is the combination of Equations 5.15 and 5.16:

$$1 < (k_{ab}^1/k_{ab}^2) < (1/k_{ab}^2) (m_a^1/m_b^1) < (m_a^1/m_a^2)/(m_b^1/m_b^2) \quad (5.17)$$

Subsequently the conditions for the substrate composition have to be considered. These conditions follow from the condition for stability (Equation 4.4). From Equations 5.11 and 5.7 it is seen that

$$\lim_{z_a/z_b \rightarrow 0} \alpha_{ab} = k_{ab}^1 (m_b^2/m_a^1) (E^1/E^2) \quad \text{and} \quad \lim_{z_a/z_b \rightarrow \infty} \alpha_{ab} = k_{ab}^2 (m_b^2/m_a^1) (E^1/E^2)$$

Substitution in Equation 4.4 yields the equilibrium conditions for the substrate composition:

$$(1/k_{ab}^1) (m_a^1/m_b^2) < (E^1/E^2) < (1/k_{ab}^2) (m_a^1/m_b^2) \quad (5.18)$$

We recognize in these limits of E^1/E^2 the values at which the equilibrium point (Equation 5.14) disappears.

The conditions for stable equilibrium, when species a is limited by nutrient 2 and species b by nutrient 1, can be derived analogous to the above. These conditions are for the species characteristics:

$$1 > (k_{ab}^1/k_{ab}^2) > (1/k_{ab}^2) (m_a^1/m_b^1) > (m_a^1/m_a^2)/(m_b^1/m_b^2) \quad (5.17')$$

and for the substrate composition:

$$k_{ab}^1 (m_b^1/m_a^2) < (E^1/E^2) < k_{ab}^2 (m_b^1/m_a^2) \quad (5.18')$$

If the initial plant ratio is such that Equation 5.8 is not met, the formulation of α (Equation 5.11) is incorrect, because the species are limited by the same nutrient. The ratio line is frequency independent at that plant ratio. It is however not necessary that Equation 5.8 holds for every possible initial plant ratio as long as it applies around the equilibrium ratio.

We will illustrate this point and some other points with the help of Figure 23. The figure shows that some of the ratio lines are 'cut off' so to say, by a straight line parallel to the diagonal.

There are two of such lines; they are the ratio lines when both species are limited by

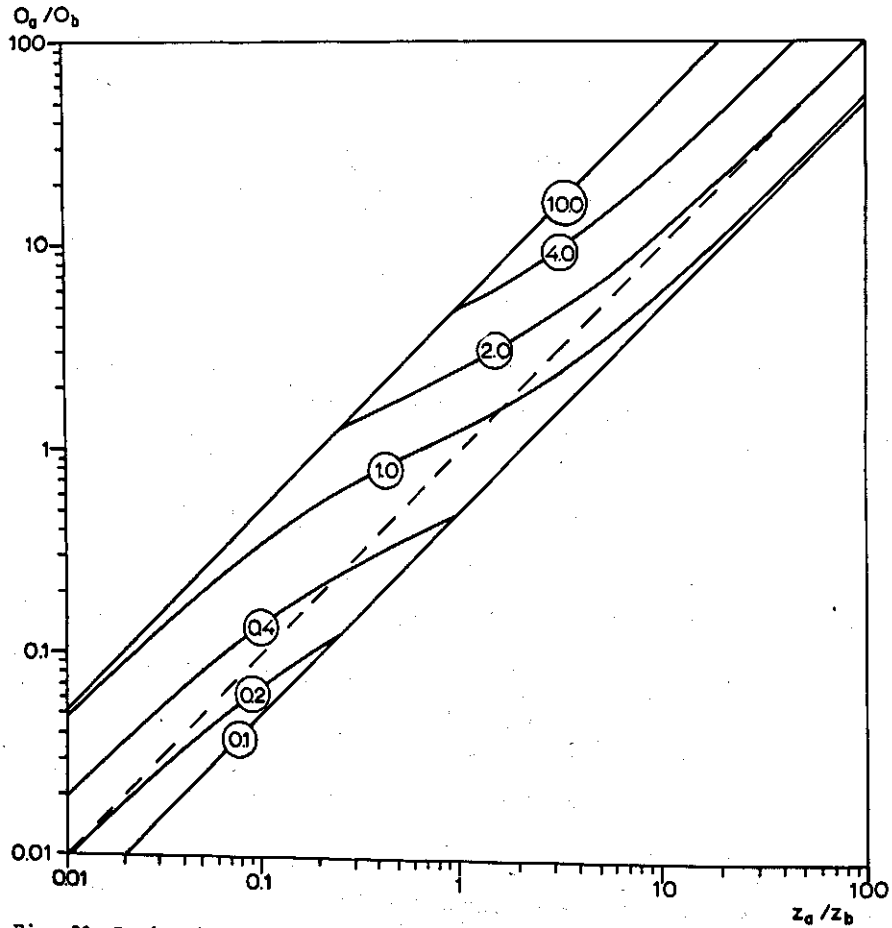


Fig. 23. Ratio diagram of a hypothetical species combination meeting the equilibrium conditions (Eqn. 5.17), calculated according to the model of Figure 22 at different substrate compositions ($E^1/E^2 = 0.1; 0.2; 0.4; 1.0; 2.0; 4.0; 10.0$). $m_a^1 = m_b^2 = 100; m_a^2 = m_b^1 = 10; k_{ab}^1 = 5; k_{ab}^2 = 0.5$.

nutrient 1 or nutrient 2, and they represent the two frequency independent values of α :

$$\alpha_{ab} = k_{ab}^1 (m_b^1/m_a^1) \text{ if nutrient 1 limits both species,}$$

$$\alpha_{ab} = k_{ab}^2 (m_b^2/m_a^2) \text{ if nutrient 2 limits both species.}$$

The frequency dependent part of the ratio line (at the frequencies where the species are limited by different nutrients) is necessarily bounded by these two frequency independent limiting ratio lines. Equilibria are only possible when these lines lie on either side of the diagonal. This visualises part of the equilibrium conditions (Equation 5.17).

The form and position of the frequency dependent part of the ratio line are involved in the other part of the equilibrium conditions (Equation 5.18). The position of the ratio line is determined by the position of its asymptotes relative to the diagonal. The form

of the ratio line is determined by the position of the asymptotes relative to each other. The asymptotes correspond with the following two extreme values of α (disregarding the limits set by the two frequency independent lines discussed before and assuming that a is limited by 1 and b by 2):

$$\lim_{z_a/z_b \rightarrow 0} \alpha_{ab} = k_{ab}^1 (m_b^2/m_a^1) (E^1/E^2)$$

$$\lim_{z_a/z_b \rightarrow \infty} \alpha_{ab} = k_{ab}^2 (m_b^2/m_a^1) (E^1/E^2)$$

The second part of the equilibrium conditions is visualized by the fact that these two asymptotes have to lie on either side of the diagonal as well. It can be seen that a possible stable equilibrium point will be reached from whatever initial plant frequency, even if the ratio line is not frequency dependent at one or both of its ends.

The quotient k_{ab}^1/k_{ab}^2 being greater or smaller than unity determines which asymptote lies above the other and, consequently, the stability or instability of a possible equilibrium point. The position of the ratio line determines whether it intersects the diagonal and consequently the existence and place of an equilibrium point. Changing the substrate composition shifts the ratio line up or down, causing the equilibrium point to move along the diagonal or disappearing eventually. The size of the range of substrate conditions allowing coexistence is solely determined by the extent to which the quotient k_{ab}^1/k_{ab}^2 exceeds unity, i.e. the difference between the species with respect to their

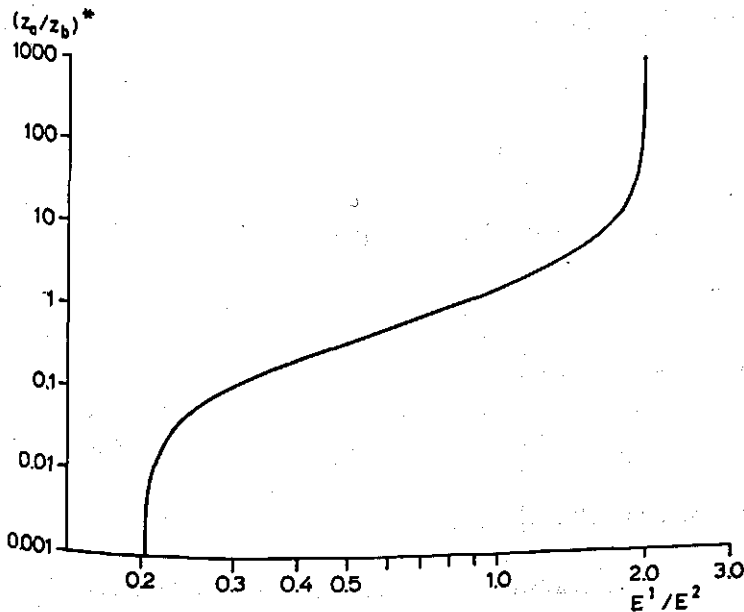


Fig. 24. Relation between the substrate composition (E^1/E^2) and the equilibrium ratio $(z_a/z_b)^*$ of the species of Figure 23.

uptake ratio's. The relation between the equilibrium ratio and the substrate composition is represented separately in Figure 24. The maximum possible elasticity of a stable equilibrium point is determined by the distances of the frequency independent ratio lines to the diagonal; i.e. by the superiority of each species in his own domain.

5.3.3 Relation between RYT and equilibria

Since an RYT value is easier to obtain experimentally than a ratio diagram, we are interested whether the $RYT > 1$ can be used as an indication of an equilibrium possibility as demonstrated in Section 4.6.

When the species are limited by different nutrients (viz. a by 1 and b by 2) at all initial plant frequencies the relative yield of species a is:

$$r_a = 0_a/M_a = (U_a^1/m_a^1)/(E^1/m_a^1) = U_a^1/E^1 = U_a^1/(U_a^1 + U_b^1)$$

and analogous to species b:

$$r_b = U_b^2/(U_a^2 + U_b^2)$$

Therefore $RYT > 1$ means that

$$U_a^1/(U_a^1 + U_b^1) + U_b^2/(U_a^2 + U_b^2) > 1$$

By multiplication we obtain:

$$U_a^1(U_a^2 + U_b^2) + U_b^2(U_a^1 + U_b^1) > (U_a^1 + U_b^1)(U_a^2 + U_b^2)$$

This can be reduced to:

$$(U_a^1/U_a^2)/(U_b^1/U_b^2) > 1$$

which after substitution of Equation 5.3 appears to be equal to

$$k_{ab}^1/k_{ab}^2 > 1$$

Similarly, it can be shown that an $RYT < 1$ means

$$k_{ab}^1/k_{ab}^2 < 1$$

when a is limited by 1 and b by 2 at all frequencies.

It is a fundamental assumption in our model that $RYT = 1$ when the species are limited by the same nutrient. This assumption however concerns only the case in which the species in monocultures as well as in mixtures are limited by the same nutrient. We have shown that the conditions for limitation by different elements (Equation 5.8) may

restrict the possible range of initial plant frequencies. While at high frequencies species a is limited by nutrient 1, species b may take up so much of nutrient 2 at low frequencies of a that it becomes limiting to a as well as to b. This occurs when the ratio line is "cut off" by a straight line parallel to the diagonal (Fig. 23).

Both species are limited by the same nutrient at the frequencies on the linear part of the ratio line. Yet the RYT is greater than unity at these frequencies, as can be seen from Figure 25, because in monoculture one of the species is limited by a different element than in the mixtures with the lower frequencies. (See also Figure 12, the middle part, where a neutral equilibrium is accompanied with $RYT > 1$). The $RYT > 1$ is a result of a reduced luxury consumption in the mixture compared with the monocultures. In the mixture each species has to give up some of the nutrient which is not limiting in the monoculture, in favour of the other species which is able to use it in extra growth. In the mixture the nutrients are used more efficiently because, due to each others uptake activities, the uptake ratio of each species is shifted in the direction of the optimum ratio which is the ratio between the minimum concentrations.

The reverse is also possible. The luxury consumption is increased in a mixture compared to monocultures, when the species are limited by different elements and each species competes best for the very element that limits the other species, that is when Equation 5.8 is met and

$$k_{ab}^1/k_{ab}^2 < 1$$

Thus $RYT < 1$ is possible when:

$$k_{ab}^1/k_{ab}^2 < 1 < (m_a^1/m_a^2)/(m_b^1/m_b^2)$$

This is an alternative explanation for $RYT < 1$ in addition to the possibility of allelopathic effects.

In conclusion one can say that an $RYT > 1$ indeed shows that part of the equilibrium conditions is met, viz. that of $k_{ab}^1/k_{ab}^2 > 1$. Whether or not there is an equilibrium point cannot be inferred from the RYT.

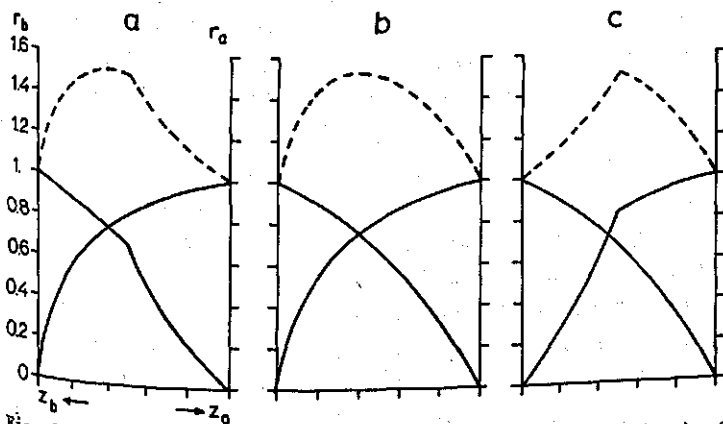


Fig. 25. Relative yields (—) and relative yield totals (---) of the species of Figure 23 at three substrate compositions: (a) $E^1/E^2 = 0.4$; (b) $E^1/E^2 = 1$; (c) $E^1/E^2 = 4$.

5.4 DISCUSSION

The model demonstrates that the combination of differences in nutrient requirements and uptake abilities offers the theoretical possibility of stable equilibria between plant species in a homogeneous environment. Bradshaw (1969) suggested this already. Philips (1973) showed the theoretical possibility of equilibria between phytoplankton species under continuous flow conditions.

Stewart & Levin (1973) considered two modes of resource exploitation: an 'equable mode' which occurs in a continuous flow system, and a 'seasonal mode' in which the resources are presented discontinuously and are exhausted each 'season'. Only a small fraction of the population is transferred to the next season. The seasonal model most resembles our model, but an important difference is that Stewart & Levin probably did not have phytoplankton in mind, but zooplankton or bacteria, because they used substitutable resources.

The simulation model of Petersen (1975) uses complementary resources. It contains no new supply of nutrients; instead it assumes a constant death rate and complete remineralization. Both the seasonal model of Stewart & Levin and the 'recycling' model of Petersen are based on Michaelis-Menten uptake kinetics. Both models show just like ours that species may coexist in homogeneous environments, while sharing resources, without violating the competitive exclusion principle. Petersen however did not include a stability analysis. Other model studies showing the theoretical possibility of coexistence between species that use the same resources are presented by Taylor & Williams (1975), by Leon & Tumpson (1975); who emphasize the difference between complementary and substitutable resources, and by Titman (1976).

Titman used a model with complementary resources, based on Michaelis-Menten kinetics and adapted to continuous flow conditions. Moreover he showed that the results of 73 competition experiments with two species of fresh water diatoms, conducted at various nutrient ratios (SiO_2/PO_4) were in general agreement with the predictions of the model. These predictions were similar to our Figure 24. All three possible outcomes were observed: coexistence and dominance of one or the other species. When a species comprised 95% or more of the total number of cells it was said to be dominant. If neither species had attained dominance at the end of the experiment (after 40 days) the results were termed "coexistence". Unfortunately, Titman had no means of judging the stability of the equilibria. It would have been profitable to include one or more replacement series in the experiments.

More recently, Tilman (1977, note the change of name) showed that the same results can be predicted by another model which he called 'the variable internal store model'. This model assumes that the internal nutrient concentrations determine the growth rate and that these concentrations are determined by the joint processes of growth and nutrient uptake, assumed to follow a Michaelis-Menten process. The model resembles ours in that both contain some minimum internal concentration and allow for luxury consumption. In this respect they are more realistic than the ones discussed above. Our model differs from these plankton models in that it dispenses with the factor time.

A great advantage of all these mechanistic resource-based models of competition, over descriptive models like that of Lotka and Volterra, is that they emphasize the role of the resource supply in determining the outcome of competition. I will elaborate this point with the help of our own model. The equilibrium conditions show that not all species may coexist in the way described by the model and that those that can, will coexist only in a specific range of environments. From Figure 24 we can see what happens when we change the environmental conditions, i.e. the substrate composition. In the centre of the range of environments the equilibrium ratio of this imaginary species combination is about unity. When we go to the limits of the range the equilibrium ratio shifts in favour of one species or the other. Outside the range the equilibrium degenerates to a monoculture of one of the species. We can imagine from this figure how unbalanced fertilizing may change the substrate in such a way that an equilibrium between species shifts and eventually disappears.

In the model only the ratio of the nutrients is important, because there are only two resources involved. Actually the concentrations of the nutrients are important as well. If too much of two limiting nutrients is added, an equilibrium will be disturbed, even if the right proportion is added, because the limitation is removed and other resources, probably not permitting coexistence, will come into the minimum. After a complete and heavy dressing nutrients will no longer be limiting. In this situation, which is probably realized in many cultivated grasslands, the possibility of coexistence by differentiation with respect to nutrient use is eliminated and light will be the predominant limiting factor for most species. This explains the low diversity in heavily fertilized grasslands, since there are only few possibilities of coexistence when only one factor is limiting.

Another interesting point is that our model sheds some light on the species patterns on environmental gradients. Species that meet the equilibrium conditions will gradually replace each other along a gradient as represented in Figure 26. In the transition zone the species coexist, because they have different niches (i.e. they are limited by different nutrients). If the species do not meet the equilibrium conditions or when other conditions make coexistence impossible, the transition zone is reduced to zero and the species will coexist only along a sharp borderline across the gradient. These two situations mimic the 'limes divergens' and the 'limes consergens' respectively, as described by Van Leeuwen (1966). When some micro-environmental heterogeneity is added to the gradient, as is done in Figure 27, the species patterns look even more natural, closely resembling the fine and smooth patterns in stable environments and the course and sharp patterns in fluctuating environments respectively.

From the above it is seen that the same differences between species characteristics may lead to niche differentiation as well as to habitat differentiation, depending on the conditions. It is therefore fundamentally impossible to measure actual niche overlap from species-characteristics, as is often attempted. This may not tempt us, however, to let the concepts of niche and habitat merge into a multi-dimensional niche, because evidently habitat differentiation and niche differentiation lead to fundamentally different ways of coexistence, which is expressed in different species patterns.

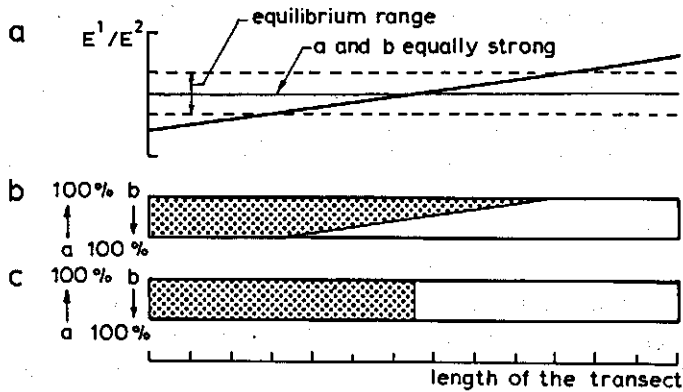


Fig. 26. Species patterns in a transect along an environmental gradient on which two species are growing.
 (a) Substrate composition (E^1/E^2) along the gradient.
 (b) Relative equilibrium density of species a (open) and b (dotted) when the equilibrium conditions (Eqn. 5.17) are met.
 (c) As in (b) when the equilibrium conditions are not met.

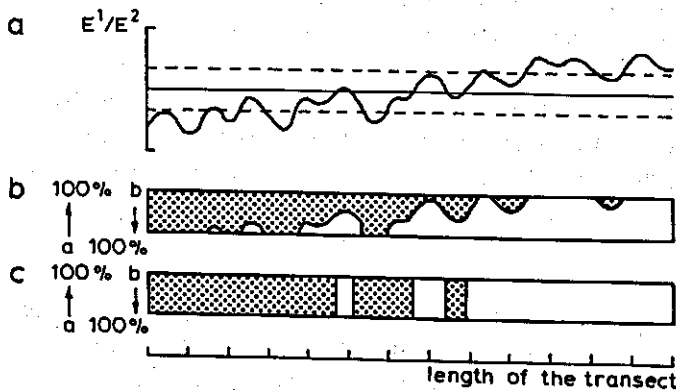


Fig. 27. Transect as in Figure 26 with micro-environmental heterogeneity added to the gradient.

An important question is whether the equilibrium conditions for the species are likely to be met or not. I already mentioned that species may differ in their relative requirements and uptake abilities of nutrients, but will these differences be in accordance with the equilibrium conditions of our model? It can be concluded from the literature and from our own experiments (see following chapters) that the differences may be great, but in most cases they are not. A reason for the supposition that the differences between coexisting species will not be great is that the species have to be adapted to the same environment. This would mean that for most species combinations the equilibrium conditions for the environment are rather strict and that the elasticity of equilibrium points will generally be low. In most cases, however, other mechanisms that are more robust, like those based on micro-environmental heterogeneity, will be acting together with the mechanism of differential resource limitation which may therefore be more important than when it was acting on its own.

In addition it should be realized that the possible number of combinations of species and limiting factors is infinitely large and no doubt there are species combinations which freely meet the equilibrium conditions. When in the course of time these species arrive in the appropriate place their combination will be preserved. The chance of differential resource limitation being important in keeping up species richness may not be judged by the chance of any species combination meeting the conditions, but only by investigating whether species that are actually living together meet the conditions or better whether they are limited by different nutrients. It does not seem impossible that natural selection of species living in a species mixture increases the extent to which the equilibrium conditions are met (Antonovics, 1978), but this remains to be investigated more deeply.

The last but not least points to be discussed concern the practicability of the model:

- Is it possible to confirm the conclusions from the model experimentally for terrestrial plants?
- Is it allowed to apply the conclusions from such a simple model to the field situation as we did above?

With respect to both questions I am rather optimistic, taking into account that Tilman (1977) both proved the predictions of his model to be valid and showed that they could be applied to the field situation, be it that this field situation was less complicated than ours. At least he demonstrated that the basis of this kind of models is sound. However, the complexity inherent to higher plants and terrestrial environments may pose some problems in the experimental verification of our model.

The model can be verified by its predictions, when they are non-trivial. Since competitive exclusion is observed in most experiments, the prediction that a stable equilibrium is not possible is trivial, unless the reason for this impossibility can be determined, which is very difficult. Verification of predicted stable (or unstable) equilibria is more significant, because these occur less frequently. The additional evidence of the species being limited by different elements would none the less be useful. For a prediction we first have to investigate the species characteristics involved for a number of species and nutrients. Then we have to choose a suitable species-nutrients combination to test the predicted non-trivial outcome of a competition experiment with these species when both nutrients are limiting.

Several problems can be foreseen, brought about by the simplicity of the model or rather by the complexity of reality. A complication occurs in determining the minimum concentrations, when these concentrations depend on conditions like age, history and parts of the plant. It is also known that in several species certain nutrients may substitute for each other functionally to some extent (Bollard & Butler, 1966; Smith, 1974).

More serious problems will arise in determining the relative crowding coefficients for the separate nutrients, because the model assumes that the processes of uptake and growth are separated. Actually, there is a positive feedback of growth and uptake ability of the species relative to each other. A small initial advantage in uptake rate will be amplified in the course of time, because it induces an advantage in growth which in

turn causes an additional advantage in uptake rate and so on. Consequently, the k-values will depend on which element determines growth rate and have to be determined at a number of substrate compositions. A similar positive feedback occurs between root and shoot competition (Trenbath, 1976). Although no allowance is made for shoot competition in the model, it will be difficult to prevent completely in experiments.

These problems occur also in the final test experiment, which should consist of several replacement series grown on a number of substrate compositions, in- and outside the equilibrium range. Since the model is based on maximum yields and minimum concentrations the species must be allowed to continue growth until they are stopped by deficiency. At that time the plants will have a most unnatural appearance. It is however an inevitable consequence of a simplistic model that nature has to be forced into a straitjacket to verify the essential conclusions of the model. The conditions in the test experiment have to be adapted to those under which the parameters have been determined and vice versa.

Since absolute k-values have to be determined in a competition experiment, we can combine this with the test experiment. Fortunately, it is possible to determine the quotient of the k-values from monocultures, because substitution of the Equations 5.3 shows that

$$(U_a^1/U_a^2)/(U_b^1/U_b^2) = (U_a^1/U_b^1)/(U_a^2/U_b^2) = k_{ab}^1/k_{ab}^2$$

U_a^1/U_a^2 and U_b^1/U_b^2 can be found in monoculture. This enables us to check whether a species combination meets part of Equation 5.17, and thereby reduce the number of competition experiments necessary to find a suitable species combination and to verify the model.

The consequence of the above complications for the execution of experiments and the evaluation of the model come up for discussion in Part II of this report. Although it would have been more convenient to avoid complications by improving the model first, an attempt was made to obtain a verification already, because knowledge was still insufficient and the experience of possible failures could be used in improving the model.

It is an act of faith to think that the mechanism of differential nutrient limitation, leading to equilibria in the simple experimental situation, should do so in the complex field situation. When equilibria are not attained because of continuous disturbances, I expect at least a stabilizing influence. Of course it cannot be expected that every species combination that attained equilibrium in an experiment will do so in the field situation, whenever the nutrient ratio agrees with the equilibrium conditions. There are too many differences between these situations. Think only of the different presentation of the nutrients, the presence of environmental fluctuations in the field situation, more competing species, more limiting factors, predation, pests and winter mortality.

It is difficult to prove the existence of any specific mechanism in the field. In a field competition experiment a tendency to a stable equilibrium can be established and some insight into its origin can be acquired by investigating the limiting factors. In an actual vegetation only the continuous co-occurring of species can be ascertained and the limiting factors investigated as already mentioned. A comparative research into the limitation of different species living next to each other is considered important.

To examine the possibility of differential nutrient limitation I suggest addition of different nutrients to plants of various species in a vegetation, in combination with removal of competitors to discriminate between the primary effects via competitive interactions. Most data of differential responses of species in natural vegetation to nutrient addition, available at present, are affected by the difficulty of discriminating between these effects.

Changes in botanical composition of grasslands as a result of fertilization are commonly observed, but in many cases these are brought about by the higher production level and the resulting increase in light competition, which favours the tall and fast growing species. Little can be inferred from such experiments about the factors limiting in the original situation. None the less differential nutrient limitation was shown to be very plausible in several instances; notably between grasses and legumes, the grasses being limited by nitrogen and the legumes by phosphorus or potassium (Van den Hende et al., 1952; Thurston et al., 1976). Addition of nutrients in dune vegetation carried out by Willis (1963) suggest that grasses were limited by phosphorus and sedges by nitrogen.

In addition to this experimental approach I suggest that much information about the occurrence of differential nutrient limitation is to be expected from observation of deficiency symptoms and especially from diagnosis of limiting nutrients with the help of chemical plant analysis.

Part II Experiments

In the next chapters a number of experiments will be discussed that were carried out partly to find an explanation for the results of an experiment of Van den Bergh & Elberse (1975) in which high RYT values indicated some niche differentiation (Chapter 6), and partly to examine the model of multiple nutrient competition, its assumptions and predictions (Chapter 7). The experiments will be discussed in relation to the views presented in the previous chapters. It should be realized that these views were developed during and partly after the experimental designs. It was however preferred to present them together instead of scattered all over the discussion of the experiments.

6 Field trials

6.1 A FIELD TRIAL WITH MULTI-SPECIES MIXTURES

The direct reason for the research presented here lies in the results of an experiment of Van den Bergh & Elberse (1975), see also Van den Bergh & Braakhekke (1978), with multi-species mixtures, carried out on a poor sandy soil at the experimental farm 'De Sinderhoeve' at Renkum near Wageningen. Seeds of 7 grass species and 6 grassland herbs, collected in 1970 from an old hay field, were sown on 3.5 m^2 plots in August 1971, including monocultures and various mixtures according to the replacement principle, replacing 1 herb seed by 3.2 grass seeds. The sowing density was 1600 viable seeds per m^2 of the grasses and 500 seeds per m^2 of the herbs in the monocultures. An area of $90 \times 90 \text{ cm}^2$ was harvested in each plot in July of the next two years and dry weights of the separate species were determined. Table 3 shows the relative yields of the species in the first and the second year in the various mixtures. 100/0 means that the seed mixture consisted of the grass species in equal proportions only; 75/25 means that the grass species were sown at 75% and the herb species at 25% of the monoculture densities. 0/100 means that the mixture consisted of the 6 herbs only.

Two herbs *Prunella vulgaris* and *Ranunculus repens* disappeared already in the first year, due to very slow establishment. In this first year *Lolium perenne* was by far the most aggressive species with very high relative yields.

It appears that the RYT of the mixture involving grass species only is about equal to one, which means that the species occupy the same niche. With the introduction of herbs in the mixtures the RYT becomes greater than one. Obviously, the grasses and the herbs show some niche differentiation. Finally the herbs among themselves show the greatest niche differentiation: RYT = 1.41.

In the second year *Lolium perenne* has almost disappeared, probably because no fertilizers were given (compare also the total absolute yields of the mixtures at the bottom of Table 3). Instead *Agrostis tenuis* has taken over the dominating position, whereas *Hordeum secalinum* and *Centaurea pratensis* have disappeared entirely. Here too, the RYT values increase from about 1 to 1.45 in passing from pure grass mixtures to pure herb mixtures. In the second year in the mixtures with herbs only the sum of the relative yields of *Chrysanthemum leucanthemum* and *Plantago lanceolata* (even on their own) is greater than 1, viz. 1.26.

This result is remarkable in view of the fact discussed in Section 4.8 that RYT values in mixtures are rarely found to exceed unity to such an extent. It indicates a considerable amount of niche differentiation and it seemed worthwhile to investigate the character of this differentiation in more detail.

In some respects the conditions for niche differentiation to find expression were

Table 3. Relative yields, RYT and absolute yields of different mixtures in the multi-species experiment in the first and second year. From: Van den Bergh & Braakhekke (1978). Explanation in text.

Seed ratio grasses/herbs	1st year					2nd year				
	100/0	75/25	50/50	25/75	0/100	100/0	75/25	50/50	25/75	0/100
<i>Lolium</i>										
<i>perenne</i>	0.68	0.77	0.64	0.49		0.05	0.01	0.02	0.01	
<i>Agrostis</i>										
<i>tenuis</i>	0.12	0.13	0.18	0.17		0.64	0.38	0.34	0.45	
<i>Anthosanthum</i>										
<i>odoratum</i>	0.05	0.05	0.06	0.05		0.18	0.13	0.15	0.11	
<i>Trisetum</i>										
<i>flavescens</i>	0.04	0.05	0.06	0.05		0.04	0.06	0.04	0.01	
<i>Hordeum</i>										
<i>secalinum</i>	0.11	0.07	0.11	0.05		-	-	-	-	
<i>Festuca</i>										
<i>rubra</i>	0.01	0.01	0.02	0.03		0.01	+	0.02	0.04	
<i>Cynosurus</i>										
<i>cristatus</i>	0.01	0.01	0.01	0.02		0.01	0.02	0.01	+	
<i>Chrysanthemum</i>										
<i>leucanthemum</i>		0.03	0.06	0.10	0.40		0.29	0.22	0.18	0.82
<i>Plantago</i>										
<i>lanceolata</i>		0.06	0.13	0.20	0.45		0.22	0.28	0.31	0.44
<i>Rumex</i>										
<i>acetosa</i>		0.06	0.09	0.25	0.53		0.03	0.06	0.07	0.19
<i>Centaurea</i>										
<i>pratensis</i>		+	0.01	+	0.03		-	-	-	-
RYT	1.01	1.24	1.37	1.31	1.41	0.93	1.14	1.14	1.18	1.45
Yield (g DM/0.8 m ²)	245	301	345	316	434	73	93	87	94	114

in this experiment better than in many other experiments. It was a long term experiment carried out under field conditions, which permits difference in growth periodicity to be expressed. The soil conditions were poor and no fertilizer or watering were applied during the experiment in order not to reduce the possibility of differential resource limitation. No pesticides were used. The seeds were collected in an old hay field, which allows for adaptation of the species populations to each others presence.

On the other hand the conditions reduced the possibility to contribute to niche differentiation for some other mechanisms. The field was made as homogeneous as possible, which reduced the possible contribution of environmental heterogeneity. Possible differences in rooting depth were reduced, because there was a gravel bank at about 40 cm depth, in which only few roots could penetrate. Although the results of this multi-species experiment seem very reliable, in view of the consistent increase of RYT with the proportion of herbs and the resemblance of the results in two subsequent years, it was decided to repeat the experiment on a smaller scale under closer observation.

6.2 COMPETITION BETWEEN *PLANTAGO LANCEOLATA* AND *CHRYSANTHEMUM LEUCANTHEMUM* AT DIFFERENT FREQUENCIES (FIELD TRIAL I)

The purpose of Field Trial I was to reproduce in a two species mixture of *Plantago lanceolata* and *Chrysanthemum leucanthemum* the RYT > 1 that was found in the experiment of Van den Bergh & Elberse (1975). Therefore it was carried out on the same field and with the same plant populations. To obtain more details about the nature and the development of the RYT deviation, five different mixtures and two harvest times were included in the experiment.

6.2.1 Material and methods

On a field adjacent to the multi-species experiment a small lime dressing of 60 kg/ha (5% MgO) was applied to attain comparable initial conditions. The grass sod was plowed under and the top layer was cultivated and homogenized. Plants of both species were collected from the plots of the multi-species experiment to be certain that vernalized plants of the same populations were used. Rhizome parts with a small shoot and some roots were separated from the old plants, washed, and divided over three size classes that were assigned proportionally to the experimental plots. Total plant density was 36 plants per plot of size 30 x 30 cm². Plant ratios were:

Plant./Chrys. = 36/0; 30/6; 24/12; 18/18; 12/24; 6/30; 0/36.

Nine replicates of each ratio were divided over the three randomized blocks. To reduce the border effect the plots were laterally bounded below ground, down to the gravel bank at a depth of 40 cm, by four asbestos plates that were placed without disturbing the soil inside the plot. The plates extended 3 cm above the ground. Green shadow gauze, allowing 50% of perpendicular incident light to pass through, was arranged around four stakes outside the corners of each plot. It was raised with the height of the vegetation in the plot.

In the first weeks after planting date (15 May 1975) the plots were regularly watered and dead plants were replaced. Other species were weeded out. To facilitate establishment a nutrient solution containing 20 meq KNO₃ per plot was applied after two weeks. Three replicates were harvested on 18 July 1975 by clipping at 3.5 cm above the surface; six replicates were harvested on 1 September 1975. On these six replicates which were maintained in the subsequent years, all the seeds were carefully collected at maturity, counted and resown on three of the plots, to investigate the role of generative reproduction relative to vegetative reproduction. Although many seedlings were observed in the autumn, not one could survive and no difference could be detected between the yields of the plots with and without resowing in the next year (1976). Therefore the seeds were not collected in the subsequent years and the six replicates were treated as equals. In 1976, 1977 and 1978 other species were removed and the gauze was refitted at the start of the growing period. Harvests were taken after the *Chrysanthemum* flowers had withered on 28 July each year, by clipping at 3.5 cm. The harvests of the same two 0/36 plots, two 18/8 plots and two 36/0 plots were analysed each year for total nitrogen, phosphorus, potassium, sodium, calcium and magnesium.

6.2.2 Results and discussion

The yields at the subsequent harvests are presented in the replacement diagrams of Figure 28. The parameters of the hand fitted curves are presented in Table 4.

In general hand fitting is preferred to the method of Thomas (1970), since the latter method obviously produced erroneous curves. This is due to the errors not being proportional to their means, in contradiction to the assumption of Thomas. The condition of proportional errors is probably seldom met, because a species' yield in a low frequency mixture is based on fewer plants per plot than in a high frequency mixture. The relative error caused by mortality and other events affecting whole plants is consequently greater, which may or may not compensate for a tendency of proportionality. Adding a rough correction for this non-proportionality to the calculus of Thomas, by weighing the observations of the different plots according to the initial frequency, produced better curves, which nevertheless could be improved by hand fitting incidentally. An advantage of fitting the curves by hand is also that it offers the opportunity to check the presence of deviating points and the possibility of frequency dependent k-values. The accuracy is not high in general, especially not for the k-values. An error of 10% for k-values around unity, rising to 40% for k-values deviating a factor 5 or more from unity seems a safe estimate for most experiments. If possible all observations should be given in replacement diagrams to allow insight in the accuracy and the possibility of frequency dependent k-values. Replacement experiments with mixtures that can be expected to show frequency dependence, like legume-grass mixtures, should therefore always include several plant ratios.

With respect to the results in Figure 28 several points can be noticed. The scattering of the points is considerable, indicating soil heterogeneity between the plots and the presence of many other factors besides the competition process determining the performance of the plants. Comparing the differences in biomass production between replicates with those in the internal nutrient concentration and in the nutrient amounts removed with the subsequent harvests (Fig. 29), it is evident that differences in the nutritional status of the plots are responsible only for a small part of the scatter. Especially in the winter period frost damage brought about great differences between plots. By using the harvest ratio of the previous year as the initial ratio in each diagram the errors are restricted to one year only. No frequency dependency of the k-values is observed, but the possibility cannot be ruled out because of the scatter of the points.

Table 4. Parameters estimated from the replacement diagrams of Figure 28.

Harvest time	k_{pc}	M_p	k_{cp}	M_c	$k_{pc} k_{cp}$	RYT extreme	$\frac{(M_p/M_c)_{t+1}}{(M_p/M_c)_t}$
18-07-1975	0.65	48	1.30	35	0.85	0.96	
01-09-1975	1.40	150	0.90	100	1.26	1.06	1.37
28-07-1976	2.00	150	0.40	160	0.80	0.94	1.50
28-07-1977	0.80	45	2.50	125	2.00	1.17	0.63
28-07-1978	1.00	11	10.00	60	10.00	1.52	0.80
							0.51

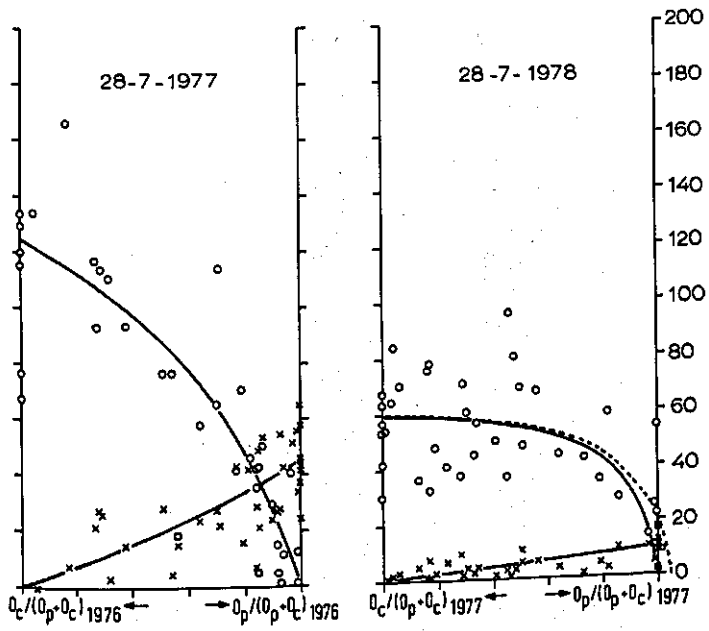
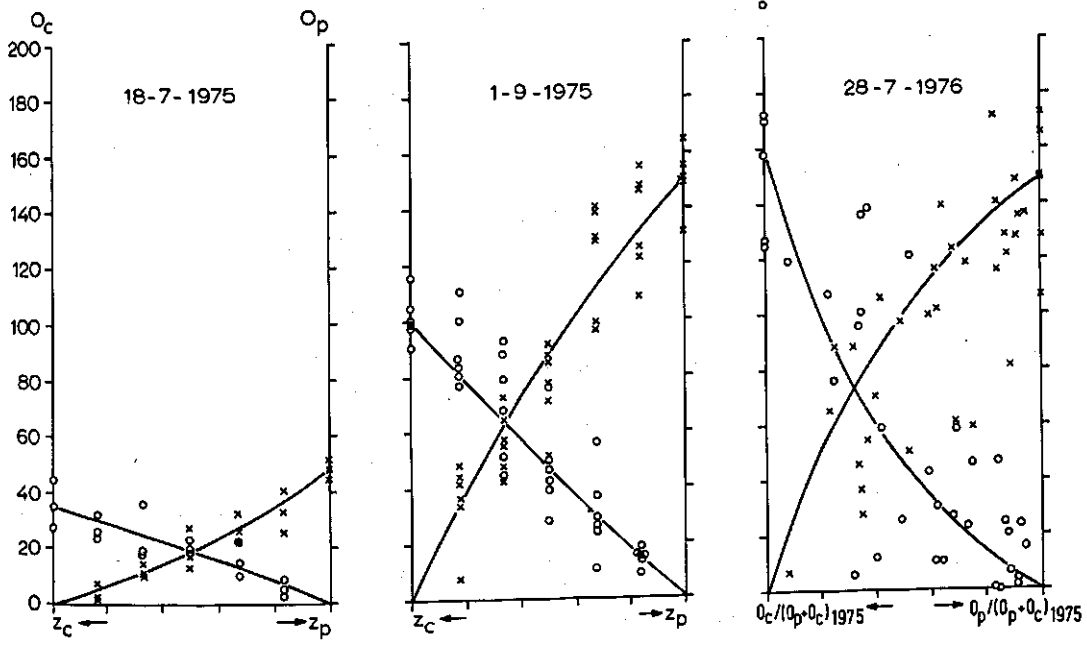


Fig. 28. Replacement diagrams of the yields (in g DM plot⁻¹) of the successive harvests of a four-year competition experiment with *Plantago lanceolata* (x) and *Chrysanthemum leucanthemum* (o) (Field Trial I).

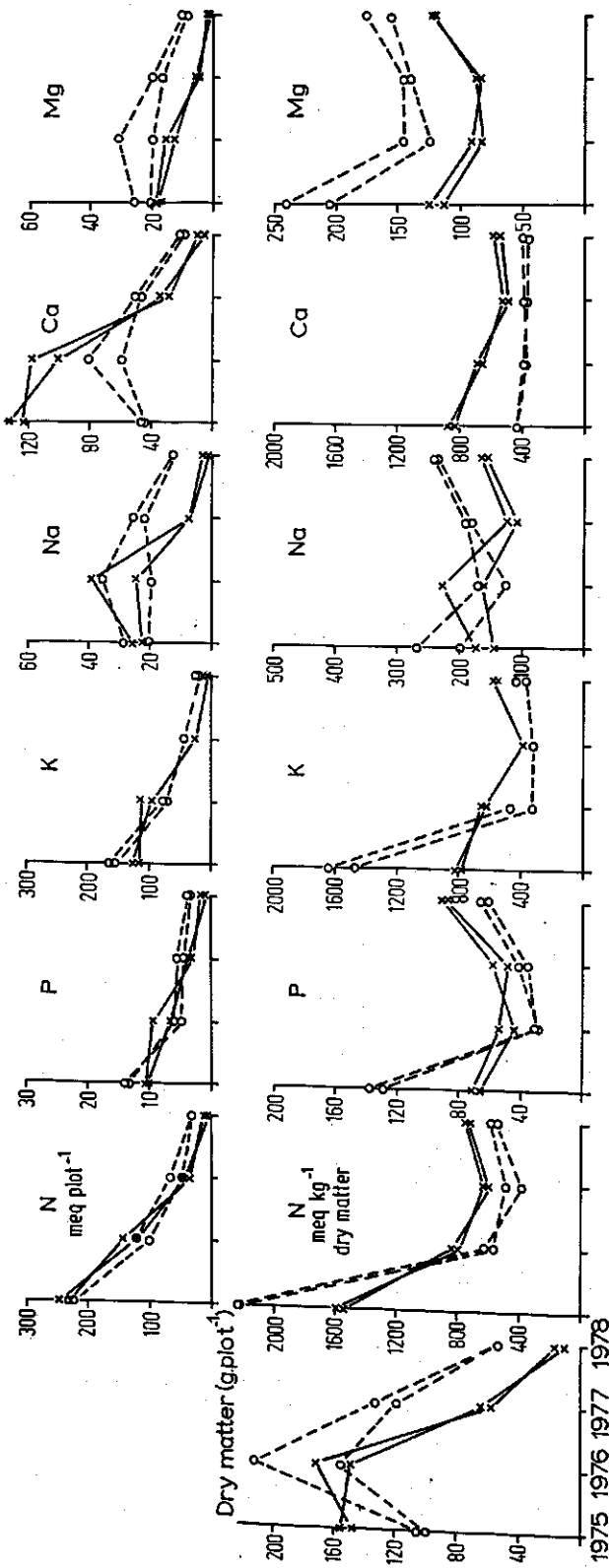


Fig. 29. Dry matter production (g plot^{-1}), nutrient contents (meq plot^{-1}) and nutrient concentrations (meq kg^{-1} DM, lower diagrams) of *Plantago* (x) and *Chrysanthemum* (o) grown in monoculture at the successive harvests of Field Trial I. Data of two replicates are given separately. Nutrient concentrations of the species grown in mixture were not much different from those in monoculture.

An inversion of the competitive dominance is shown during the first year (1975), *Chrysanthemum* being stronger on 18 July, *Plantago* being stronger on 1 September. This may indicate a different growth rhythm. Light interception measurements on 18 July showed an average interception of 92% in *Chrysanthemum* monocultures, 83% in *Plantago* monocultures and 88% in the 18/18 mixtures. Both species being approximately of the same height on this date, *Chrysanthemum* probably had an advantage in light competition, since its leaves were less erect than the *Plantago* leaves, absorbing more light in the upper layer.

On 1 September *Plantago* leaves were observed to extend over the *Chrysanthemum* plants which remained mainly vegetative (in spite of the use of vernalized plants) and did not increase in height after the first harvest. This indicates an advantage for *Plantago* in light competition at the second harvest. The inversion of dominance may explain the small positive deviation of the $k_{pc} k_{cp}$ product on 1 September (RYT extreme = 1.06; this is however not considered significantly different from unity).

Chrysanthemum flowered in the subsequent years, but a difference in growth rhythm remained present. Until flowering the tall *Chrysanthemum* plants overshadowed *Plantago*, but after flowering the *Chrysanthemum* stem leaves wither, passing through the light to the *Plantago* plants.

There is a remarkable decrease in yields, especially of *Plantago*, in the third and the fourth year (1977, 1978). In the first year production was high. From the monoculture yields it can be inferred that *Plantago* produced 102 g per plot above ground between the two harvests, which comes to $258 \text{ kg ha}^{-1} \text{ day}^{-1}$. Apparent production of *Chrysanthemum* was less (65 g per plot), but much was invested in rhizomes which were not harvested. The productivity of *Plantago* was considerably higher than the maximum potential production of $200 \text{ kg/ha}^{-1} \text{ day}^{-1}$ estimated for our region (De Wit et al., 1970). Probably this excess is due to light entering the plots laterally in spite of the shadow gauze. Evidently, no soil factor was limiting growth in the first year, which is explained by the mineralisation of the old sod. Therefore the species were light limited. This can also be inferred from Figure 29 where the internal concentrations of some major nutrients are plotted in the subsequent years. At the second harvest in 1975 all the concentrations are above the level where growth depression usually occurs (De Wit et al., 1963).

In 1976 the yields of *Plantago* were still high, but growth could have been less in that year, since the plants could make use of built up reserves of the previous year. The increased yield of *Chrysanthemum* was due to flowering which involved the production of many stems with a low nutrient content. This caused the internal nutrient concentrations, except for Mg, to fall below that of *Plantago* (Fig. 29). The nitrogen concentrations in both species came to the level where growth depression usually occurs ($< 1000 \text{ meq kg}^{-1}$ dry matter). Since 1976 had an extremely dry summer both species were probably also limited by water supply and little growth was possible for *Plantago* after the flowering of *Chrysanthemum*, explaining the $k_{pc} k_{cp}$ product of 0.80 (corresponding with RYT extreme of 0.94) which is not significantly different from unity.

In 1977 the monoculture yield of *Plantago* was reduced with 70% and in 1978 with 75% compared to the previous yield. The reason for this decrease can hardly be found in the exhaustion of the soil nutrient store, since the internal concentration of the limiting

nutrient (nitrogen) increased in 1978, as did the other concentrations. Comparison of the amounts of nitrogen removed with the *Chrysanthemum* and *Plantago* monoculture harvests show that *Plantago* did not exhaust the nitrogen supply to the utmost.

A decrease in the yield of *Plantago* after one or two years was observed earlier by Milton (1943). Recently Newman & Rovira (1975) connected this with their observation of a significant autotoxic capacity of *Plantago*. The observation of poor seedling establishment of *Plantago* in the neighbourhood of parent plants by Sagar (1960), quoted in Harper (1961), and the striking behaviour of this species in a long term fertilizer experiment at Wageningen (Fig. 14 in Van den Bergh, 1979) may also point to autotoxic activity. The frequency percentages of this species in the latter experiment showed a distinct rise-and-fall curve, completed within 12 years. The rise might be explained by an abnormally high seed production in 1967. The gradual return to the original level must have meant the death of many individuals. Senescence or allelopathic selfinhibition may have been responsible for this. According to Van Groenendael, the vitality of *Plantago* rootstocks decreases considerably in a few years. Observations in dune grasslands indicated a half life of two years (pers. comm.).

Observations in our own plots revealed that germination and early establishment of seedlings was not noticeably hampered, but the survival and development of *Plantago* seedlings, in monocultures as well as mixtures, was low and, obviously, could not compensate for the degeneration of the original plants.

In the present experiment *Chrysanthemum* seems to have profited from the spontaneous retreat of *Plantago*, in view of its sixfold increased relative crowding coefficient in 1977, resulting in a $k_{pc} k_{cp}$ product of 2.0. This corresponds with RYT extreme = 1.17, which is considered just about a significant deviation from unity. In 1978 the *Chrysanthemum* monoculture yield was reduced 50% compared to 1977. Considering the increase in the internal concentration of the limiting nutrient (nitrogen) this suggests autotoxic activity of *Chrysanthemum* as well. Nevertheless *Chrysanthemum* seems to have profited again from the much greater yield reduction of *Plantago* (75%), in view of its increased relative crowding coefficient ($k_{cp} = 10$). *Chrysanthemum* apparently is hardly influenced by the presence of the *Plantago* plants. *Plantago* in its turn seems to have found some "space" where it can subsist. Although the low accuracy makes it impossible to assess a reliable relative crowding coefficient for *Plantago*, the $k_{pc} k_{cp}$ product must be significantly higher than unity. We estimated a value of 10, corresponding with RYT extreme = 1.52.

In consequence of the above the Relative Replacement Rate must have been frequency dependent in 1978. Notwithstanding the considerable scatter of the points this is also shown by the ratio diagram (Fig. 30). The slope of the ratio line estimated by linear regression (broken line) is significantly smaller than unity in 1978 ($P < 0.01\%$). The continuous line is computed with the M- and k-values obtained from the replacement diagrams.

Frequency dependency of RRR is also apparent from the course lines (Fig. 31). After an initial change in favour of *Plantago* the yield ratio falls rapidly, favouring *Chrysanthemum*. This fall is less steep when starting from a low ratio than from a high

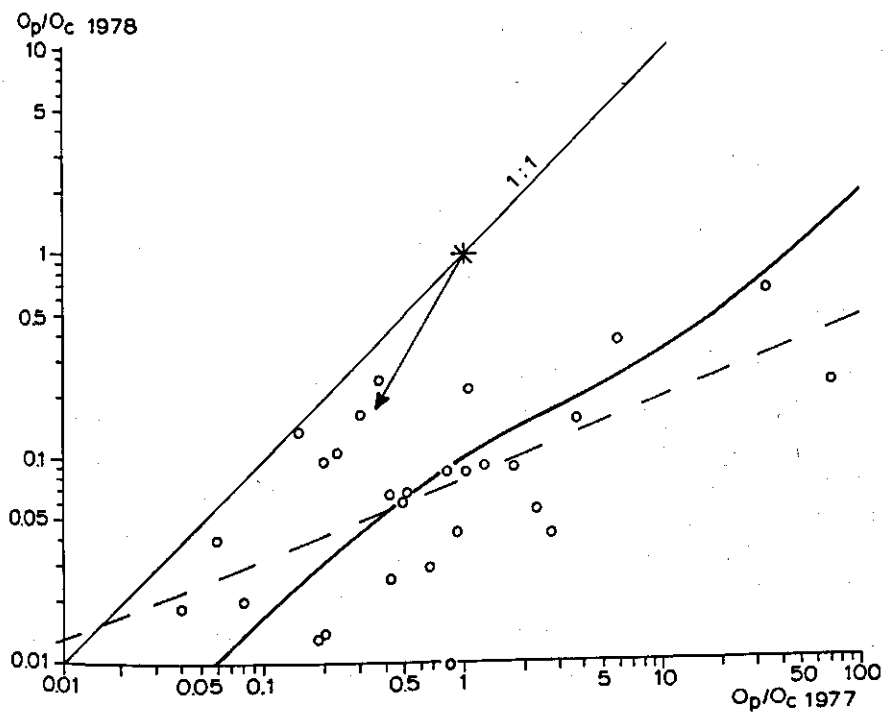


Fig. 30. Ratio diagram of the 1978-harvest of Field Trial I. The arrow indicates the distance over which the coordinate system shifts when relative yield ratios are used instead of absolute yield ratios. (----) regression line; (—) ratio line calculated with the parameters estimated from the replacement diagram (Fig. 28).

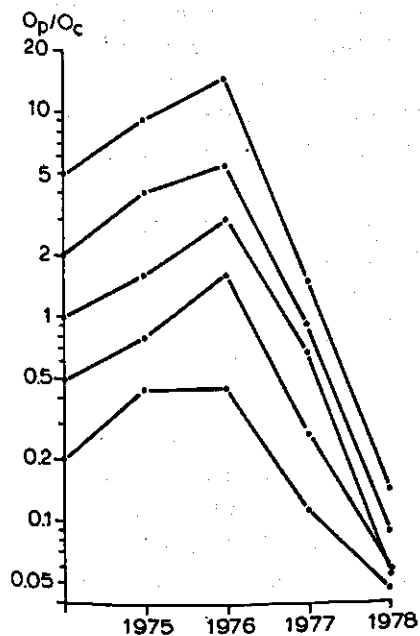


Fig. 31. Course of the yield ratio O_p/O_c in mixtures of *Plantago* and *Chrysanthemum* with different initial plant ratios. (Field Trial I).

ratio, which causes the course lines to converge. However, this does not mean that an equilibrium will be attained, because for an equilibrium the ratio line has to intersect the diagonal and the course lines have to level off and converge to one horizontal asymptote which is obviously not or not yet the case.

To predict the eventual outcome of competition from the ratio diagram, we have to consider the population ratios N_p/N_c rather than the yield ratios (see Section 4.4). Since the double quotient of the monoculture yields is not constant (Table 4), we cannot be certain that the double quotient of the monoculture populations has settled on unity. Consequently it is precarious to use ρ as an estimate of RRR.

When we do take the relative yield ratios instead of yield ratios the coordinate system moves over the indicated distance in the direction of the arrow in Figure 30. It appears that the continuous line still does not intersect the diagonal. It is, however, possible that by mowing we have obtained an ever lower proportion of the biomass of *Plantago*, eventually decreasing to zero, when not only the population density decreases, but also the size of the individuals grows smaller. In that case *Plantago* may disappear from the harvest, but will still be present in the mixture. It is also possible that the double quotient of the monoculture yields will change further, favouring equilibria, when the *Chrysanthemum* yields continue to decrease and the *Plantago* monoculture settles at about 10 g per plot.
10 g per plot.

The experiment will be pursued to obtain the answer. The main thing now is that a frequency dependent RRR is found, indicating reduced competition. In the last year the *Plantago* monocultures have been infested with *Chrysanthemum*, degenerating to mixtures. As argued in Section 4.9.6, this may account for an artificial stabilizing effect, and an $RYT > 1$. Without this effect of immigrating *Chrysanthemum*, the points on the right-hand side of the ratio diagram would have been situated higher, the relative yields of *Plantago* would have been lower, as well as the k -value of *Chrysanthemum*.

Fitting a replacement curve by hand with an indeterminate origin through the yields of *Chrysanthemum* reveals, however, that the seed immigration had only little influence on the relative crowding coefficient (dotted line in the right-hand diagram of Fig. 28), and accounts only for a small part of the high $k_{pc} k_{cp}$ product, leaving the observed frequency dependency for the greater part to be explained otherwise.

6.3 GROWTH RHYTHM IN MONOCULTURES AND MIXTURES (FIELD TRIAL II)

6.3.1 Material and methods

To investigate the possibility of niche differentiation between *Plantago* and *Chrysanthemum* by means of different growth rhythms, an experiment was planned at 'De Sinderhoeve' with monocultures and 50/50 mixtures of both species, including 5 series to be harvested at different times, each replicated three times. The net size of the plots was 1 m^2 with a border area of 50 cm around.

Seeds were collected from the multi-species experiment and the germination percentage was determined on filterpaper. The species were sown with a total density of 500

viable seeds per m^2 in October 1975. Weeds were removed by hand several times during the experiment.

Germination and establishment was good, but during the next winter period many of the young plants were killed by frost, in consequence of which the plant density was low and irregular in 1976. The following extremely dry summer aggravated this situation, so that we had to remove the plants remaining and resow the experiment, which was completed in September 1976.

In 1977 plant density was better, but production and height of the vegetation were too low to obtain a harvest by mowing large enough for a reliable determination of the population ratios in the mixtures. Since these ratios had already visibly changed and grown different again, the initial ratios in 1978 were unknown and we had to approach the question at issue differently.

To ensure a better harvest a light dressing of 300 kg fertilizer/ha (12% N, 10% P, 18% K) was applied in March 1978. This was considered admissible, since growth periodicity and not nutritional differentiation was studied in this experiment. Instead of taking subsequent harvests on different plots, we chose to follow the growth in time on the same plots by repeated non-destructive determination of biomass, at intervals of approximately two weeks. To this end we used the point quadrat method with the apparatus, as described by Warren Wilson (1963), with a sharp needle, movable in vertical direction. The needle was gradually lowered to ground level at two hundred points regularly spaced at 4 cm distance on eight rows per plot. Contacts of the needle point were recorded with leaves only, distinguishing between *Plantago*, *Chrysanthemum*, weeds and bare soil. Since more hits per point were possible 'hit score' may exceed 100%.

The relation between the hit score and living aerial biomass was determined on separate plots at intervals of one month. To this end one quarter of a plot was sacrificed each time, the plots being selected for structural resemblance with the plots continually followed. Since the analysis as described above is very time-consuming no replicates could be taken.

6.3.2 Results and discussion

The hit scores are represented in Figure 32a as hits per 100 points per plot of one square meter. The relation between hit score and biomass is represented in Figure 32b as the hit percentage at a density of 1 gram dry matter per $0.25 m^2$. One curve was fitted through the observations in monocultures and mixtures. This curve was used to calculate from Figure 32a the standing crop, points and curves, represented in Figure 32c. The relative yields, represented in Figure 32d, were calculated directly by dividing in Figure 32a the hit scores of the mixtures by those of the monocultures; the relative yield curves are obtained by dividing the curves in Figure 32a.

Looking first at *Chrysanthemum* we see a rapid increase in hit score in April and May, a maximum during flowering, which started in mid-May, and decrease in June, July and August. The hit score per gram per $0.25 m^2$ decreases from April to August, indicating a change in structure, i.e. an increasing proportion of stems initially, and a withering of leaves later on, after flowering. The increase in September is attributed to the

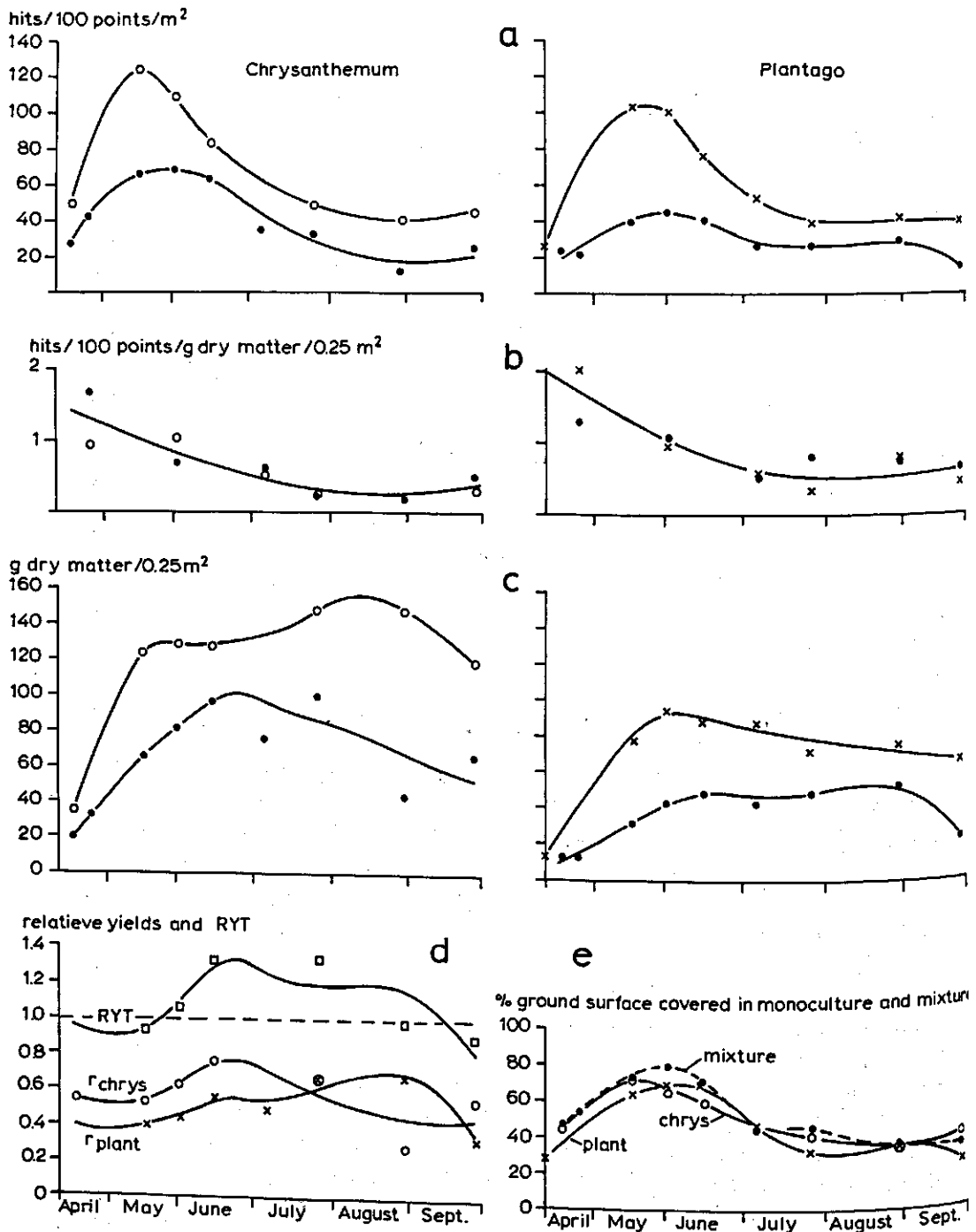


Fig. 32. Results of Field Trial II.

- Course of the hitscores of *Chrysanthemum* (o) and *Plantago* (x) growing in monoculture and mixture (●), obtained by point quadrat analysis.
- Changes during the season in the relation between hitscores and aerial biomass of both species, calculated as the hitscore at a density of 1 g DM/0.25 m².
- Course of the aerial biomass of the species in mixture and monoculture.
- Course of the relative yields and the RYT calculated from (a).
- Percentage of soil surface covered by one or both species in monoculture or mixture during the season.

production of young rosette leaves.

The biomass increases, reaching a plateau in the monoculture in the second half of May and in the mixture about one month later, in consequence of which the relative yield increases. A possible explanation for this difference between monoculture and mixture is that in the mixture side branches and additional stems could be formed, as a result of the more open top layer of the vegetation.

In July and August the biomass increases still somewhat in the monoculture, in contrast to the mixture. Consequently the relative yield decreases. An explanation for this difference may be that in the mixture the formation of young rosette leaves is hampered by the dark micro-climate in the lower vegetation layer, due to the *Plantago* leaves. The observed differences in the behaviour in monoculture and mixture agree with the change in competitive relation observed in Field Trial I in 1975, *Chrysanthemum* in the mixture having an advantage initially and a disadvantage later on.

The hit score of *Plantago* shows roughly the same picture as *Chrysanthemum*, except for the small increase in September. The hit score per gram per 0.25 m² decreases as a result of the formation of stems and the erection of the leaves.

The biomass increases until May. It then decreases gradually in the monoculture. In the mixtures, however, it stabilizes, even increases a little in July, and decreases only in September. Consequently the relative yield increases gradually until September, when it falls back again rapidly. The explanation for this advantage of the mixture might be that after flowering the stem leaves of *Chrysanthemum* begin to wither, passing through more light to the *Plantago* plants in the lower vegetation layer.

The simultaneous increase in relative yield of both species results in an appreciable increase of the RYT in May and June, leading to a maximum at the time when the plants are usually harvested. The percentages soil surface covered in the monocultures and in the mixture (Fig. 32e) show that the mixture has a coverage higher than or equal to the most dense monoculture. Since there were no replicates the absolute value of the RYT has little meaning; between-plot soil heterogeneity could easily result in RYT values deviating from unity throughout. The important observation is the increase in RYT during the most productive phase and a high value lasting all the summer.

The wilting of the *Chrysanthemum* stem leaves can only be of advantage to *Plantago* in mixture when light is a limiting factor. From the low production level it is evident that soil conditions are limiting the production of the vegetation as a whole. The mechanism of different growth rhythms may, however, still be effective as the above ground behaviour is reflected by the root activities.

Even when light is not limiting growth of the vegetation as a whole, it may be limiting one or more of the component species, and the position in light competition of a species may determine its share of the limiting resource to a great extent. Virtually, there will be a gradual transition between light and nutrient limitation, as plants are known to maintain a functional equilibrium between root and shoot growth (Brouwer, 1962). This implies that there is an equilibrium between light and nutrient limitation which shifts as the conditions change.

This experiment provides more evidence that *Plantago* and *Chrysanthemum* have different niches under the conditions concerned. About the nature of this niche difference

we can conclude from Field Trial II that the development of the high RYT results from certain differences in the behaviour of the species in monoculture and mixture, for which we have some tentative explanations, involving a difference in growth rhythm. The explanations (viz. the formation of more stems and side branches per plant by *Chrysanthemum* as a result of a more open upper vegetation layer in the mixture, and the higher production of *Plantago* plants in the mixture as a result of the withering of *Chrysanthemum* stem leaves after flowering) have to be checked first. Even if they prove to be correct, the difference in growth rhythm does not remove our need for other explanations, because it cannot account for all of the niche differences. One question remaining is why the increase of the relative yield of *Chrysanthemum* in May and June does not result in a corresponding decrease in the relative yield of *Plantago*. Mechanisms other than different growth rhythms must be responsible for this.

6.4 ROOT DISTRIBUTION

To check the presupposition that differences in rooting depth between *Plantago* and *Chrysanthemum* are prevented at 'De Sinderhoeve' by the occurrence of a gravel bank at about 40 cm depth, we determined the root distribution of two adjacent monocultures in Field Trial II. To this end blocks of soil were cut out of the walls of a pit between the plots. These samples, measuring 30 x 30 x 10 cm, were washed and sieved, separating the roots and the gravel fraction > 7 mm.

From the results as represented in Figure 33 it is seen that only few roots penetrate into the gravel bank which is situated at 40 to 50 cm depth. Maximum rooting depth is 70 cm for both species.

The root density in the layer of 10 to 30 cm is overestimated, especially in the *Plantago* plot, because the roots were contaminated by the remains of the old sod which could not be separated from them. Although the exact amounts of roots are not known in this layer, it is evident that differences in root distribution are small and will not have contributed to the observed niche differentiation.

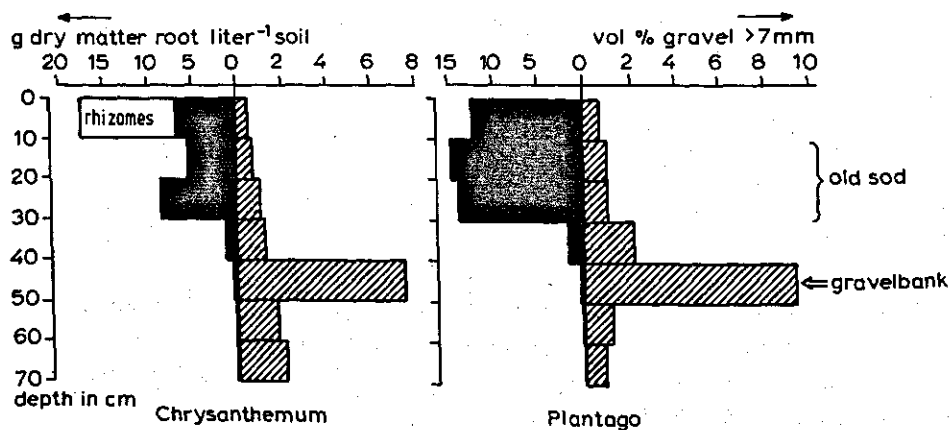


Fig. 33. Root distribution of *Plantago* and *Chrysanthemum* grown in monoculture in Field Trial II.

6.5 CONCLUSIONS FROM THE FIELD TRIALS

All three experiments carried out at 'De Sinderhoeve' indicate that *Plantago lanceolata* and *Chrysanthemum leucanthemum* are in some respect niche differentiated under the prevailing conditions. In the second year of the multi-species experiment the sum of their relative yields was 1.26. In Field Trial I the RYT-extreme was significantly greater than unity: 1.17 and 1.52 in the third and fourth year respectively. In the fourth year the frequency dependency of the relative replacement rate was also visible from the ratio diagram. In Field Trial II an appreciable increase in RYT with 0.4 was observed in the period of the highest productivity. We are not sure that this niche differentiation will lead to an equilibrium. If so, the equilibrium population density of *Plantago* will be very low.

About the nature of the niche difference we may already have some speculations with the help of Table 1.

1. Spatial differentiation between the species could have been of little importance, since the plots were homogenized carefully and the effect occurred also in the very small plots of Field Trial I. Besides it would have resulted in S-curves in the replacement diagrams of Field Trial I.
2. The effect of immigration of seeds in the plots was probably not important initially, since seedling establishment was poor in the first years of Field Trial I. Immigration of *Chrysanthemum* was observed in the last year of Field Trial I, but it accounts only for a small part of the frequency dependency of RRR observed in this year.
3. Temporal differentiation between the species as meant in point 3 of Table 1, in which the competitive dominance regularly alters as a result of changes in the environment, the $k_{ab} k_{ba}$ product being unity throughout, evidently does not apply here.
4. Some of the possible functional differences between species have to be considered in more detail.

Since predation of pathogens (4b) were not observed we let this matter rest until other explanations fail. The same applies to the category 'other mechanisms' (4c), with the exception of allelopathy. The remarkable decrease in monoculture yield of *Plantago* suggests autotoxic activity. It explains the high RYT value, but it does not result in equilibria. Senescence in combination with self-inhibition of seedling establishment will make the occurrence of *Plantago* dependent on continual establishment on new places. This was referred to in Sections 3.1 and 3.4.1 as transient autogenic micro-environmental heterogeneity, leading to cyclic succession and shifting mosaic patterns.

Special attention has to be paid to differentiation in resource use (4a). Spatial differentiation of resource exploitation (4.a.2) seems, however, not important, since the rooting patterns were much alike. Seedlings grown in sand culture had approximately the same root diameters and amounts of root hairs. Only the branching pattern is slightly different. Mycorrhiza and root nodules are not observed nor recorded in the literature (Sagar & Harper, 1964; Howarth & Williams, 1968).

From the observation of a change in competitive dominance in the first year of Field Trial I and from the results of Field Trial II it is plausible that a difference in growth rhythm (viz. the reduced vegetative activity of *Chrysanthemum* after flowering, as opposed

to the continued vegetative growth of *Plantago*) contributed to the niche differentiation (4.a.3). However still another mechanism must be involved, because different growth rhythms cannot explain the simultaneous increase of the relative yields of both species in May and June.

The possibility that differences in uptake efficiency by the species of some resource (4.a.4) is responsible for this simultaneous increase is small, because differences in uptake efficiency have to act together with differences in time or place of uptake as was argued in Section 3.3.1. Differences in time are out of the question when simultaneous increases are concerned and differences in place are not likely at first sight, as mentioned above.

The possibility remains that differences in the limiting resource (4.a.1) may contribute to niche differentiation between *Plantago* and *Chrysanthemum*. This possibility was investigated in several experiments, described in the next chapters, emphasizing the cation nutrition, because it was previously established that *Plantago* and *Chrysanthemum* often differ in their K and Ca contents. Although the results of these experiments showed no equilibrium in the competition for these nutrients, other nutrient combinations may offer better possibilities. Especially nitrogen and phosphorus are important in this respect, since these were the major limiting elements in the field trials.

In summary we have reduced the number of possible causes of the observed niche differentiation to a difference in growth rhythm and the possibility of autotoxic activities of one or both of the species; the possibility of a difference in the use of nitrogen and phosphorus remains to be investigated. Other causes are less likely but not excluded.

7 Experiments under controlled conditions

7.1 PRELIMINARY EXPERIMENTS WITH PLANTAGO AND CHRYSANTHEMUM IN SOIL CULTURE (TONNEYCK, 1974)

In succession of the experiment of Van den Bergh & Elberse (1975; see Section 6.1) a spacing experiment and a competition experiment were carried out with *Plantago lanceolata* and *Chrysanthemum leucanthemum* on two contrasting soils in a climate room (Tonneyck, 1974). The results of these experiments will be summarized in this section.

The two soils were a sandy soil, poor in nutrients (pH-KCl 3.7), limed up to pH 5.6, and a fertile sandy soil (pH-KCl 5.6) with an additional dressing of fertilizer (NPK). Both experiments were carried out in six-liter pots. Plant densities in the spacing experiment were 1, 2, 4, 8 and 16 plants per pot. The plants were harvested 10 weeks after sowing. The results are given in Figure 34.

As a matter of course the productions on both soils were very different. Interesting is the fact that *Chrysanthemum* shows a clear depression at the highest densities on the fertile soil. This supports our suggestion that autotoxic activity may have occurred in the field experiments.

The competition experiment was carried out at two total plant densities (4 and 12 plants per pot) and included the two monocultures and a 50/50 mixture. Different series

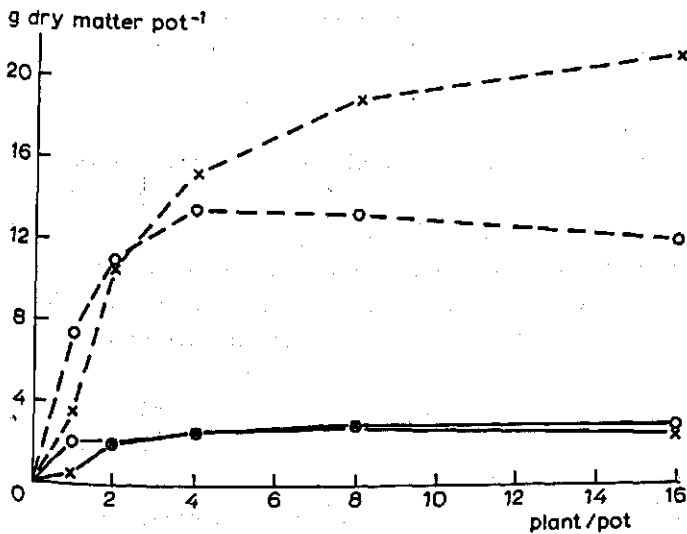


Fig. 34. Yield-density relationship of *Plantago* (x) and *Chrysanthemum* (o) on a poor (—) and a fertile (---) soil. (Tonneyck, 1974)

were harvested approximately 8, 13 and 17 weeks after sowing. On both soils and at both densities *Plantago* was the stronger competitor. This was attributed to its more vigorous root development and its longer leaves which overshadowed *Chrysanthemum* on the fertile soil. In none of the mixtures the RYT was significantly different from unity. Evidently, the species were competing for the same 'space', this being a nutrient, probably nitrogen, on the poor soil, and light on the fertile soil.

7.2. DIFFERENTIAL LIMITATION OF K AND Ca FOR *PLANTAGO LANCEOLATA* AND *CHRYSANTHEMUM LEUCANTHEMUM*.

It was concluded on theoretical grounds in Chapter 5 that species may coexist in a stable equilibrium when they are limited by different nutrients. We arrived at this conclusion after analysing the equilibrium conditions of a simple competition model for two nutrients. In Chapter 6 we concluded that such a differential nutrient limitation was one of the possibilities remaining to explain the observed frequency dependent relative replacement rate and the RYT greater than one, observed in the field trials. It could, however, not be demonstrated that this mechanism was actually working, because the experiments were not designed to that end.

We argued in Section 5.4 that the complexity inherent in higher plants and terrestrial environments would make it difficult to show the occurrence of this equilibrium mechanism in the field. The model developed in Chapter 5 is too elementary with respect to its description of the environment and it cannot be expected that the equilibrium conditions obtained for the substrate are applicable to the field situation.

The experiments described in the following sections were designed to investigate whether *Plantago* and *Chrysanthemum* at least showed the essential differences in nutrient requirements and uptake abilities, and whether elimination of the complexity of the soil makes it possible to evaluate the essential conclusion of Chapter 5 that differential nutrient limitation permits stable coexistence in a homogeneous environment.

7.2.1 *Choice of nutrients*

In searching for adequate differences in nutrient requirement and uptake between *Plantago* and *Chrysanthemum* we had to reduce the number of nutrient combinations to be investigated. For several reasons the combination of potassium and calcium seemed a good choice. In the first place it is known that K and Ca concentrations in species growing in the same vegetation may differ considerably. Such differences are often greater than differences in the chemical composition of the same species growing in different places (De Vries & Dijkshoorn, 1961; Horak, 1971).

Of our two species most data are available of *Plantago*, as it was included in several studies on the relation between botanical and chemical composition of pasture herbage (Fagan & Watkins, 1932; Thomas & Thompson, 1948; Thomas et al., 1952; Van der Kley, 1957; Said, 1959; De Vries & Dijkshoorn, 1961). It is generally appreciated as a good source of minerals for animals, especially of Ca, of which it contains fairly high concentrations compared to other species. According to Horak (1971) it belongs to

the physiological type of plants called 'calcitrophic'. This type of plants contains high concentrations of soluble calcium, often higher than potassium concentrations.

From experiments described by De Wit et al. (1963) it is known that *Plantago* has little preference for a specific cation. This was concluded from the straight lines in the nutrient replacement diagrams of Figure 35. Whereas other species investigated (most Gramineae, belonging to the K-type of plants, see below) seem to possess two uptake systems (one 'four-ion system' by which K, Na, Mg and Ca are taken up and a 'monovalent-ion system', which takes up K and Na with a high preference for K). *Plantago* apparently possesses only a four-ion system with about equal preference and capacity for the uptake of the four cations.

Less information is available of *Chrysanthemum*. According to analysis of Fagan & Watkins (1932) its K/Ca ratio is somewhat higher than that of *Plantago*. It was not included in the investigation of Horak (1971), but he concluded that most of the Compos-

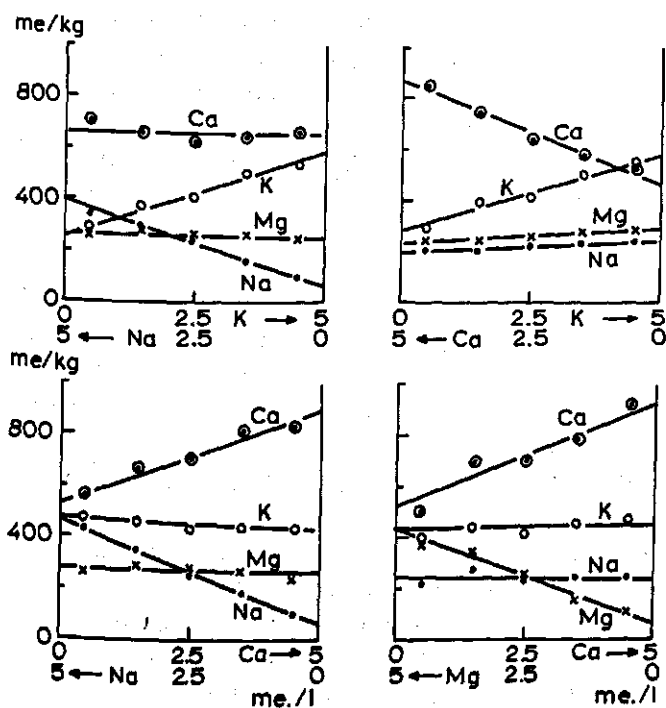


Fig. 35. Cation replacement diagrams for the herbage of *Plantago* (From De Wit et al., 1963). Initial composition of the solutions in meq l⁻¹;

	Na-K	Ca-K	Na-Ca	Mg-Ca
K	x	x	2.5	2.5
Na	5-x	2.5	x	2.5
Mg	2.5	2.5	2.5	x
Ca	2.5	5-x	5-x	5-x
NO ₃	5	5	5	5
H ₂ PO ₄	2.5	0.83	0.83	0.83
SO ₄	2.5	2.5	1.67	1.67
Cl	0	1.67	2.5	2.5

Period of growth on the treatments: 4 weeks
 Renewal of solutions : 1x
 Average yield per container : 25 g

itae are of the so-called 'potassium type' of plants. This physiotype contains little free calcium and high concentrations of potassium. The K/free Ca ratio is in excess of 10 for many Compositae species (1.37 for *Plantago*). The mean K/Ca-total ratio of the 17 species included in his study was about 2 (1.06 for *Plantago*).

In addition to the fact that cation concentrations are easy to manipulate in nutrient solutions this conjectured difference in K and Ca nutrition between *Plantago* and *Chrysanthemum* motivated us to investigate whether this combination of species and nutrients meets the condition for stable coexistence.

7.2.2 K and Ca requirements (Experiment I)

From the above data one can only infer a difference in the nutrient uptake ratios of the species, but not a difference in the nutrient requirements, since no information on growth in relation to internal nutrient concentration is available. To determine whether *Plantago* and *Chrysanthemum* differ in their K and Ca requirements we investigated the minimum concentrations. This was done by growing both species separately in a series of nutrient solutions with different K and Ca concentrations, designed according to the replacement principle. These solutions were not renewed and the plants were allowed to exhaust the solutions and to produce the maximum possible yield. In Figure 11 we have shown what results can be expected of such an experiment with different mutual relations of the two nutrients in determining growth.

7.2.2.1 Experimental technique

Seeds of *Plantago* and *Chrysanthemum* collected from plots of the multi-species experiment (see Section 6.1) were sown in a glasshouse on a soil poor in nutrients, which was limed to increase the pH. On 22 April the seedlings were transplanted. Four plants per pot were mounted with foam-plastic strips in holes of the lids of 1.3 liter pots containing the experimental nutrient solutions. Initial weights, K and Ca contents are given in Table 5. Due to the lime treatment of the soil the initial Ca content of *Plantago* was fairly high in view of the amounts supplied with the nutrient solutions.

The composition of the ten experimental solutions is given in Table 6. Iron was added as Fe-EDTA which was prepared with NaOH. Micro-nutrients were supplied at 1 ml per pot of the 'A-Z solution', according to Hoagland & Arnon (1938; in Hewitt, 1966). Demineralized water was used to prepare the solutions and to replenish the transpired water. The concentrations of the major nutrients were chosen so to make sure that no

Table 5. Initial dry weights, K and Ca concentrations and contents of the plants in Experiment I.

	Dry matter g pot ⁻¹	Potassium		Calcium	
		meq kg ⁻¹ DM	meq pot ⁻¹	meq kg ⁻¹ DM	meq pot ⁻¹
<i>Plantago</i>	0.12	222	0.027	1027	0.123
<i>Chrysanthemum</i>	0.10	237	0.024	509	0.051

Table 6. Composition of the ten nutrient solutions (in meq pot⁻¹) in Experiment I.

K	x											
Ca	0.6-x											
Mg	1.4											
Na	1.4											
NH ₄	2.5											
Solution no.	I	II	III	IV	V	VI	VII	VIII	IX	X		
x =	0.10	0.15	0.20	0.25	0.30	0.35	0.40	0.45	0.50	0.55		

other nutrient than K and Ca could become limiting. This required a relatively high amount of nitrogen, which was supplied mainly as NH₄NO₃ and not as Na- or Mg-nitrate to prevent high Na and Mg concentrations interfering with K and Ca uptake.

The experiment included four harvest series and was replicated five times. Placement of the pots was changed daily to reduce effects of environmental heterogeneity in the glasshouse. The four series were harvested after 22, 33, 47 and 50 days. Roots and shoots were separated and the shoots were divided in living and dead parts. The roots were rinsed in demineralized water and blotted to remove adherent water. After determination of dry weight the replicates were mixed for chemical analysis. Of the third harvest all parts were analysed for K, Ca, Na and Mg by the chemical department of the CABO according to routine procedures using flame photometry.

During the experiment the glasshouse was fumigated with nicotine twice against aphids, which was however not very successful and seemed to harm *Plantago*. Another complication was that the cooling of the glasshouse was not sufficient for the tropical heat of the 1976 summer, resulting in temperatures of over 40°C in the air and nutrient solutions. In addition substantial amounts of Ca and K may have been emitted by the nebulizer.

7.2.2.2 Deficiency symptoms

At the first harvest, deficiency symptoms were already visible in the plants on the solutions poor in Ca. At the second and third harvest, severe deficiency symptoms were observed in the plants on all the solutions. The fourth harvest was taken earlier than planned, because the plants were dying on the extreme solutions and there was a risk of losing weight by rotting.

The deficiency symptoms were fairly well confirming to the description in the literature (Wallace, 1961; Sprague, 1964). Symptoms of potassium deficiency started in both species with necrotic spots on the older leaves, followed by a browning of the leaf margins and subsequent death of these leaves. Young leaves retained a healthy appearance relatively long. In *Plantago*, a typical pattern of interveinal spots, and in *Chrysanthemum* a bluish-green tinting was sometimes observed.

Symptoms of calcium deficiency developed earlier and were far more dramatic of appearance. The rapidity with which Ca-deficiency can be induced is illustrated by the observation that a stay of only two days on a solution without Ca was enough for young *Plantago* plants to develop the specific black and hooked tips in the youngest leaves, which appear-

ed several days later when the Ca supply had already been restored. In *Chrysanthemum*, the leaf area of the young leaves was reduced, in contrast to the leaf stalk. With continuing deficiency, the growing point died, and lateral tillers formed with only leaf stalks as well, giving the plant a strange spiny appearance. In *Plantago*, the growing-point also died and the scapes wilted just below the spikes.

7.2.2.3 Results and discussion

The results of the third harvest are presented in Figure 36 and Figure 37 in the same way as applied in Figure 11. Due to the complications mentioned before the experimental error is rather great as can be seen in Figure 36. In drawing the curves it has been taken into account that errors are more likely to decrease than to increase the yields. The left ends of the curves have been drawn with the assumption that the amount of potassium initially present in the plants (K load) is freely movable. Since the relative redistribution of Ca in most species is small (Loneragan & Snowball, 1969 a and b), the initial amounts of Ca (Ca load) are assumed to be not available for growth and have consequently been left out of consideration in drawing the right parts of the curves. Both K and Ca are assumed to be essential nutrients.

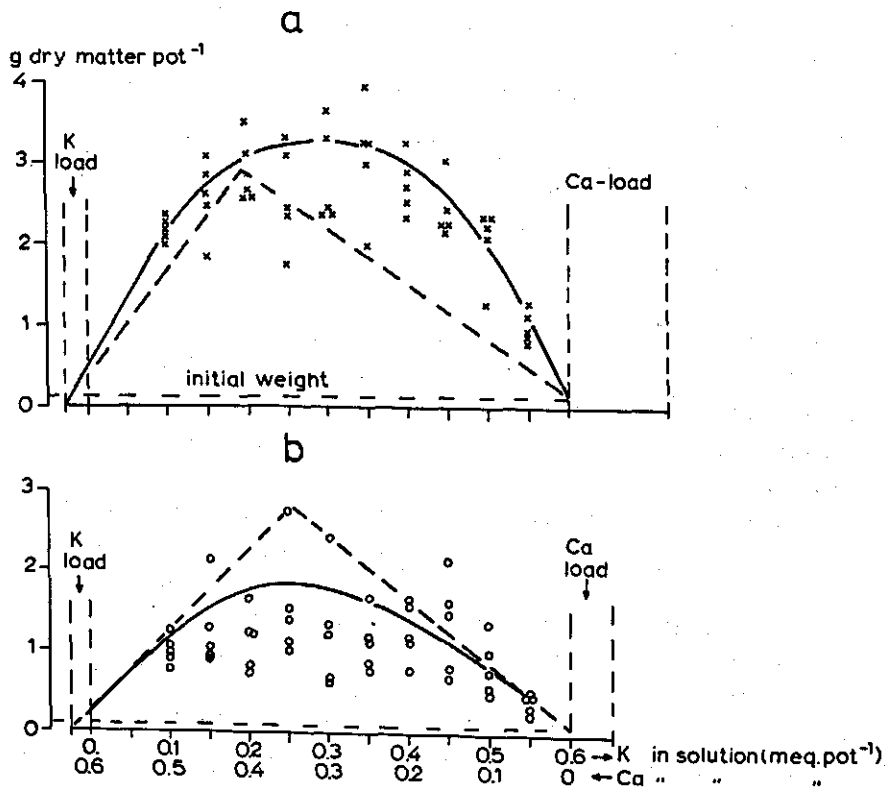


Fig. 36. Yields in a K-Ca replacement series (Exp. I, 3rd harvest), (a) *Plantago*; (b) *Chrysanthemum*. Explanation in text.

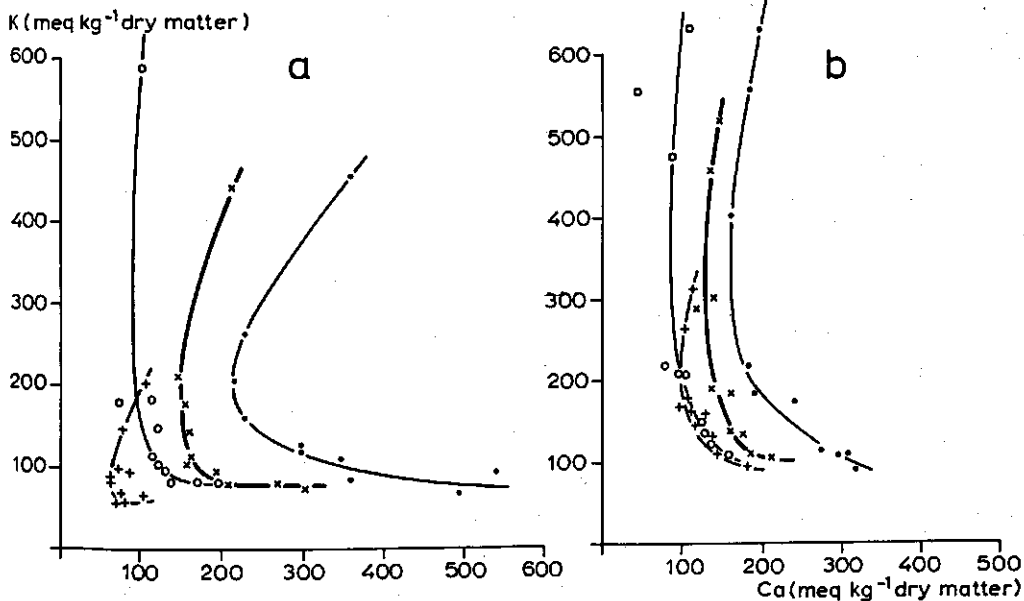


Fig. 37. K and Ca concentrations of plants grown in a K-Ca replacement series (Exp. I, 3rd harvest); in the roots (+), in the living shoot material (o), in the dead shoot material (•) and in the whole plant (x).

(a): *Plantago*; (b) *Chrysanthemum*.

The yields predicted from the minimum concentration, red off in Figure 37, and the amounts of K and Ca supplied, are indicated in Figure 36 with auxiliary lines, assuming exact functional complementarity of these nutrients. The actual yields of *Plantago* are well above these predicted yields, especially where Ca is limiting, suggesting extra supplies of Ca. This is attributed to emission of considerable amounts of Ca by the nebulizer in the glasshouse. Apparently *Chrysanthemum* could not use this extra supply as well as *Plantago*.

It is difficult to decide which of the uptake-yield relations suggested in Figure 11 fits best to these results. The application of a smooth curve does not imply that the suggested relation of interacting nutrients (Fig. 11e) suits best. The relation of two nutrients with one specific and one common function (Fig. 11d) may also apply. Even the complementary relationship (Fig. 11a) may be appropriate, taking into account that we do not know whether the observed yields are maximum yields. Since the higher maximum yields in the middle take a longer time and more of the other resources to be realized than the lower maximum yields at the extremes of the nutrient replacement series, they are more likely not to be attained. The curve might have been more pointed if we had succeeded in eliminating limiting factors other than K and Ca. The assumption made in the model of Chapter 5, that the nutrients are complementary may well hold in principle for K and Ca. In practice, however, we have to reckon with a gradual transition from K-limitation to Ca-limitation, which complicates the evaluation of the equilibrium conditions.

In Figure 37 the internal K and Ca concentrations in the different parts and in the whole plants of the third harvest are plotted against each other, obtaining minimum con-

centration curves. The curves are evidently more complicated than suggested in Figure 22, which is mainly due to the behaviour of Ca in the plant. The concentration of Ca in the different parts of the plants is not the same. Since Ca is not redistributed, growth stops almost immediately after the exhaustion of Ca in the nutrient solution, and tissues very low in Ca are not produced in an exhaustion experiment. The Ca concentrations in the oldest leaves reflect the situation before the experiment. The Ca concentration in the younger leaves reflect the uptake-growth ratio at advancing stages during the exhaustion of the solution. The dead parts of the shoot were mainly composed of the older leaves. The cause of their death could not have been Ca deficiency, as the living parts have much lower Ca concentrations.

Remarkably, plants on the most Ca deficient solution have higher Ca concentrations in the dead parts than plants growing on less Ca deficient solutions. This is reflected in the concentration of the whole plants, and, since the roots were not separated in dead and living parts, they also exhibit this behaviour. This phenomenon, which causes a C shaped concentration-yield curve (discontinuous line in Fig. 20) is called the 'Steenbjerg effect' (reviewed by Bates, 1971).

An explanation for this effect in our case may be that with the extreme Ca-deficient solution hardly any production occurred and the internal Ca concentration remained close to the initial concentration, whereas with the other solutions substantial production occurred of tissue with a lower Ca concentration until the solution was exhausted and growth stopped. Since most of the older leaves with high Ca concentrations are dead, this is not reflected in the concentration in the living parts. The possibilities mentioned by Bates (1971) that the dead leaves have lost some of their dry matter and that deficiency destroys the potential for growth irreversibly and earlier than the potential for uptake, may also apply.

The K concentrations are much less different between tissues at their minimum than the Ca concentrations. Only the roots of *Plantago* seem to have a somewhat lower K requirement. The highest concentrations show that, in contrast to the root, the shoot accumulates K to a large extent when it is in excess.

The uneven concentration in the plant and the 'Steenbjerg effect' make it difficult to determine a minimum concentration of Ca. A reasonable estimate is obtained by taking the concentration in the youngest leaves. A better way would be the use of continuous flow cultures with low Ca concentrations (Loneragan & Snowball, 1969b) if it were not for the fact that exhaustion is inherent in a competition experiment.

In quantifying the minimum concentrations as parameters for our model we have to use concentrations in the whole plant, since they will be used in calculating the total production possible with a consumed amount of a nutrient. Taking the lowest concentrations attained by the curves of whole plants, we obtained the following minimum concentrations ($\text{meq kg}^{-1} \text{ DM}$):

$$m_p^K = 75; m_p^{\text{Ca}} = 150; m_c^K = 100; m_c^{\text{Ca}} = 130.$$

This means that the double quotient of minimum concentrations is different from unity, which is a part of the equilibrium condition (Eqn 5.17).

$$\left(\frac{m_p^{Ca}}{m_p^K}\right) / \left(\frac{m_c^{Ca}}{m_c^K}\right) \approx 1.5$$

Owing to the absence of Ca redistribution, the 'Steenbjerg effect' and the gradual transition from K limitation to Ca limitation, it depends to some extent on the history of the plants and the composition of the nutrient solution, whether these minimum concentrations will be attained. These complications will make yield predictions based on the minimum concentrations somewhat questionable.

7.2.3 Competition for K and Ca (Experiment II)

In addition to the observed difference in the minimum K and Ca requirements of *Plantago* and *Chrysanthemum* a difference in the relative uptake abilities is required to permit coexistence by differential resource limitation. To obtain information about the relative uptake abilities the relative crowding coefficients, k_{pc}^K and k_{pc}^{Ca} , were measured in competition experiments carried out on K and Ca deficient nutrient solutions, respectively.

To this end nutrient solutions were chosen with K/Ca ratios corresponding with Solutions II and VIII of Experiment I. From Figures 36 and 37 can be seen that in these solutions K and Ca were limiting for both species, respectively, that the 'Steenbjerg effect' did not occur and that the production was reasonable.

In addition to these solutions one intermediate solution (V) was included in the experiment to see how the relative crowding coefficients behave when both elements are limiting in the same degree, and also on the chance of this solution meeting the equilibrium conditions for the substrate (Eqn 5.18), in case the species might satisfy their equilibrium condition (Eqn 5.17), in which case the RYT is expected to exceed unity.

7.2.3.1 Experimental technique

Seeds of *Plantago* and *Chrysanthemum* collected from the field trials were sown on a moderately fertile soil in a glasshouse. On 1 November the seedlings were transplanted in six-liter pots containing the experimental nutrient solutions. The plant density was 16 plants per pot; the frequencies were $Z_p/Z_c = 16/0; 12/4; 10/6; 8/8; 6/10; 4/12; 0/16$. The plants in a pot were grouped together per species to reduce inter-specific light competition and intermingling of the roots. Initial dry weights, K contents and Ca contents of the monocultures are given in Table 7.

The composition of the nutrient solutions is given in Table 8. Addition of iron and

Table 7. Initial dry weights, K and Ca concentrations and contents of the monocultures in Experiment II.

	Dry matter g pot ⁻¹	Potassium		Calcium	
		meq kg ⁻¹ DM	meq pot ⁻¹	meq kg ⁻¹ DM	meq pot ⁻¹
<i>Plantago</i>	0.73	351	0.26	1532	1.12
<i>Chrysanthemum</i>	0.64	648	0.42	545	0.35

Table 8. Composition of the three nutrient solutions used in Experiment II (in meq pot⁻¹).

K	x	NO ₃ ⁻	34.8
Ca	4.8-x	SO ₄ ⁻	5
Mg	15	H ₂ PO ₄	5
Na	15	Fe	10 mg l ⁻¹
NH ₄	10		

Micro-nutrients as in Table 6

x= 1.2 (Sol. II); 2.4 (Sol. V); 3.6 (Sol. VIII)

micro-nutrients and watering was applied as in Experiment I. Air was blown through once a day to mix the solution. The experiment included two harvest series and was replicated three times. It was carried out in climate room at 18°C and 50 W m⁻² illumination by HPL lamps during 15 hours a day. Humidity was not regulated to prevent Ca contamination through the air. Placement of the pots was changed daily. The climate room was fumigated once against aphids.

Harvests took place after 38 and 49 days. At the latter date the plants were in a state of deficiency comparable to the third harvest of Experiment I. Roots and shoots were harvested separately. The roots of the species were separated carefully, rinsed in demineralized water and blotted to remove excess water. After determination of dry weight the replicates were combined for analysis of K, Na, Ca and Mg concentrations in the whole plants.

7.2.3.2 Results and discussion

The results of the second harvest are presented in Figures 38 to 43. Since no tendency to S-curves is visible the curves in Figure 38 are calculated using the De Wit formulas with constant relative crowding coefficients. The parameters of the curves are given in Table 9.

For comparison with Experiment I Figure 39 and 40 are given. With Solution II both species show a K concentration higher than the minimum concentration found in Experiment I. It can however be concluded from the form of the curves in Figure 39 and 40 that *Plantago* is limited by K on this solution. *Chrysanthemum* on the other hand seems to be limited by Ca on all solutions. Absence of aerial Ca contamination may be put forward as an explanation for the fact that its Ca concentration is lower than the minimum concentration found in Experiment I (see Section 7.2.2.3). In *Plantago* this is probably compensated by its higher initial Ca concentrations, so that it attains approximately the same minimum Ca concentration as in Experiment I.

The relative crowding coefficients and their products for K and Ca uptake and for biomass production, estimated from gross uptake and gross yield figures, are plotted in Figure 41 against the substrate composition to facilitate comparison of the competitive ability for different nutrients and the impact of different limiting conditions on growth in mixture. (Note that the relative crowding coefficients estimated for gross uptake and

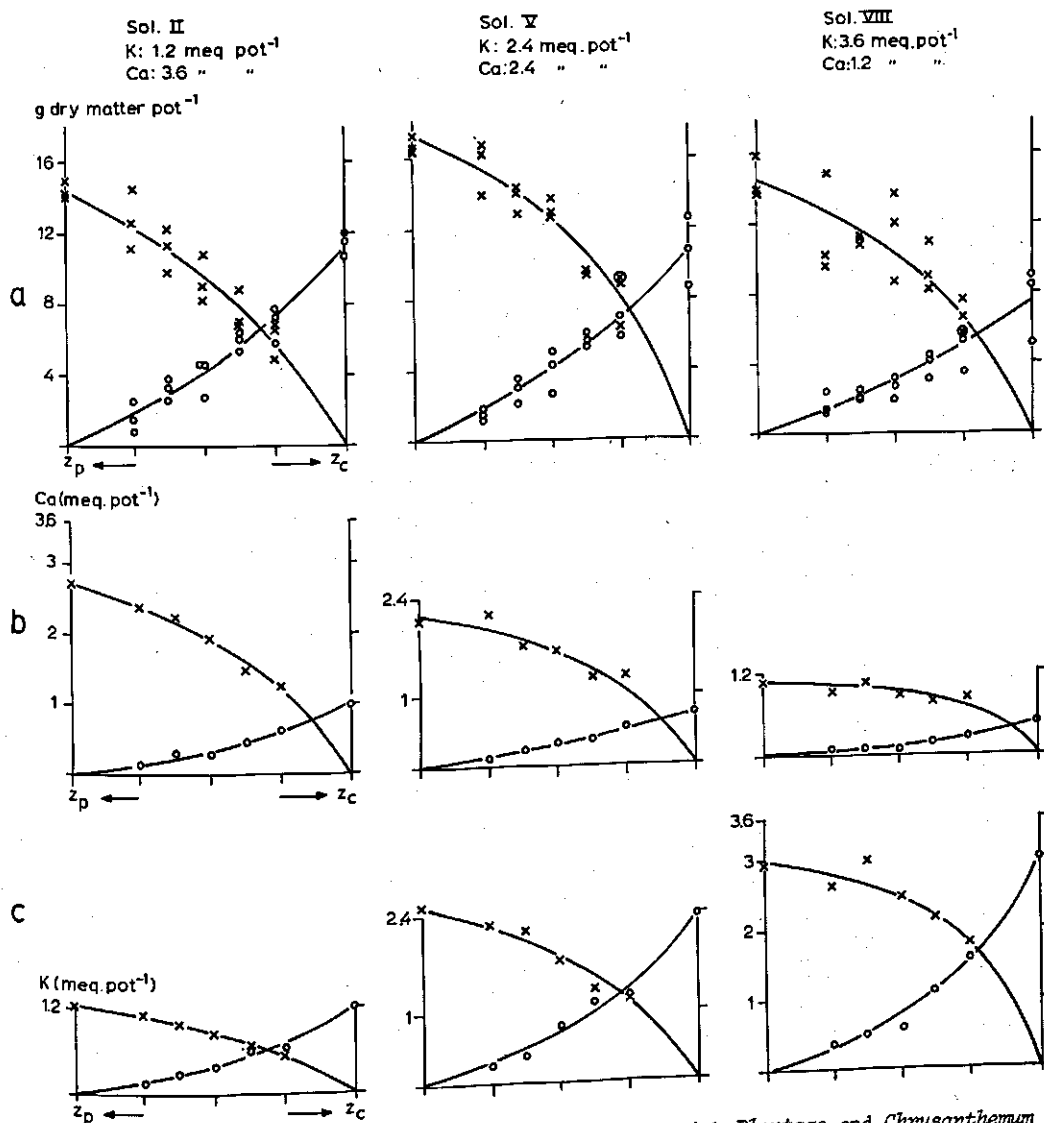


Fig. 38. Replacement diagrams of a competition experiment with *Plantago* and *Chrysanthemum* on nutrient solutions with different K/Ca ratios (Exp. II, second harvest). (a) Dry matter yields (in g DM pot⁻¹), (b) Net Ca uptake and (c) net K uptake (in meq pot⁻¹).

Table 9. Parameters of the curves in Figure 38.

	Solution	k_{pc}	M_p	K_{cp}	M_c	$k_{pc} k_{cp}$	RYT extreme
Dry matter (Fig. 38a)	II	2.05	14.38	0.60	11.20	1.23	1.05
	V	2.70	17.20	0.60	10.80	1.62	1.12
	VIII	2.50	14.50	0.66	7.50	1.65	1.13
Net Ca Uptake (Fig. 38b)	II	2.35	2.73	0.50	1.00	1.18	1.04
	V	3.00	2.15	0.70	0.71	2.10	1.18
	VIII	6.00	1.05	0.40	0.47	2.40	1.22
Net K Uptake (Fig. 38c)	II	2.20	1.25	0.50	1.21	1.10	1.02
	V	2.50	2.50	0.45	2.34	1.13	1.03
	VIII	4.50	3.00	0.35	3.00	1.58	1.12

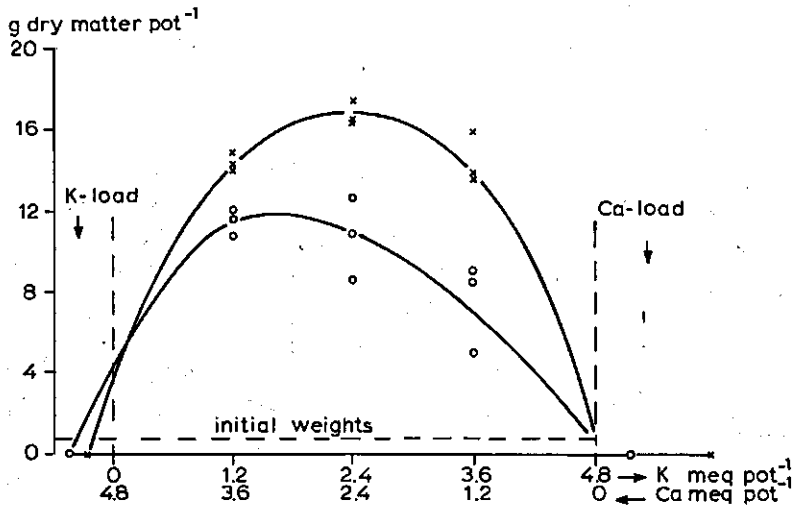


Fig. 39. Yields of the monocultures of Experiment II (second harvest) plotted in the same way as Figure 36. (x) *Plantago*; (o) *Chrysanthemum*.

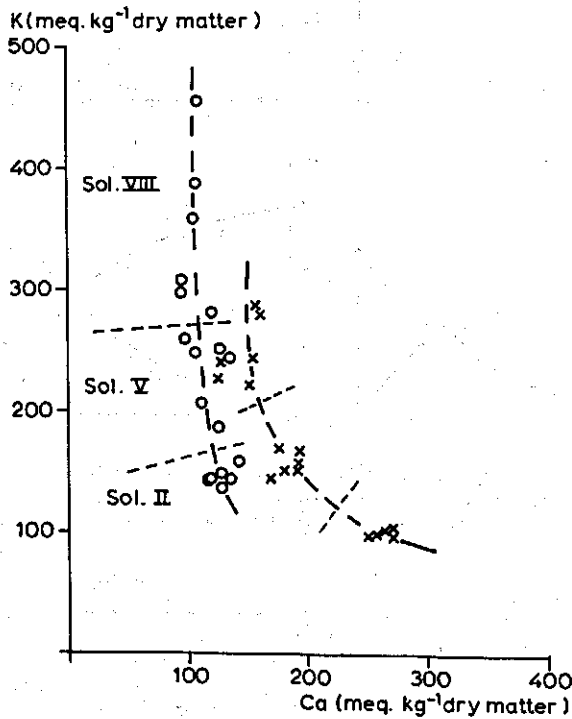


Fig. 40. K and Ca-concentrations in whole plants of *Plantago* (x) and *Chrysanthemum* (o) grown in monoculture and in different mixtures on nutrient solutions with different K/Ca ratios II, 2nd harvest).

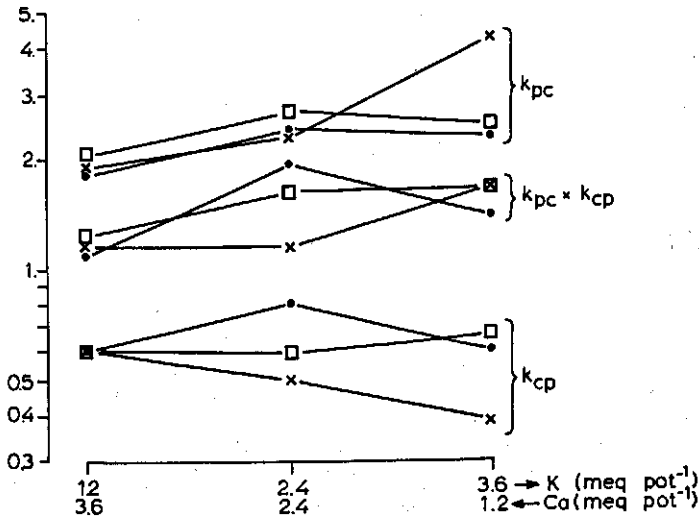


Fig. 41. Relative crowding coefficients of *Plantago* with respect to *Chrysanthemum* (k_{pc}) and *vice versa* (k_{cp}) and their product, estimated for gross yield (□) and gross K (x) and Ca (●) uptake (incl. initial contents) on nutrient solutions with different K/Ca ratios (Exp. II, 2nd harvest). Note that the relative crowding coefficients estimated for gross uptake are somewhat different from those calculated for net uptake (Table 9).

net uptake are slightly different). It appears that *Plantago* is the stronger competitor on all the solutions, which agrees with the findings of Tonneyck (see Section 7.1). The differences in the relative crowding coefficients for K, Ca and dry matter on the same solution are considered not significant, except perhaps on Solution VIII.

The deviating k^K values on Solution VIII suggest that *Chrysanthemum* does not accumulate K as fast as *Plantago*, especially when it is not limiting. This disadvantage adds to the handicap *Chrysanthemum* already has in the Ca competition. The relative crowding coefficient of dry matter remains close to that of Ca, as Ca is limiting in Solution VIII. This results in a frequency dependent K concentration which can also be seen in Figure 40 where the points from Solution VIII are more or less arranged in vertical direction with the monoculture at the top for *Chrysanthemum* and at the bottom for *Plantago*.

Figure 41 shows that the products $k_{cp} k_{pc}$ for dry matter as well as for K and Ca on Solution VIII and for dry matter and Ca on Solution V deviate slightly from unity. This deviation is considered just about significant (compare: a value of 1.5 corresponds with RYT extreme = 1.10). The deviation of the Ca product on Solutions V and VIII, where Ca is limiting, reveals that the assumption made in the model, that the species exclude each other in competition for the separate nutrients does not hold for Ca.

The explanation for this phenomenon can be inferred from Figure 38b: *Chrysanthemum* does not take up all the Ca supplied, even when Ca is limiting. Evidently, it is not able to take up Ca at low concentrations in solution (< 0.1 meq l⁻¹), leaving a Ca refugium for *Plantago* that can exhaust Ca to a much lower concentration (compare Section 4.9.4). This results in RYT values for Ca exceeding unity, which is accompanied by an increased RYT for dry matter when Ca determines growth (on Solution V and VIII) and also by an in-

Sol. VIII

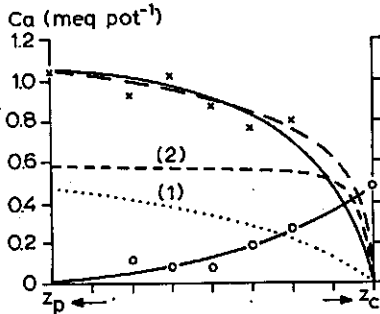


Fig. 42. Compound and simple replacement curve of *Plantago* (x) for net Ca uptake on Solution VIII of Exp. II (second harvest). The compound curve (----) is composed of (1) a replacement curve, representing the competitive process with *Chrysanthemum* (o) for the fraction of Ca taken up at higher concentrations ($M_p = M_c$; $k_{pc} = 1/k_{cp}$); (2) a spacing curve, representing the non-competitive uptake by *Plantago* alone of the remaining fraction of Ca. The simple curve (—) is directly fitted through the points ($k_{pc} = 6.$; $M_p = 1.05$), according to Equations 5.3.

creased RYT for K, when enough K is present (as in Solution VIII, where not all K is consumed). The relevant curves of *Plantago* are thought to be composed of a replacement curve and a spacing curve. Strictly, the use of constant relative crowding coefficients in Figure 38 is not correct, but the difference with a compound curve is negligible in view of the scatter of the points (Fig. 42).

Checking the fulfillment of the equilibrium conditions, however, we did not use the relative crowding coefficients, to avoid difficulties arising from their non-reciprocity and to avoid the use of formulas based on assumptions that have been disproven. Instead we calculated the double quotient

$$(U_p^{Ca}/U_p^K)/(U_c^{Ca}/U_c^K)$$

from the net uptake. Figure 43 demonstrates that *Plantago* has a Ca/K uptake ratio which is on an average 2.3 times as high as that of *Chrysanthemum* which agrees with our inference from Horak (1971) that we are dealing with a calciotropic and a potassium type of plant. The double quotient is independent of the plant frequency. Although the uptake ratios depend closely on the substrate ratio (indicated with -----), the quotient of uptake ratios is remarkably independent of the substrate ratio.

Under the assumptions of the model, the double quotient is identical to k_{pc}^{Ca}/k_{pc}^K . Its numerical value 2.3 evidently does not lie between unity and the value of the double quotient of minimum concentrations which was 1.5. Therefore the combination of *Plantago* and *Chrysanthemum* with K and Ca as limiting nutrients does not meet the condition for coexistence by differential resource limitation as derived from our model (Eqn 5.17).

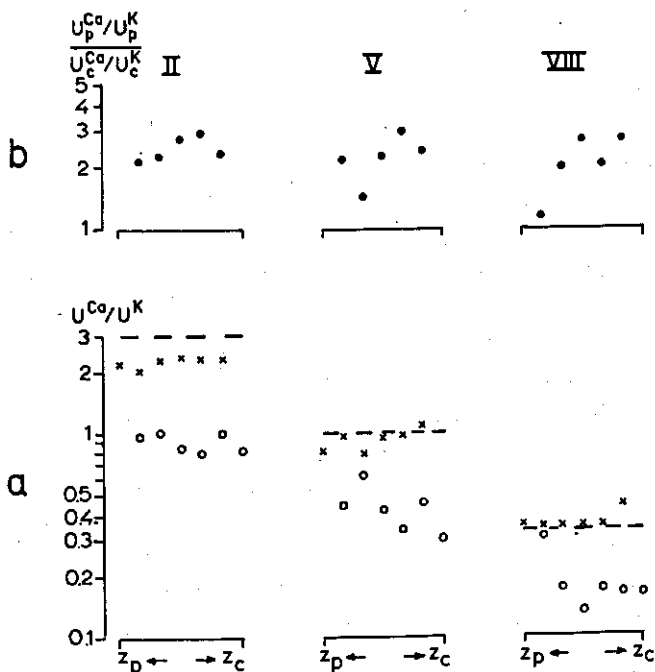


Fig. 43. (a) Net Ca/K uptake ratios of *Plantago* (x) and *Chrysanthemum* (o) in monoculture and in different mixtures on nutrient solutions (II, V and VIII) with different Ca/K ratios (indicated with -----). (Exp. II, 2nd harvest).
 (b) Quotients of the net Ca/K uptake ratios of *Plantago* and *Chrysanthemum*.

7.2.4 Conclusions

From Experiments I and II it can be concluded that *Plantago* and *Chrysanthemum* indeed differ in their K and Ca nutrition, as was expected from the literature. Only the differences do not meet the equilibrium conditions derived from our model of multiple resource competition (Eqn 5.17). The difference in uptake of K and Ca is greater than the difference in K and Ca requirements, whereas the reverse is required for coexistence.

Nevertheless the experiments support our opinion that differential nutrient limitation may contribute to species diversity, since the kind of species differences required for two equilibrium mechanisms have been shown to exist. Taking the infinite number of possible species-nutrients combinations into account, there certainly will be combinations that meet the equilibrium conditions.

The results also reveal a difference in Ca-uptake ability at low concentrations. The inability of *Chrysanthemum* to take up Ca at low substrate concentrations resulted in a resource refugium for *Plantago*. It was argued in Sections 3.3.1 and 4.9.4 that this may lead to equilibria between species. In the present case this was not possible, as the species with the refugium was already stronger in the competition for the common resource, i.e. the amount of Ca available at higher concentrations.

The determination of the relative crowding coefficients k_{ab}^1 and k_{ab}^2 from competition experiments, which are very labourious, is complicated by the fact that they may be

frequency dependent and interconnected. Therefore it is more convenient first to determine the uptake ratios of a number of species separately, which is much easier. Interesting species combinations may then be studied in more detail in competition experiments.

The model developed in Chapter 5 has been shown to give a poor representation of the facts at some points. In the first place there is a gradual transition from K limitation, instead of the assumed sharp breaking point. In the second place the nutrients are taken up incomplete by one of the species. In consequence of the above the relative crowding coefficients of the separate nutrients may be non-reciprocal and frequency dependent in contrast to what was assumed.

These shortcomings would perhaps not be serious, should the equilibrium conditions be met liberally. However, the species differences are only small. All conditions being favourable the observed value of 2.3 of the K/Ca uptake double quotient theoretically permits an RYT-extreme of 1.33. The double quotient of minimum concentrations should be about 5.0 and the substrate conditions should be within a narrow range to realize this RYT. The shortcomings of the model may have exaggerated the expected RYT and the stabilizing effect. In reality they may be smaller and experimental errors will make them difficult to detect in practice, even in waterculture. Therefore it is not possible to evaluate the model and its essential conclusion that differential resource limitation permits stable coexistence, with species that only hardly meet the equilibrium conditions.

7.3 RATIOS OF CATION UPTAKE BY SOME GRASSLAND SPECIES IN THE FIELD

Since the previous experiments confirmed that differences in relative uptake and relative requirement of nutrients do occur between species, but that the differences in K and Ca nutrition between *Plantago* and *Chrysanthemum* do not meet the equilibrium conditions of our model, we intended to investigate whether these species differ in other aspects of their nutrition more closely conforming to the equilibrium conditions and whether differences observed in water culture also occur in the field situation. At the same time we wanted to find some species-nutrient combination meeting the equilibrium conditions liberally enough to evaluate the essential conclusion from our model.

In consequence of the above we had to test more species and more nutrients. To make a sensible choice from the infinite number of possible species-nutrients combinations, a preliminary chemical analysis was carried out of a number of species co-occurring on plots of a field experiment. It concerned a 20 year old fertilizer experiment in a hay-field on clay soil (Van den Bergh, 1979), next to the field where the seed populations used in our experiments were collected. The plots received the following fertilizer applications each year:

0 = no fertilizer

Ca = 1000 kg ha⁻¹ CaO (lime)

P = 120 kg ha⁻¹ P₂O₅ (superphosphate)

K = 400 kg ha⁻¹ K₂O (potassium sulphate)

PK = 120 kg ha⁻¹ P₂O₅ and 400 kg ha⁻¹ K₂O

In addition pairs of species co-occurring in a number of chalk grasslands were analysed. The results of these analyses will be discussed in detail elsewhere (Braakhekke & Elberse, in prep.).

Some results are condensed in Figure 44, showing the K/Ca ratios (on equivalent basis) in the aerial biomass of the five species growing in the five plots of the field experiment sampled in June 1977. The advantage of using uptake ratios is that the influence of differences in growth on nutrient concentrations are largely eliminated. Evidently, the different treatments, especially the potassium fertilization, considerably affect the K/Ca uptake ratio of most species. This illustrates, incidentally, the risk of making inferences about species differences in mineral nutrition from analyses of plants growing in different places.

On the other hand it is clear that there are great differences between the uptake ratios of different species in the same plot. It is apparent also that the species respond differently to the various fertilizer treatments. Whereas their K/Ca uptake ratios vary between plots with a factor six, a constant difference of a factor two is maintained on all plots between the K/Ca uptake ratios of *Plantago lanceolata* and *Chrysanthemum leucanthemum*. This difference is in remarkably good agreement with the results obtained on waterculture (Experiment II). In contrast to these species the K/Ca uptake ratio of *Cerastium holosteoides* is hardly influenced by the fertilizer treatments. *Rumex acetosa* takes an intermediate position between these species, in that it is affected in the same way, but to a less extent than the first two species. *Centaurea pratense* demonstrates its

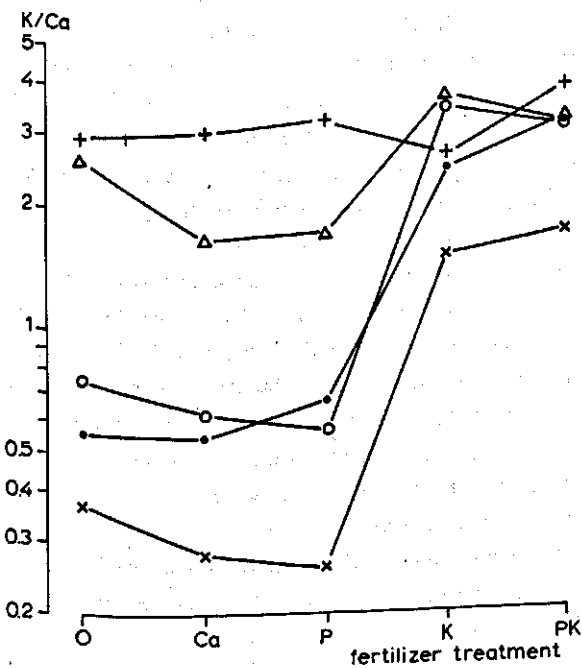


Fig. 44. K/Ca ratios (on equivalent basis) in the aerial biomass of five species co-occurring in five plots of a 20 year old fertilizer experiment. (+) *Cerastium*; (Δ) *Rumex*; (o) *Chrysanthemum*; (●) *Centaurea*; (x) *Plantago*.

family relationship with *Chrysanthemum* in showing approximately the same pattern and values of the uptake ratios.

Inspection of the nutrient concentrations reveals that the differences in K/Ca uptake ratio of species between the five plots originated mainly from variation in the K concentrations. The differences between the species originated from differences in K concentration and Ca concentration as well. K fertilization much reduced the between-species differences, in K/Ca uptake ratio. The Ca and Mg concentrations were less influenced by the treatments than the K and Na concentrations. Consequently, the Ca/Mg uptake ratios showed less variation between plots. There were, however, considerable differences between species. The Ca/Mg ratio of *Plantago* varied between 4 and 6, that of *Chrysanthemum* between 1.8 and 2.7 and that of *Cerastium* between 1.2 and 1.6.

The differences in K/Na uptake ratios were very great: a factor 12 to 30 between plots (depending on the species) and a factor 6 to 40 (!) between species (depending on the plot). The lowest K/Na ratio was observed in *Plantago*, i.e. 0.2. High K/Na ratios were found in *Cerastium*, namely up to 75. (A value of 225 was found for *Lotus corniculatus*, a species not further discussed here, because it was not present in all the plots.) These results agree with the earlier findings of Collander (1941) that species differences with respect to the relative Na concentration are very pronounced.

From these results it is evident that the differences in cation uptake ratios between *Plantago* and *Chrysanthemum* are easily surpassed by other species combinations. Interesting species combinations in this respect are *Plantago* with *Cerastium* or *Rumex*. From the analyses of plants growing in chalk grasslands two more interesting species emerged. *Anthyllis vulneraria* showed a K/Ca ratio of 0.4 which is remarkably low compared to the K/Ca ratio of 2.3 of *Chrysanthemum* growing in the same place. This suggests a K/Ca uptake ratio even lower than that of *Plantago*. In fact *Anthyllis* is known as 'das Musterbeispiel einer calciotropen Pflanze' (Horak, 1971, p. 44).

The other interesting species is *Sanguisorba minor*. The K/Mg uptake ratio of this species was 0.9, whereas *Plantago* growing next to it had a K/Mg ratio of 5.2. This is a great difference, since the species differences in K/Mg ratio were only small in the fertilizer experiment. Horak (1971) found approximately the same K/Mg ratio for *Sanguisorba* and relatively low K/Mg ratios for some other *Rosaceae* as well. Among the sixteen grassland species grown on the same soil by Thomas et al. (1952) *Sanguisorba* (= *Poterium sanguisorba*) had the highest Mg concentration and the lowest K/Mg ratio. An additional reason for *Sanguisorba* to be interesting for our experiments arises from the fact that Ca was shown to be not an easy nutrient for the purpose of evaluating our model, as it is not redistributed within a plant, which makes minimum concentrations difficult to determine. As the relative redistribution of Mg is in general better, species combinations with different K/Mg ratios are preferred.

These considerations, together with the availability of seeds led us to the choice of the following six species to be studied in more detail in the subsequent experiments with respect to their relative K, Ca and Mg uptake:

Plantago lanceolata
Chrysanthemum leucanthemum
Rumex acetosa
Cerastium holosteoides
Anthyllis vulneraria
Sanguisorba minor

These species often co-occur in grasslands, though not all together and in all combinations.

7.4 RATIOS OF CATION UPTAKE BY SIX GRASSLAND SPECIES ON WATER CULTURE (EXPERIMENT III)

7.4.1 Introduction

As explained in the previous section we intended to test a number of species for differences in the relative uptake of a number of nutrients. The nutrients K, Ca and Mg and the species *Plantago lanceolata*, *Chrysanthemum leucanthemum*, *Rumex acetosa*, *Cerastium holosteoides*, *Anthyllis vulneraria* and *Sanguisorba minor* were chosen for this purpose because of their different cation composition while co-occurring in the field.

It was demonstrated in Experiment II that the cation uptake ratio of plants depends closely on the substrate ratio when the solution is not replenished, which is not surprising. A difference between the uptake ratios of the species was maintained on different solutions, in monoculture as well as in mixtures, because they differed in the extent to which the solution could be exhausted. The analysis of plants growing in the field also demonstrated that the uptake ratio was dependent on the substrate ratio. However, in this case the differences between some of the species were highly variable. This makes it precarious to determine the differences between the uptake ratios of species by growing them on one substrate only.

In the experiment described in this section the relative uptake of three cations by the six species mentioned above was studied in relation to the composition of the substrate, by growing them together on nutrient solutions with different K, Ca and Mg concentrations, which were kept constant within certain limits. In this way the species were subjected to exactly the same substrate conditions, differences arising from different uptake ratios are avoided, as well as competition. In contrast to Experiments I and II uptake is determined only by the concentration and composition of the substrate and not by the amounts that are supplied.

7.4.2 Experimental technique

Seeds of *Plantago* and *Chrysanthemum* were collected from the field trials. Seeds of *Rumex* were obtained from plants in a nursery, coming from a population coexisting with the original populations of *Plantago* and *Chrysanthemum* used in the experiments. *Cerastium* seeds came from a derelict lawn near the laboratory and seeds of *Anthyllis* and *Sanguisorba* were obtained from a commercial seed trader.

To reduce concentration fluctuations we used large volumes of nutrient solution in

215 liter containers covered with plastic foil inside. To avoid difficulties arising from pretreatments differing from the experimental treatments and consequent transplantations, the plants were grown on the experimental solutions from the start.

The seeds were sown on synthetic cloth supported by narrow p.v.c. frames with nylon gauze that were mounted just at the water surface in the containers. After germination the roots of the seedlings penetrated through the cloth and floated in the nutrient solution. The solution was aerated and mixed continuously by pumping it at a rate of 30 l min^{-1} from the bottom of the container through a distributing system with perforated pipes, squirting it from just above the water surface along the roots.

The composition of the nutrient solutions is given in Table 10. Originally, the experiment included thirteen solutions in twofold. The first seven solutions form three series, in each of which the concentration of one cation was lowered ten and a hundred times, starting from Solution 1 in which K, Ca, Mg and Na were present to an equivalent of 2 meq l^{-1} . In the Solutions 8 to 13 the concentration of two cations was reduced simultaneously ten or a hundred times. When, two weeks after the start of the experiment, it became evident that hardly any growth was possible on the Solutions 5 and 11 with $0.02 \text{ meq Ca l}^{-1}$, it was decided to replace these solutions by one solution with $0.05 \text{ meq Ca l}^{-1}$ and two solutions in which the concentrations of the three cations were decreased simultaneously ten or a hundred times.

Sodium was present in all solutions with 2 meq l^{-1} , serving as a counter ion in order to provide sufficient amounts of the anions. The anions were supplied in all solutions in the same proportions, but, necessarily, in different total concentrations. The solutions were prepared and replenished with demineralized water. They were analysed weekly and later on twice a week for the cations present at 0.2 and 0.02 meq l^{-1} , to calculate the gross uptake rates. The amounts taken up were replenished by stock solutions containing the anions in the proportions mentioned above. This was done frequently

Table 10. Composition of the nutrient solutions in Experiment III (in meq l^{-1}).

Solution	K	Ca	Mg
1	2	2	2
2	0.2	2	2
3	0.02	2	2
4	2	0.2	2
5	2	0.02	2
6	2	2	0.2
7	2	2	0.02
8	0.2	0.2	2
9	0.2	2	0.2
10	2	0.2	0.2
11	0.02	0.02	2
12	0.02	2	0.02
13	2	0.02	0.02
27	0.2	0.2	0.2
28	0.02	0.02	0.02
29	2	0.05	2

In all solutions: Na 2 meq l^{-1}
 $\text{NO}_3 : \text{H}_2\text{PO}_4 : \text{SO}_4 = 4:1:1$ (as equivalents)
 Fe and micro-nutrients as in Table 6

enough (twice a day at the end) to keep the concentration fluctuations within 20%.

The experiment was carried out from 11 October until 3 January in a heated glass-house at approximately 20°C, with additional illumination from 3.00 to 9.00 a.m. Depending on growth the species were harvested in one, two or three portions at different times during the experiment. On several solutions harvest was not possible because the plants died soon after germination due to severe Ca deficiency. *Chrysanthemum* and *Rumex* failed to establish on many containers due to rooting difficulties and subsequent fungal attack. In harvesting the plants were clipped just above the supporting cloth. Roots and shoots were carefully rinsed in demineralized water and blotted. After determination of fresh and dry weight they were combined for chemical analysis for K, Na, Ca and Mg.

7.4.3 Results and discussion

7.4.3.1 Growth

The experimental technique was not a great success in so far as the support of the plants was concerned. Because the plants intermingled and fell-over, it was not possible to harvest comparable numbers of plants in subsequent harvests, so that an intended determination of growth rates was not possible. A reasonably qualitative indication was nevertheless obtained through independent visual judgement by different persons.

The low K concentrations caused a small reduction in the growth of *Sanguisorba* only. The low Mg concentrations caused some growth reduction in *Anthyllis* and little or no reduction in the other species. Obviously, most species are able to take up these nutrients from the present low concentrations rapidly enough to maintain a maximum growth rate. For K this was already known from the literature (Williams, 1961; Asher & Ozanne, 1967; Wild et al., 1974). Mg concentrations often have to be higher to prevent Mg deficiency ($> 0.4 \text{ meq l}^{-1}$ for *Helianthus annuus*, according to Madhok & Walker, 1969).

In contrast to the above, little or no growth was possible at the lowest Ca concentrations. This is surprising in view of the findings of Loneragan et al., (1968a and b) who found at this concentration relative growth rates greater than half the maximum growth rate for most of the thirty species investigated. Some improvement was observed when the Mg concentration was low as well. Apparently, the hundred fold higher Mg concentrations hampered the Ca uptake from the lowest concentrations (see Moore et al., 1961; Legget & Gilbert, 1969; Maas & Ogata, 1971). This would also explain the differences with the experiment of Loneragan et al. (1968) as these authors used K, Mg and Na concentrations of only 0.25, 0.2 and 0.01 meq l^{-1} respectively. The reduction in K concentration simultaneously with Ca caused no relief of the Ca deficiency, but seemed to deteriorate conditions even more.

On the solutions with the intermediate concentrations of the three cations most species grew best. A concentration of 2 meq l^{-1} seems already above the optimum concentration, provided of course that the supply is adequate.

Severe Ca deficiency symptoms were observed on the solutions with the lowest concentrations. Symptoms of Mg deficiency were less marked and no symptoms of K deficiency were found.

7.4.3.2 Cation concentrations

The K, Na, Ca and Mg concentrations of the whole plants are shown in Figure 45 (average values of all harvests and replicates available). The nutrient solutions are grouped according to the concentration of the relevant cation, except for the figure with Na concentrations where the solutions are ordered according to the total cation concentration. The effect of the substrate concentration of a cation on its concentration in the plants is seen by comparing the level of the concentration lines of the groups. The effect of the substrate concentration of a cation on the internal concentration of other cations is seen from the concentration differences within each group.

The internal concentrations of Ca and Mg are much influenced by their own substrate concentrations as well as by those of the other cations (excluding Na of course). The internal K concentration remains relatively constant, revealing a strong ability of the species to take up K at low substrate concentrations and to avoid excess uptake when other cations are in short supply.

The concentrations show a reasonably consistent pattern, the ranking of the species being the same in most solutions. *Cerastium* and *Chrysanthemum* have the highest, and *Sanguisorba* the lowest K concentration. The highest Ca concentrations are found in *Anthyllis* and *Plantago*, while *Cerastium*, *Rumex* and *Chrysanthemum* have low Ca concentrations. *Sanguisorba* has the highest Mg concentrations and *Chrysanthemum* the lowest. *Plantago* has the highest Na concentrations and *Anthyllis* the lowest. Apart from their Na concentrations these latter two species show a remarkably similar pattern.

Presumably minimum concentrations are approached only for calcium. Extremely low Ca concentrations are observed on Solution 29. Loneragan and Snowball (1969) found such low concentrations only in some cereals growing at substrate concentrations more than ten times lower. Although the relevant data are not available from the present experiment, it can be inferred that the minimum Ca concentrations of *Plantago* and *Chrysanthemum* measured in Experiment I (150 and 100 meq kg⁻¹ respectively) are too high. Evidently, a continuous limited supply is the proper way to obtain reliable information about the minimum Ca requirement of plants (Loneragan & Snowball, 1969a).

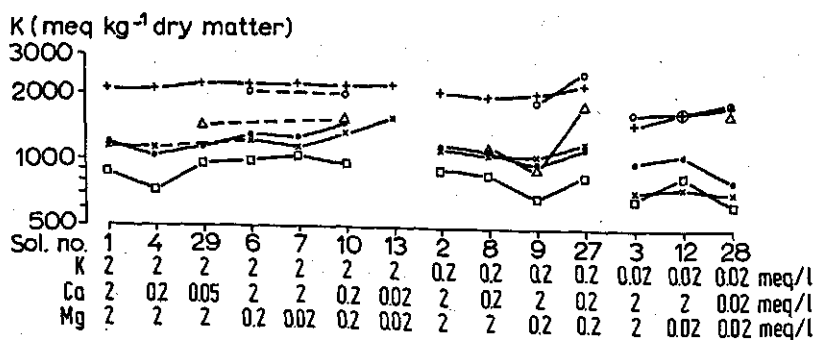
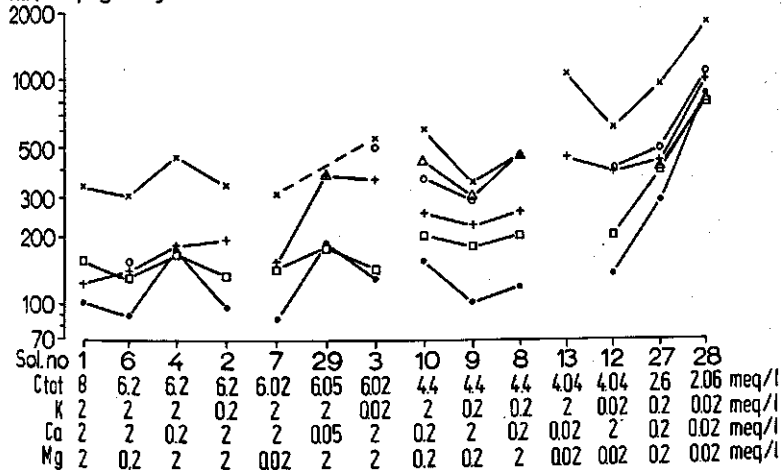
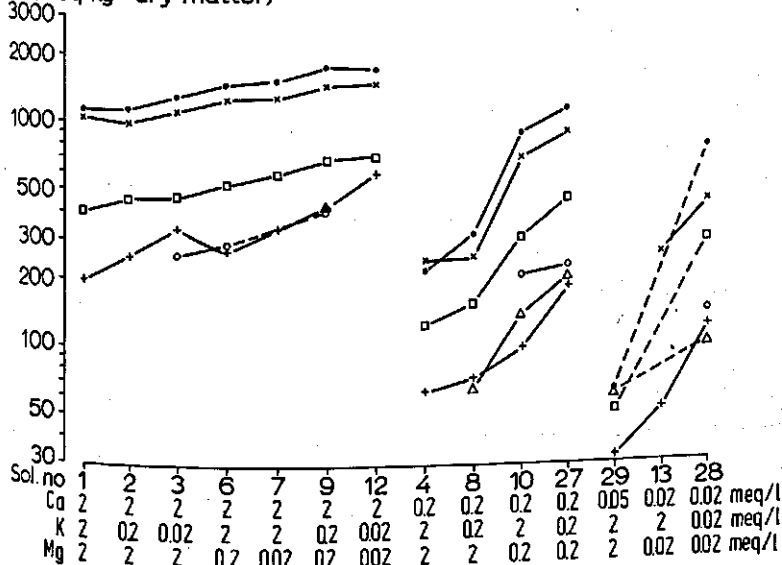


Fig. 45. K, Na, Ca and Mg concentrations (meq kg⁻¹ DM) in six species grown on nutrient solutions with different K, Ca and Mg concentrations, which were kept constant (Exp. III). (+) *Cerastium*; (Δ) *Rumex*; (x) *Plantago*; (o) *Chrysanthemum*; (●) *Anthyllis*; (□) *Sanguisorba*.

Na (meq kg⁻¹dry matter)



Ca (meq kg⁻¹dry matter)



Mg (meq kg⁻¹dry matter)

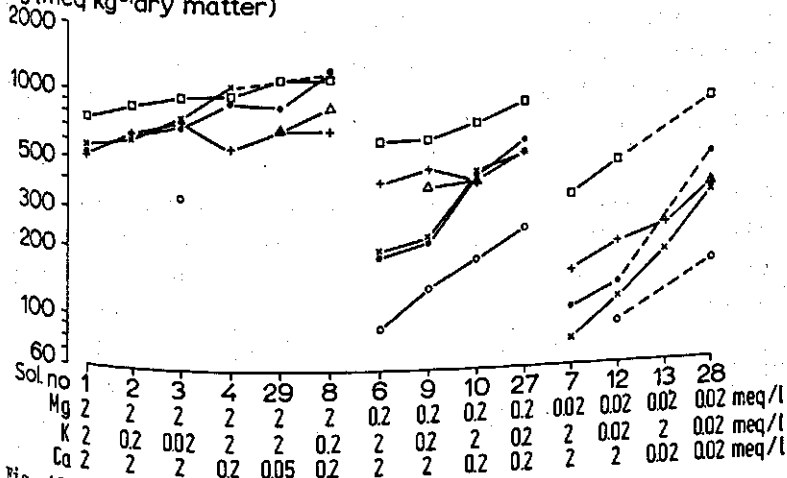


Fig. 45. (continued)

7.4.3.3 A triaxial ratio diagram

The results of the chemical analysis reveal a rather complicated relationship between the cation composition of the substrate and the plants growing in it. To enable a comprehensive view and to facilitate comparison of the species, I developed a triaxial ratio diagram to represent this relationship for three cations.

Commonly the relative amounts of three nutrients are presented in a triangular diagram, as shown in Figure 46a, in which the percentages of the nutrients are plotted along three axes that are perpendicular to the sides of an equilateral triangle. Such a diagram serves reasonably well when the nutrients are present in approximately equal amounts. However, when the relative composition is more extreme, in the sense that one of the nutrients occupies a low or a high percentage, relative differences in nutrient composition are displayed less clearly.

This is demonstrated by comparing the distances between the points A and B, C and D, E and F. The difference within each pair of these points, which may represent plants or nutrient solutions, concerns only the Ca and Mg concentrations (see Table 11). Since the Ca and Mg concentrations of A, C and E as well as those of B, D and F are chosen equal, this difference is exactly the same within each pair. Yet the distances in the diagram suggest otherwise.

Similar deception is encountered when the positions of the 13 initial solutions of Experiment III in a triangular diagram are compared. Solution 2 differs from Solution 1 in having a ten times lower K concentration. The same difference exists between Solution 3 and 2. The distance between 3 and 2, however, is only a fraction of that between 2 and 1. In fact distances in a triangular diagram may not be used as a measure for differences in relative composition.

This problem does not exist when we plot ratios instead of percentages along the three axes, and use logarithmic scales for this. We see in Figure 46b that in the triaxial ratio diagram the distances between A and B, C and D, E and F are equal and parallel. A, C and E as well as B, D and F differ only in their distance perpendicular to the Ca/Mg axis. The perpendiculars to the axes indicate the direction in which the position of a point changes when two ratios vary to the same extent while the third ratio remains constant (bisector between two axes). This is what happens when the concentration of one of the nutrients is varied, while the concentration of the two other nutrients remains constant. The axes have been situated such that an increase in the concentration of K, Ca or Mg causes a positional change in a direction comparable to that in the triangular diagram (arrows).

Both methods make use of the principle that the coordinates on two of three axes lying in the same plane, determine the coordinate on the third axis completely: two of the percentages of three components determine the percentage of the remaining third component; two of the three possible different ratios between three components (not counting the reciprocal ratios) determine the remaining third ratio. Only the last method has the advantage that the same distance represents the same difference in relative composition everywhere in the diagram, which is essential for a comparison of species responses to changes in nutrition.

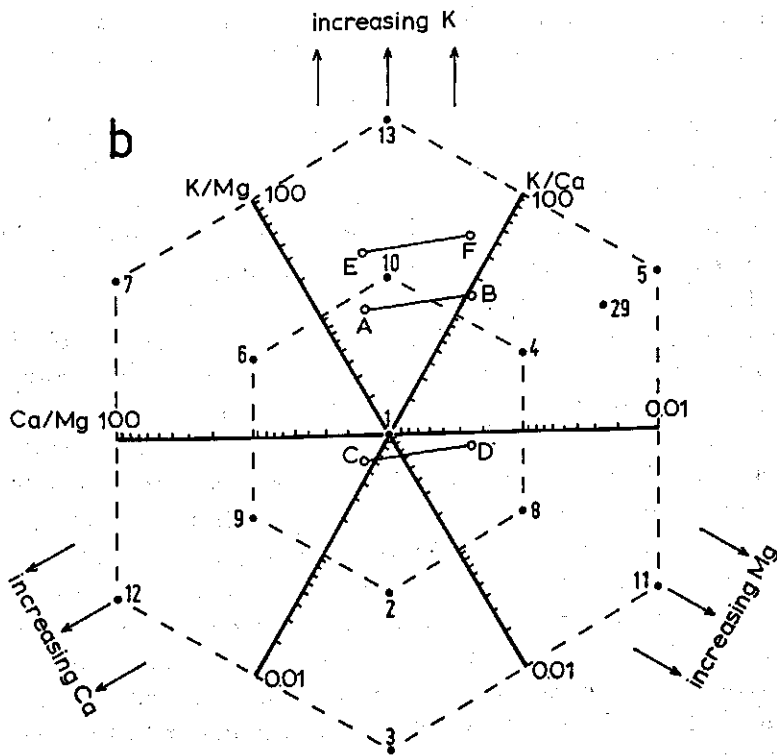
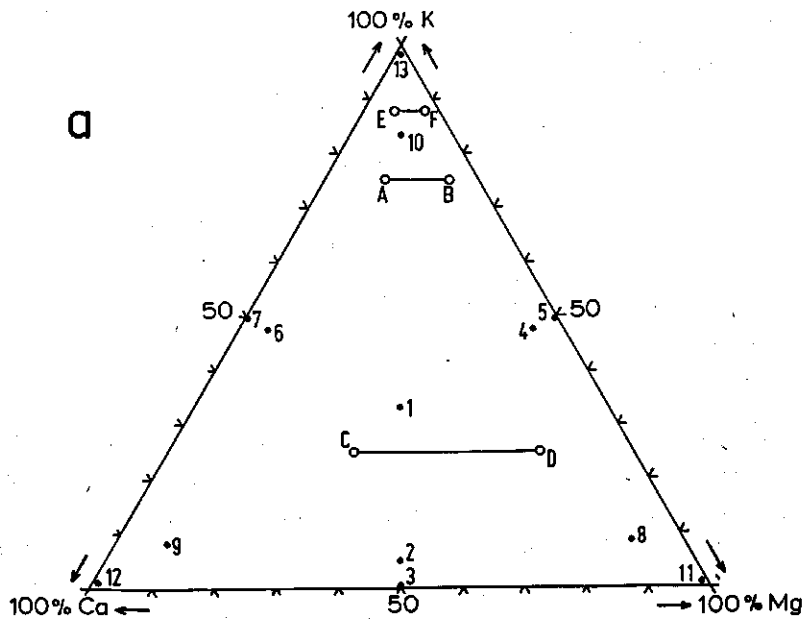


Fig. 46. Comparison of the position of some points in a triangular diagram (a) and in a triaxial ratio diagram (b). The points A-F represent six arbitrary nutrient compositions listed in Table 11. The points 1 to 13 represent the nutrient solutions used in Experiment III (Table 10). The arrows in Figure b indicate the direction in which a cation increases. Further explanation in text.

Table 11. Six arbitrary cation compositions plotted in Figure 4b.

	Concentrations			Percentages			Ratios		
	K	Ca	Mg	K	Ca	Mg	K/Ca	K/Mg	Ca/Mg
A	1500	300	200	75	15	10	5.00	7.50	1.50
B	1500	100	400	75	5	20	15.00	3.75	0.25
C	167	300	200	25	45	30	0.55	0.83	1.50
D	167	100	400	25	15	60	1.67	0.42	0.25
E	3500	300	200	87.5	7.5	5	11.67	17.50	1.50
F	3500	100	400	87.5	2.5	10	35.00	8.75	0.25

The above is once more illustrated by the position of the 13 solutions of Experiment III in Figure 46b. Solutions 1 and 2 differ only in their K concentration. This causes an equal difference in position along the K/Ca and K/Mg axis, resulting in a shift along their bissector. The same holds for Solution 2 and 3. The distance between 1 and 2 is the same as that between 2 and 3, since both represent a decrease in K concentration with a factor 10. The relative change from Solution 10 to 1 is equal to the change from Solution 1 to 2, only is it not accomplished by changing the K concentration but by decreasing the Ca and Mg concentration with a factor 10. The same holds for the difference between 13 and 10.

Owing to the systematic way of variation in the cation concentrations in Experiment III, the points representing the first thirteen nutrient solutions form two nested, regular hexagons, with Solution 1 in the center. When we plot the cation composition of the plants of the same species grown in these thirteen solutions one expects to find something like an image of these hexagons, might it be transposed, reduced, or deformed. Looking at the diagram of *Cerastium* (Fig. 47a) this indeed is just what we see.

Of the outer species' hexagons several points are missing, because no species could grow on the solutions concerned. The hexagons of *Rumex* and *Chrysanthemum* are still more incomplete due to failure of seedling establishment. To complete the picture the composition of plants grown in Solution 29 is also incorporated in the outer species' hexagons, although this solution does not fit in the outer regular hexagon of substrate composition.

Concentrations are not visible in these diagrams. The solutions in the same hexagon do not all have the same total cation concentration. However, comparison of the composition of plants growing in the Solutions 1, 27 and 29 reveals that even a hundredfold reduction in the total concentration of the three cations causes only a minor shift in the relative cation composition of the species. It was said before that with the low total concentration we used, the species could not grow on a sector of the outer hexagon due to low Ca concentrations in that sector. With higher total concentrations, however, an increasing number of solutions at the opposite side of the diagram becomes hard to realize because of precipitation of calcium phosphates.

The first to be noticed is that the ability of selective uptake reduces the differences in the relative cation composition of the thirteen solutions to much smaller differ-

ences inside the plants, and that this ability varies among species. Differences in size, place, shape and inclination of the species' hexagons demonstrate differences in degree of selectivity, in preference for a specific cation and in interactions between the three cations during the uptake processes.

All species considerably reduce the variation in the ratios in which potassium is involved. From solutions with low K proportions they take up relatively much K and from solutions with high K proportions they take up relatively little K. The relatively extended form of the hexagons of *Anthyllis* and *Plantago*, meaning much variation along the Ca/Mg axis, indicates that these two species discriminate less between Ca and Mg than other species. The influence of variation in the proportion of one cation on the uptake ratio of the other two can be seen from the inclination of the species hexagons with respect to the relevant axis of the diagram. Ca, for example, has a considerable effect on the K/Mg uptake ratio of *Plantago* and *Anthyllis*, because Ca interferes more with Mg uptake than with K uptake by these species (more variation along the Ca/Mg axis than along the K/Ca axis).

Evidently, the triaxial ratio diagram has a great potential for studying interactions in nutrient uptake. This however will not be further exploited here. Our main concern is the differences between the cation uptake ratios of the species.

There is a general agreement with the species differences inferred in the field (Section 7.3). *Chrysanthemum* shows the highest preference for K, which justifies its denomination as a K-type of plant. It can however replace K by Ca when it is in short supply as is demonstrated by the low K/Ca ratios on some of the plots in the fertilizer experiment. A high preference for K is also shown by *Cerastium* and to a less extent by *Rumex*, but these species do not replace it by Ca to the extent that *Chrysanthemum* does. In fact, they seem to need only small amounts of Ca, firstly because it is taken up reluctantly and secondly because it is inactivated as oxalate (Lötsch & Kinzel, 1971). As expected *Sanguisorba* has the highest preference for Mg and the lowest for K. *Anthyllis* and *Plantago* justify their classification as calcitrophic plants only in so far as their hexagons, are the closest to the Ca angle of the diagram. The term 'calcitrophic' may however need adjustment when other species of this type should also prove to be better characterized by a lack of selectivity between Ca and Mg.

Comparing the hexagon of *Plantago* with the results of De Wit et al. (1963), shown in Figure 35, a discrepancy is seen. The uptake of K, Ca and Mg through a 'four-ion system' with approximal equal preference for the cations, as was inferred by De Wit et al. (1963), can impossibly yield the pattern we observed. Instead a species' hexagon with approximately the same size and position as the substrate hexagon would have been the result. This discrepancy is still unexplained. Perhaps the fact that the plants of De Wit et al. contained considerable amounts of the cations already at the start of the experiment may have influenced the pattern. Anyhow, uptake through a 'four-ion system' alone is a too simple representation of the cation uptake by *Plantago*.

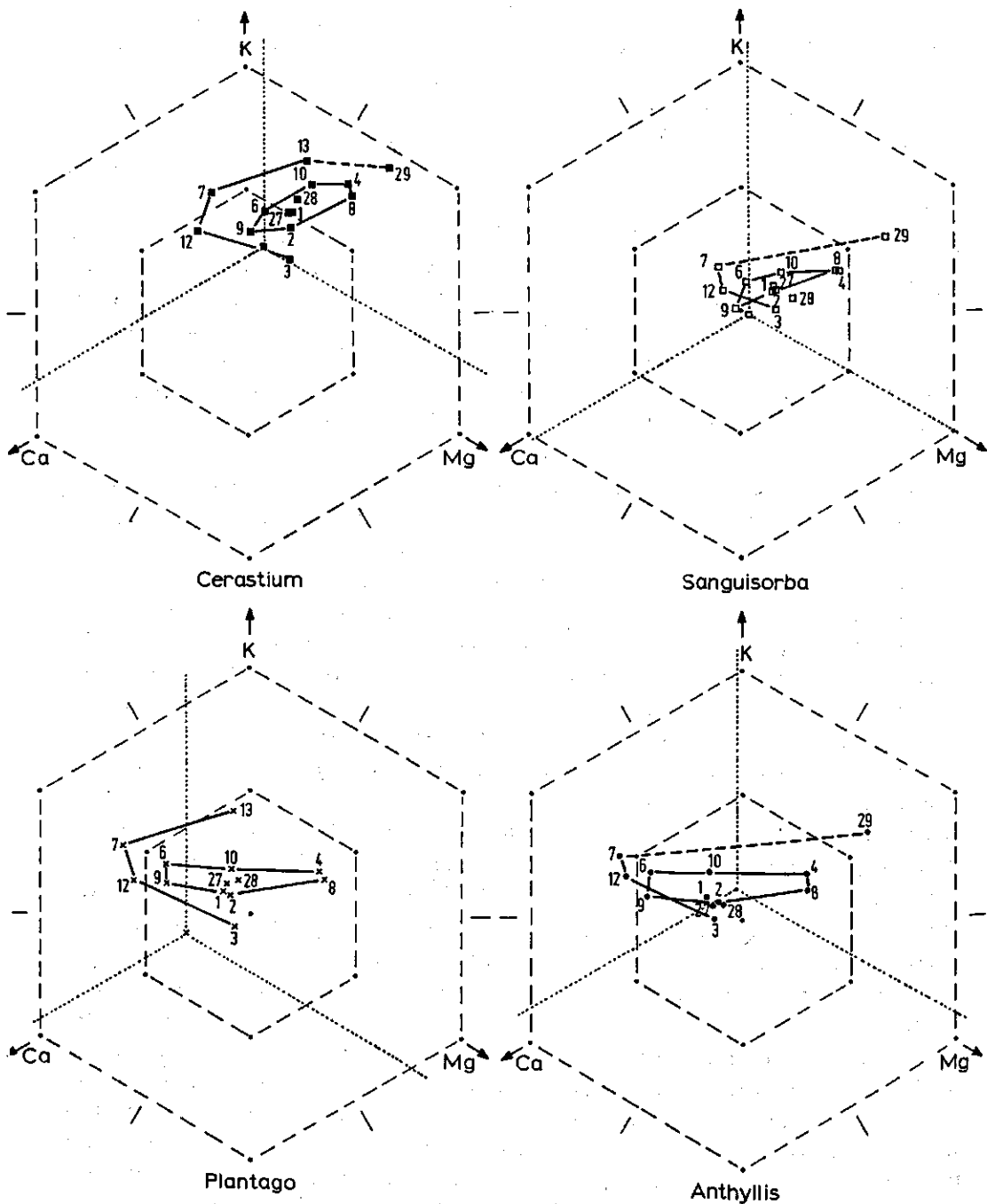


Fig. 47. The relative cation composition of the six species of Experiment III, plotted in triaxial ratio diagrams. The numbers refer to the nutrient solution on which the plants were grown. The composition of the nutrient solutions is indicated by the angular points of the two hexagons (for numbers see Fig. 46b). The nutrient requirements of the species, listed in Table 13, are used to divide the diagrams into segments, in each of which one of the cations is limiting. Further explanation in text.

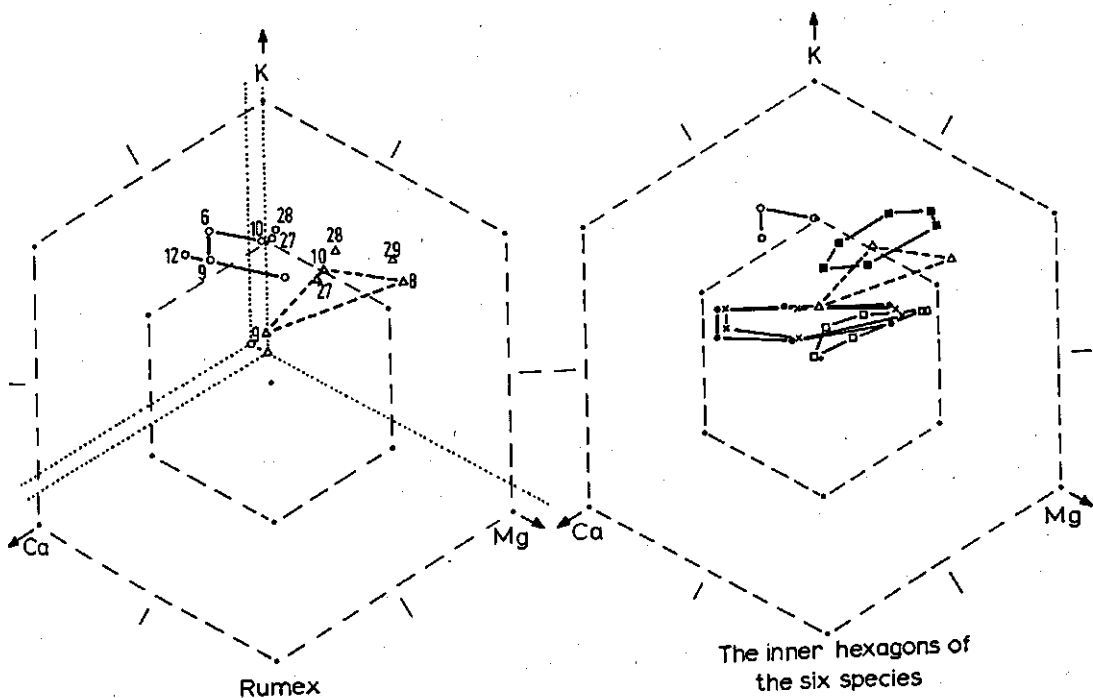


Fig. 47. (continued).

7.4.3.4 Uptake ratios for substitution in the equilibrium conditions

To evaluate the equilibrium possibilities of a species combination according to the equilibrium condition (Eqn 5.17) of our model of multiple resource competition, two nutrients have to be selected as limiting resources. In testing predicted equilibrium possibilities experimentally, care has to be taken that only these two nutrients act as limiting factors; other nutrients have to be supplied liberally. This must be taken into account in determining the species parameters on the score of which the equilibrium possibilities are evaluated, since we have seen that the substrate concentration of a third nutrient may influence the uptake ratio of other cations. Therefore we should compare uptake ratios of two cations in the presence of an excess of the third cation, say a concentration ten times as high as the first two when these are present in equal amounts. The uptake ratios of the species on the solutions meeting this condition are listed in Table 12.

The greatest difference in uptake ratios is found between the K/Mg ratios of *Chrysanthemum* and *Sanguisorba*, resulting in a double quotient

$$(U_c^K/U_c^{Mg})/(U_s^K/U_s^{Mg}) = 12.1$$

The greatest differences in the K/Ca and Ca/Mg uptake ratios are found between *Anthyllis* and *Cerastium* resulting in double quotients of 7.7 and 8.7, respectively. This, however, does not imply that these species combinations are the most suitable for our purpose,

Table 12. Cation uptake ratios of the six species in Experiment III at unity substrate ratio and a tenfold excess of the other cations (calculated on equivalent basis).

Cation ratio Solution number	K/Ca 8	K/Mg 9	Ca/Mg 10
<i>Cerastium</i>	27	4.3	0.24
<i>Chrysanthemum</i>	10 ¹	13.3	1.1
<i>Rumex</i>	17.7	2.4	0.34
<i>Plantago</i>	4.3	4.5	1.5
<i>Anthyllis</i>	3.5	4.4	2.1
<i>Sanguisorba</i>	5.6	1.1	0.42

¹ Estimated

since the relative nutrient requirements are also involved in the equilibrium conditions. The present experiment gives no information about relative requirements, only about relative uptake abilities.

7.4.3.5 Nutrient requirements in a triaxial ratio diagram

Relative nutrient requirements can well be plotted in a triaxial diagram. Under the simplifying assumption that the nutrients are perfectly complementary and no other limiting factors are involved, the diagram may be divided in three segments in each of which one cation is limiting. The segment in which, for example, Ca is limiting, is situated opposite to the arrows indicating increasing Ca concentrations. This segment is delimited by two lines, starting at the point that represents the optimum cation composition, and running perpendicular to the Ca/Mg axis or the K/Ca axis, respectively, to the direction in which K or Mg increase. A third line perpendicular to the K/Mg axis forms the border between the two other segments.

The species hexagons are divided in parts by these lines. The nutrient solutions in which a particular cation will be limiting for a particular species are found by looking which substrate compositions belong to the cation composition situated in that part of the species hexagon that indicates limitation by the cation in question.

Running ahead of the presentation of Experiments IV and V, we already followed this approach in Figure 47, using for the minimum concentrations the lowest concentrations measured in whole plants in the Experiments I to IV (Table 13). Since the Ca minimum

Table 13. Lowest concentrations of K, Ca and Mg (meq kg⁻¹ DM) in six grassland species (whole plants) found in Experiments I to V, and their ratios.

	K	Exp.	Ca	Exp.	Mg	Exp.	K/Ca	K/Mg	Ca/Mg
<i>Cerastium</i>	104	VI	25	IV	36	IV	4.16	2.89	0.69
<i>Chrysanthemum</i>	72	V	45	IV	31	V	1.60	2.32	1.45
<i>Rumex</i>	80	V	50	IV	47	V	1.60	1.70	1.06
<i>Plantago</i>	51	V	150	I	36	V	0.34	1.42	4.17
<i>Anthyllis</i>	104	IV	63	III	55	IV	1.65	1.89	1.15
<i>Sanguisorba</i>	53	IV	52	III	59	V	1.02	0.90	0.88

concentrations differ considerably between experiments, when determined in exhaustion experiments, the segmentation of the diagrams has little practical value, rather serving to illustrate the principle.

7.4.4 Analogy of competition between plants and competition between cations

Even with a constant proportion of the third cation the differences in the uptake ratios between species are not the same on all substrate ratios. To enable a more detailed insight into this matter I plotted the K/Mg uptake ratio of the species against the K/Mg substrate ratio in Figure 48. Solutions with a constant proportion of Ca but a varying K/Mg ratio are joined. These are situated in Figure 46b on lines parallel to the K/Mg axis, viz.: the Solutions 3, 9 and 7; Solutions 2 and 6; Solutions 8 and 10 and Solutions 11, 4 and 13. The Solutions 12, 1 and 5 remain separate. In doing so one obtains ratio lines comparable to those used in representing the outcome of competition between two plant species (Fig. 4, p.), now used to represent the outcome of competition between cation species in the process of being taken up by a plant.

De Wit et al. (1963) have shown that competition processes between cations during the uptake by plants may be described by the Equations 4.3. The elaboration of the De Wit-theory presented in this paper, permits to exploit this possibility to a greater extent and, as the experiments provide suitable data to demonstrate this, I will shortly consider this side-issue.

De Wit et al. (1963) did not use the ratio diagram to represent the results of their experiments. Looking at the ratio diagrams (Fig. 48) it is seen from the relatively flat ratio lines that the two competing cations, K and Mg, are 'niche differentiated' to a large extent. Similar ratio diagrams have been made of the K/Ca and Ca/Mg ratios. The three ratio lines of *Cerastium* are shown together in Figure 49. The slope of the Ca/Mg ratio line is the steepest (though still less than 45°), indicating that Ca and Mg are much alike in respect of their uptake. All ratio lines intersect the diagonal (dashed line), suggesting some sort of 'equilibrium ratio' at which the species take up the cations in the ratio at which they are supplied. This ratio should however not be interpreted as an 'ideal substrate ratio' as it is not necessarily coincident with the ratio in which the cations are required for optimal functioning of the plant.

The obvious explanation of the observed 'niche differentiation' is that the cations are competing for different uptake mechanisms with a reasonable though not perfect selectivity. In Section 4.9 some more complicated ways of competition were analysed. I suggest that the model of competition for substitutable resources (Section 4.9.3) also provides a basic description of the competitive cation uptake processes. Equations 4.11' and 4.12 can be rewritten as

$$U^1 = x_U^1 + y_U^1 \text{ and } U^2 = x_U^2 + y_U^2 \quad (4.12')$$

$$x_U^1 = x_k^{1,2} c^1 (x_k^{1,2} c^1 + c^2)^{-1} x_M^1 \quad (4.11')$$

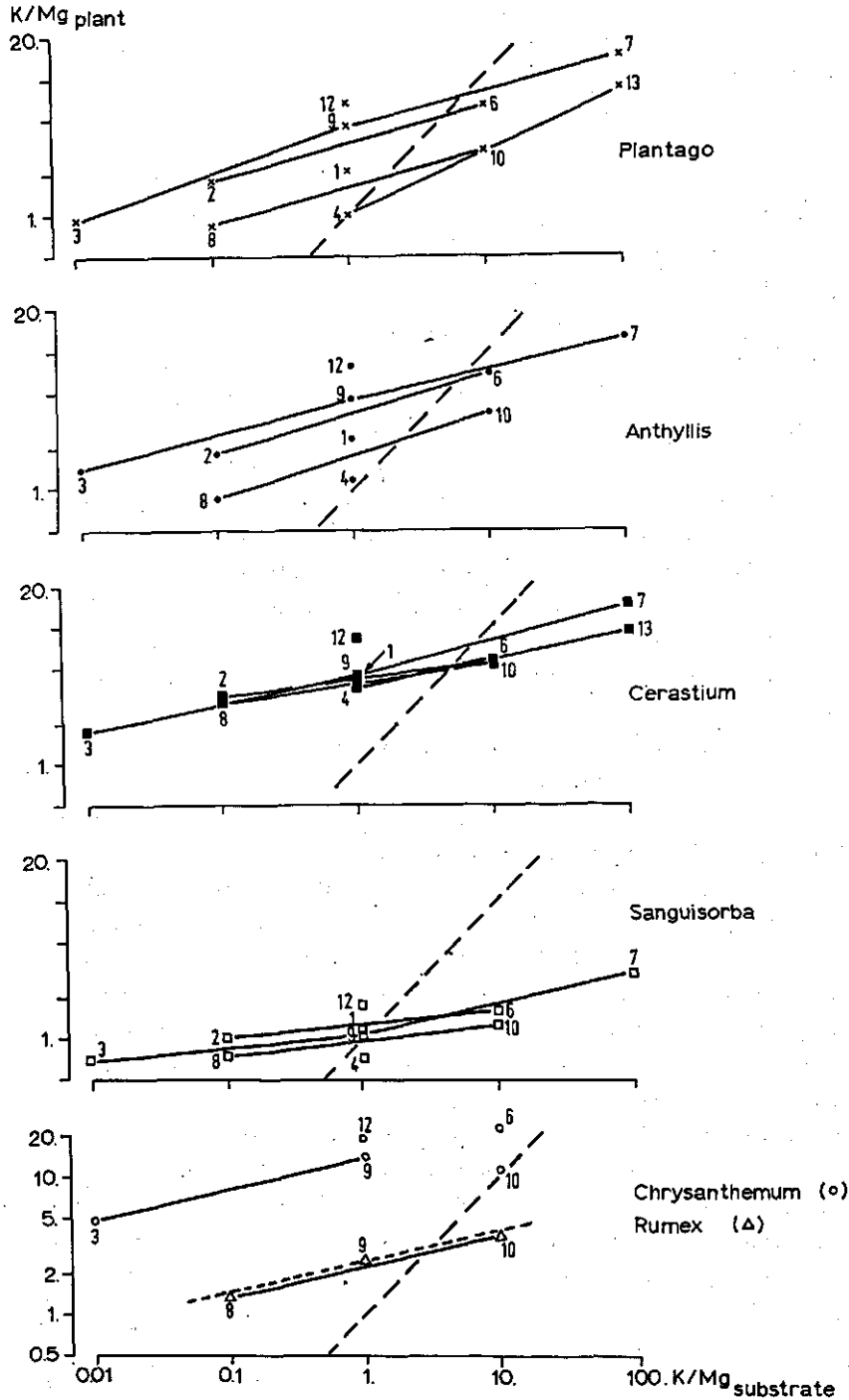


Fig. 48. K/Mg uptake ratios of the species in Experiment III, in relation to the K/Mg ratio in the nutrient solution, at different relative proportions of Ca. The points of solutions that are situated on lines parallel to the K/Mg axis in Figure 46 are joined. The diagonal of the ratio diagram is indicated with an interrupted line.

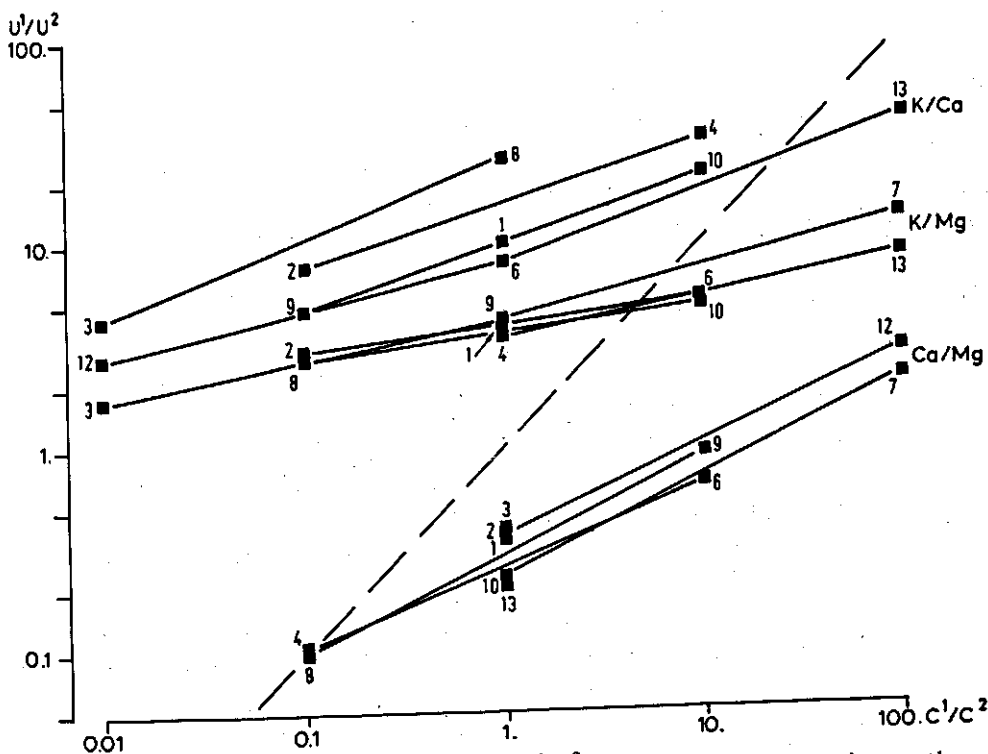


Fig. 49. K/Ca, K/Mg and Ca/Mg uptake ratio (U^1/U^2) of *Cerastium* in relation to the substrate ratios (C^1/C^2).

$$x_U^2 = c^2(x_k^{1,2}c^1 + c^2)^{-1} x_M^2 \quad (4.11'')$$

$$y_U^1 = y_k^{1,2} c^1 (y_k^{1,2} c^1 + c^2)^{-1} y_M^1 \quad (4.11''')$$

$$y_U^2 = c^2 (y_k^{1,2} c^1 + c^2)^{-1} y_M^2$$

in which U^1 is the total amount of cation 1 taken up per root unit per day; x_U^1 and y_U^1 are the amounts of 1 taken up through mechanism x and y, respectively; M is an amount taken up from a 'mono-cation solution' with a concentration C; c^1 and c^2 are the relative concentrations of 1 and 2 in solution, whereby $c^1 + c^2 = C$; $x_k^{1,2}$ is the relative crowding coefficient of cation 1 with respect to cation 2 in the uptake through mechanism x, and may be interpreted as the selectivity of this uptake mechanism.

The distinction of different mechanisms of uptake is common (Yoshida, 1964; Schuffelen, 1974; Yoshida & Kohno, 1976), but the representation in a ratio diagram brings out some consequences more clearly. The slope of the ratio line is determined by the relative selectivity of the two mechanisms and the position is determined by their capacities, indicated by x_M and y_M , and also by the selectivities.

In a ratio diagram it can easily be seen how the uptake ratio of two cations is

influenced by the presence of a third cation. By increasing the Ca concentration the K/Mg uptake ratio of all six species is increased at all K/Mg substrate ratios with approximately the same factor. Likewise the K/Ca ratio line shows a parallel upward shift when the Mg concentration is increased.

The effect of the concentration of a third cation on the level of the ratio line may be caused by its unequal ability to compete for the two uptake mechanisms x and y . When cation 3 competes with cation 2 rather than with cation 1, the uptake capacity of cation 2 will be reduced more than the uptake capacity of cation 1 by increasing the concentration of cation 3. This means that with high concentrations of 3 the position of the ratio line of cation 1/cation 2 will be higher than with low concentrations of cation 3.

The unequal ability to compete for two uptake mechanisms may be inferred from the slopes of the ratio lines of cations 1 and 3 and cations 2 and 3, since a steep line indicates much competition and a flat one indifference. Thus the Ca/Mg ratio line of *Cerastium* being steeper than the K/Ca and the K/Mg ratio lines agrees with the observation that the K/Ca ratio line shifts upward with increasing Mg concentrations as does the K/Mg rate line at increasing Ca concentrations.

When indeed the above formulas provide a valid description of the competitive uptake processes, this would mean that the amounts taken up (U^1 and U^2) plotted in a replacement diagram are situated on a S-shaped curve (compare Fig. 12, p. 45). Only a few nutrient replacement experiments described in literature include enough different solutions to establish S-curves. Yet we found S-curves in experiments of Dijkshoorn et al. (1974: Fig. 3) and Van Schoor (1954; in Homès & Van Schoor, 1966: Fig. 25). Although differently explained and neglected by the authors respectively, these examples increase the analogy between plant competition and cation competition. Detailed studies of the S-curve and resolution into its components would enable us to obtain more information about the relative selectivity and capacity of the separate uptake mechanisms.

7.5 K, Ca AND Mg DEFICIENCY IN SIX GRASSLANDS SPECIES (EXPERIMENT IV)

To see whether the differences observed in cation selectivity influence the performance of the six species of Experiment III in the competition for cations, and to obtain an indication of their K, Ca and Mg requirements, we induced deficiency of the cations by growing them together in three nutrient solutions, in each of which one of the cations was in short supply.

7.5.1 *Experimental technique*

The 215 liter containers of Experiment III were used with an improved plant supporting system. Seeds were germinated in silver sand, supplied with a little nutrient solution poor in Ca. Transplantation to the containers with nutrient solution was done as soon as the first leaf of most seedlings had emerged, so that the initial nutrient amounts in the plants were negligible. The seedlings were planted in small incisions in rubber disks (cut out of a bicycle tube) placed over holes in the bottom of plastic pots.

Table 14. Initial composition of the nutrient solutions in Experiment IV. The reduced concentrations are placed between brackets. (Concentrations in meq l⁻¹)

K	0.2 (0.02 in Sol. 1)	NO ₃	0.42 (0.45 in Sol. 2)
Na	0.2	H ₂ PO ₄	0.1
Ca	0.2 (0.05 in Sol. 2)	SO ₄	0.1
Mg	0.2 (0.02 in Sol. 3)		
Fe and micro-nutrients as in Table 6			

The pots were mounted, upside down, with their bottoms just above the water level, in order to keep the root systems of the plants from intermingling. Later on cuffs of pvc-pipe were placed around the pots to keep the shoots upright. Each container carried six pots of each species with three or more plants in it, depending on the size of the seedlings.

The nutrient solution was pumped continuously from the bottom of the containers via a distribution system through the pots, to keep it homogeneous. The solutions were replicated once. The initial composition is given in Table 14. Demineralized water was used throughout the experiment. After 18 and 28 days the same amounts of nutrient were supplied again except for the deficient cations and the micronutrients. Because the K and Ca deficiency symptoms appeared already when the plants were rather small, we delayed the growth arrest for some time, by supplying to the deficient solutions, little by little, approximately half of the initial amount of K and Ca from the 28th to the 35th day.

The experiment was carried out in a climate room at 20°C, 70% air humidity and 50 W m⁻² illumination with HPL lamps during 17 hours a day. The plants were harvested in two portions after 35 and 45 days. After determination of dry weight the replicates coming from the same container were combined for chemical analysis of the whole plants.

7.5.2 Deficiency symptoms

It was argued in Section 3.5 and 5.4 that determination of factors limiting coexisting species is of great importance in understanding the species richness of grassland vegetation. Although nutrient deficiency in the field will seldom be so pronounced as in our experiment and 'hunger' will remain latent in many cases, the following description of the K, Ca and Mg deficiency symptoms might possibly aid in recognizing limiting factors in the field. The symptoms observed agreed reasonably well with the general description in the literature (Wallace, 1961; Sprague, 1964).

In all six species K deficiency occurs first in the old leaves with the development of yellow spots which become necrotic later on, followed by withering of the leaf. In *Cerastium* the necrotic areas are pale and situated on the margins of the leaves. *Chrysanthemum* shows interveinal yellowing at the tips and margins of the older leaves. Large light brown necrotic spots develop and may merge later. *Rumex* shows brown marginal scorch and curling of the leaves. *Plantago* shows interveinal chlorosis at the tip and margins. Later rows of pale brown necrotic spots with dark purplish margins develop and the leaf withers from the tip to the basis. *Anthyllis* shows brown necrotic areas at the

tips and margins of the older leaves. *Sanguisorba* shows chlorotic tips and margins of the distal leaflets on the oldest leaves, which grow brown and necrotic later on.

Ca deficiency invariably begins in the youngest leaves which become distorted and reduced near their tips, while the remainder of the plant keeps a healthy appearance. In *Cerastium* these tips are pale green and narrowed to a point. The youngest leaves of *Chrysanthemum* are drastically reduced and curled forward or backward. *Rumex* has reduced leaf tips and margins of the youngest leaves, which are curled and ragged with a chlorotic marginal band. *Plantago* produces characteristically reduced black hooked tips on its youngest leaves. The youngest leaves of *Anthyllis* are folded with a reduced hooked tip. The youngest leaf of *Sanguisorba* consists of a few leaflets only, the other leaflets and the stalk being reduced to a little, scorched, dark brown tip.

Mg deficiency is generally characterized by intervenal chlorosis of the oldest leaves, but other colours and necrosis may also occur. The oldest leaves of *Cerastium* show a pattern of yellow, pale and brown spots with the latter concentrated at the tip and margin. The mid nerve and base of the leaves remain green for a long time. *Chrysanthemum* shows intervenal chlorosis all over the oldest leaves, which may become very pronounced before necrosis develops. *Rumex* shows a pattern of pale necrotic spots in purplish discoloured areas between the veins over the whole leaf. *Plantago* shows intervenal chlorosis proceeding from the tip to the basis of the older leaves. Necrosis starts at the tips and margins. *Anthyllis* shows a pale green necrotic tip and small chlorotic spots with a pale necrotic center between the veins at the margins of the older leaves. *Sanguisorba* shows a slight intervenal chlorosis and pale green withered dents at the margin of the older leaves.

7.5.3 Results and discussion

The differences in the amounts of a cation taken up by each of the six species are difficult to interpret, because these amounts are absorbed at changing concentrations and depend on several interrelated factors such as uptake rate, growth rate and nutrient requirement. Moreover, initial size and number of the seedlings and interspecific interactions are important in this experiment. However, when we compare the average percentages of the three cations taken up by the same species from the solutions in which they are limiting (Fig. 50), we see roughly what we already found in Experiment III.

Cerastium and *Chrysanthemum* performed better in the competition for K than in the competition for Mg or Ca, which agrees with the preference for K they showed in Experiment III. *Rumex* absorbed the highest amounts of K and Mg of all species, which is due to the combination of a moderate preference for these elements and fast growth, while the species with the highest preference for K (*Chrysanthemum* and *Cerastium*) and Mg (*Sanguisorba*) were growing relatively slow. The behaviour of *Plantago* was the reverse of that of *Rumex*. It competed extremely well for Ca, using almost half of the total amount of Ca consumed. Because of its fast growth and extensive root system it performed also well in the competition for K and Mg. Like *Plantago*, *Anthyllis* performed best in competition for Ca but, since it grew slowly, it absorbed only small amounts of all three cations. *Sanguisorba* performed best in competition for Mg. Its very subordinate position in the

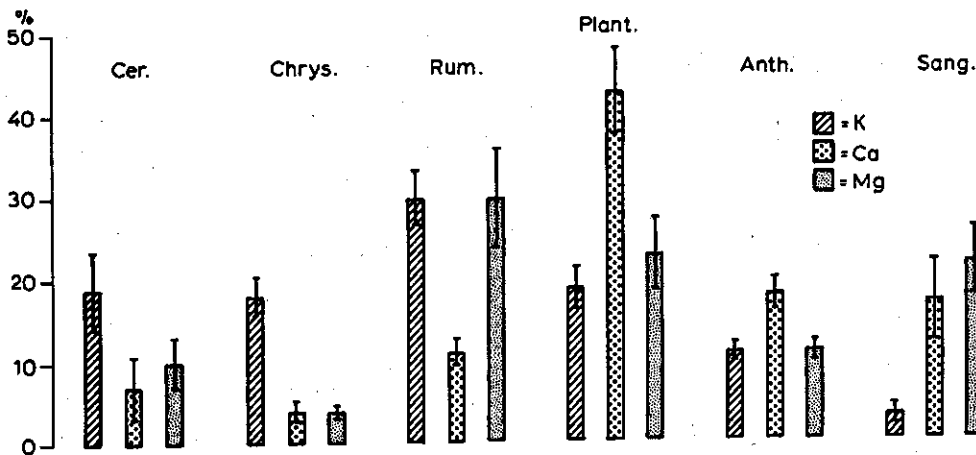


Fig. 50. Percentages of the total amounts consumed of K, Ca and Mg, absorbed by the six grassland species, when grown together on nutrient solutions in which the cation concerned was limiting (Exp. IV). Average percentages of two harvests and two replicates are shown. The vertical bars indicate the standard deviation.

competition for K is due to the combination of a low preference for K and a slow growth rate.

The internal K, Ca and Mg concentrations of the six species when grown on the solutions poor in these cations are listed in Table 15. The lowest concentrations are found in the last harvest, except for Ca in *Cerastium* and *Chrysanthemum*. The extra supply of Ca during the experiment was probably used less efficiently by these species, because their growth lagged behind the increase in uptake rate so that some biomass was produced with a relatively high Ca concentration. In four cases lower concentrations have been found in previous experiments, viz. a K concentration of 100 meq kg⁻¹ in *Chrysanthemum*, a Ca concentration of 150 meq kg⁻¹ in *Plantago*, both observed in Experiment I, and Ca concentrations of 63 and 52 meq kg⁻¹ in *Anthyllis* and *Sanguisorba*, respectively, observed in Experiment III.

The above results demonstrate clearly that differences in cation selectivity between

Table 15. Internal concentration (in meq kg⁻¹ DM) of K, Ca and Mg in six grassland species (whole plants) grown on nutrient solutions in which these cations were in short supply. The lowest concentrations of a species are in italics (Experiment IV).

Cation	K				Ca				Mg			
	1		2		1		2		1		2	
	1	4	1	4	2	5	2	5	3	6	3	6
Container No.	1	4	1	4	2	5	2	5	3	6	3	6
<i>Cerastium</i>	191	192	110	104	25	26	59	59	69	62	36	42
<i>Chrysanthemum</i>	249	245	144	161	45	84	81	80	43	45	33	32
<i>Rumex</i>	193	196	111	118	53	53	59	50	98	87	60	67
<i>Plantago</i>	109	103	64	71	223	239	179	180	81	63	57	44
<i>Anthyllis</i>	208	187	124	104	400	410	278	296	87	81	55	70
<i>Sanguisorba</i>	74	94	53	56	125	113	87	94	230	20	97	81

species are important in determining their performance in the competition for different cations. On the other hand it is evident that other features like growth rate and root morphology are important as well. Besides, the resultant competitive ability, as measured from biomass production, depends also on the concentration of the limiting cation in the plants, which is bounded by the minimum requirement of the species.

7.6 K AND Mg REQUIREMENTS OF FIVE GRASSLAND SPECIES (EXPERIMENT V)

7.6.1 Introduction

It is evident from the previous experiments that the minimum concentration of calcium in whole plants, measured in an exhaustion experiment, is not a reliable parameter for the Ca requirement of a species. This is due to important differences in the minimum Ca concentrations measured in different experiments, depending on the pretreatment, the amount of biomass produced and the trend in the Ca substrate concentration during the experiment. Moreover, notwithstanding possible differences between their functional requirements, plants will be limited by Ca almost concurrently in an exhaustion experiment, since potential reserves of Ca in the plants cannot be exploited, because they are immobile.

Obviously, our model of multiple resource competition is not applicable when Ca is involved as a limiting nutrient. Therefore it was preferred to try K and Mg as limiting factors in an attempt to evaluate the equilibrium conditions of the model. Since the previous experiments only gave defective information about the species' requirements of K and Mg an experiment was carried out to determine the minimum K and Mg concentrations in four of the species studied in Experiments III and IV, i.e. *Plantago*, *Chrysanthemum*, *Rumex* and *Sanguisorba* and in one additional species, *Anthoxanthum odoratum*. Moreover, we intended to investigate whether the underlying assumption of our model of the nutrients being perfectly complementary is justified with K and Mg as limiting nutrients. Both ends may be achieved by growing the species on a nutrient replacement series.

7.6.2 Experimental technique

Seeds of the five species were germinated in silver sand. The seedlings were transplanted to six-liter pots containing the experimental nutrient solutions as soon as the first leaf emerged, so that their initial nutrient contents were negligible compared to the amounts supplied in the solutions. Ten seedlings per pot were planted in small incisions in rubber disks placed over holes in the lid of the pot. Later on they were replanted in pieces of thick walled rubber gas tube that were cut open lengthwise, and pressed into the holes in the lid of the pot.

The composition of the seven nutrient solutions is given in Table 16. They were prepared and replenished with demineralized water and aerated continuously. The plants were allowed to exhaust the solutions as far as possible. Harvesting took place when deficiency symptoms were observed on all the plants and no further growth was observed.

Table 16. Composition of the seven nutrient solutions in Experiment V (in meq pot⁻¹).

K	x						
		NO ₃	19.2				
Mg	1.2-x	H ₂ PO ₄	6				
Ca	18	SO ₄	6				
Na	12						
Fe and micro-nutrients as in Table 6							
Solution no.:							
	I	II	III	IV	V	VI	VII
	x = 0.2	0.4	0.6	0.7	0.8	0.9	1.1

This was 36 days after transplantation for *Plantago* and *Sanguisorba* and after 44 days for the other species. After determination of dry weight the roots and shoots were analysed separately for K, Na, Ca and Mg. The experiment was replicated three times. It was carried out in a climate room at 20°C, 60% air humidity and 50 W m⁻² illumination by HPL lamps during 17 hours a day. The 105 pots were placed on eleven mobile frames that were moved daily.

7.6.3 Results and discussion

The yields of the species are presented in Figure 51. The curves are hand fitted through both origins. Notwithstanding the considerable scattering of the points, it is evident that there are remarkable differences between the species, concerning the size as well as the place of the optimum yield. The K and Mg concentrations in the whole plants are presented in Figure 52 in the form of minimum concentration curves (see Fig. 11, p. 43).

The place of the yield optima of the species agrees reasonably well with that calculated from the minimum concentrations measured on the extreme solutions. However, the curves are far from angular so that the optimum yields are much lower than predicted, viz. approximately 50% of the maximum yield calculated from the minimum concentrations. This means that either the yields in the middle of the nutrient replacement series had not yet attained their maximum at the time of harvest, or that factors other than K and Mg were limiting on these solutions, or that K and Mg were functionally substitutable to some extent.

Nutrients may be partly substitutable in different ways. They may fulfill two (or more) nonspecific functions in the plant with different efficiencies or at least one nonspecific function apart from their specific functions. It may also be that they are interacting in realizing their function. The consequences of these possibilities for the yield curves and the minimum concentration curves are shown in Figure 11c, d and e. Since K and Mg are both known to be essential to the functioning of higher plants, the first possibility is ruled out. Of the remaining possibilities the first one is the most attractive, because some of the yield curves seem to be composed of three more or less linear parts, similar to the graph in the last column of Figure 11d. The middle part is inclined towards the left side, which would mean that K is more efficient in realizing the common function. Numerous yield curves composed of three parts have been published by Homès (1961). (Nevertheless, this author claims that his formula, which involves the product

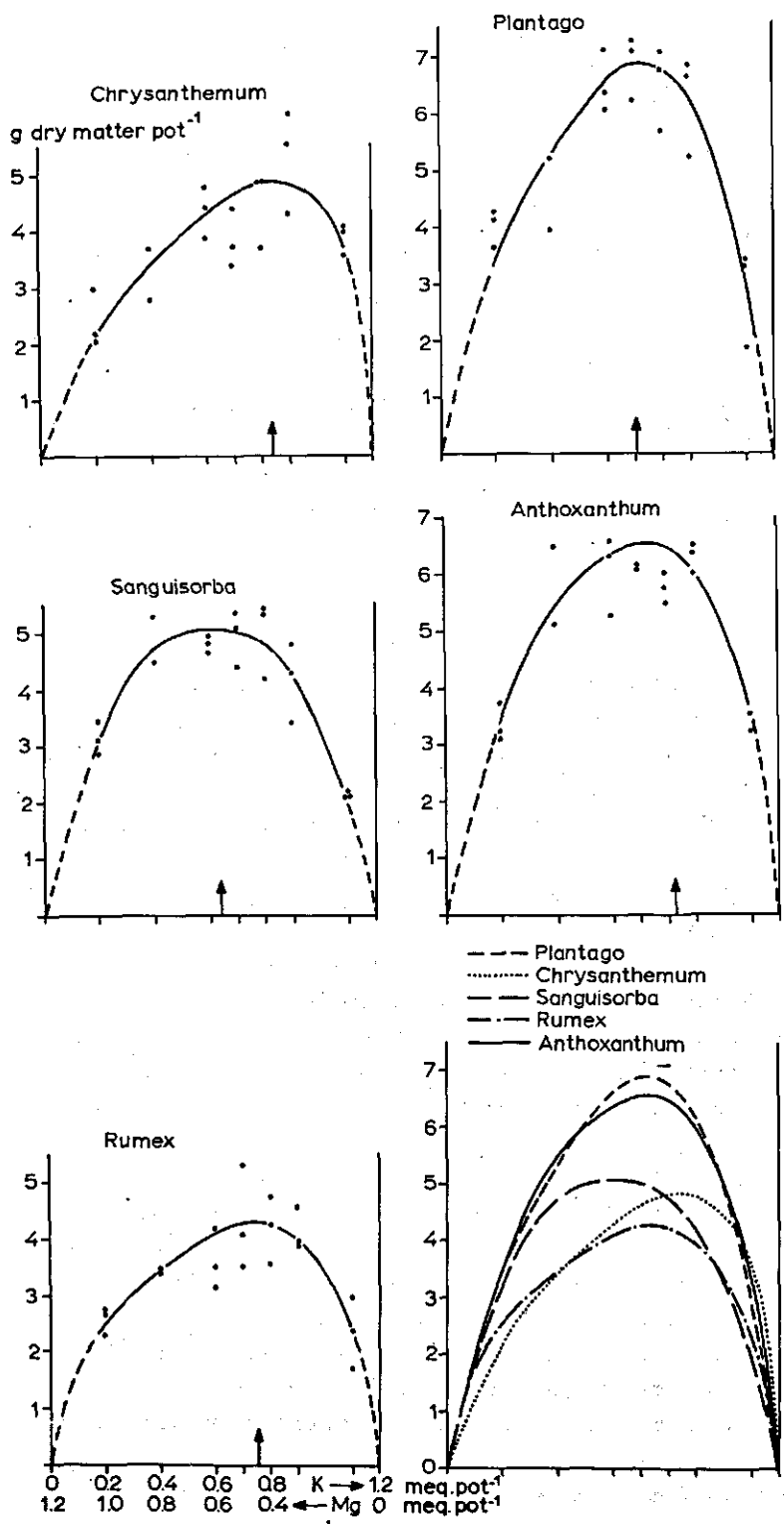


Fig. 51. Yields (g DM pot⁻¹) of five grassland species grown on a K-Mg replacement series (Exp. V). The arrow indicates the place of the yield optimum calculated from the minimum concentrations measured at the extremes of the replacement series.

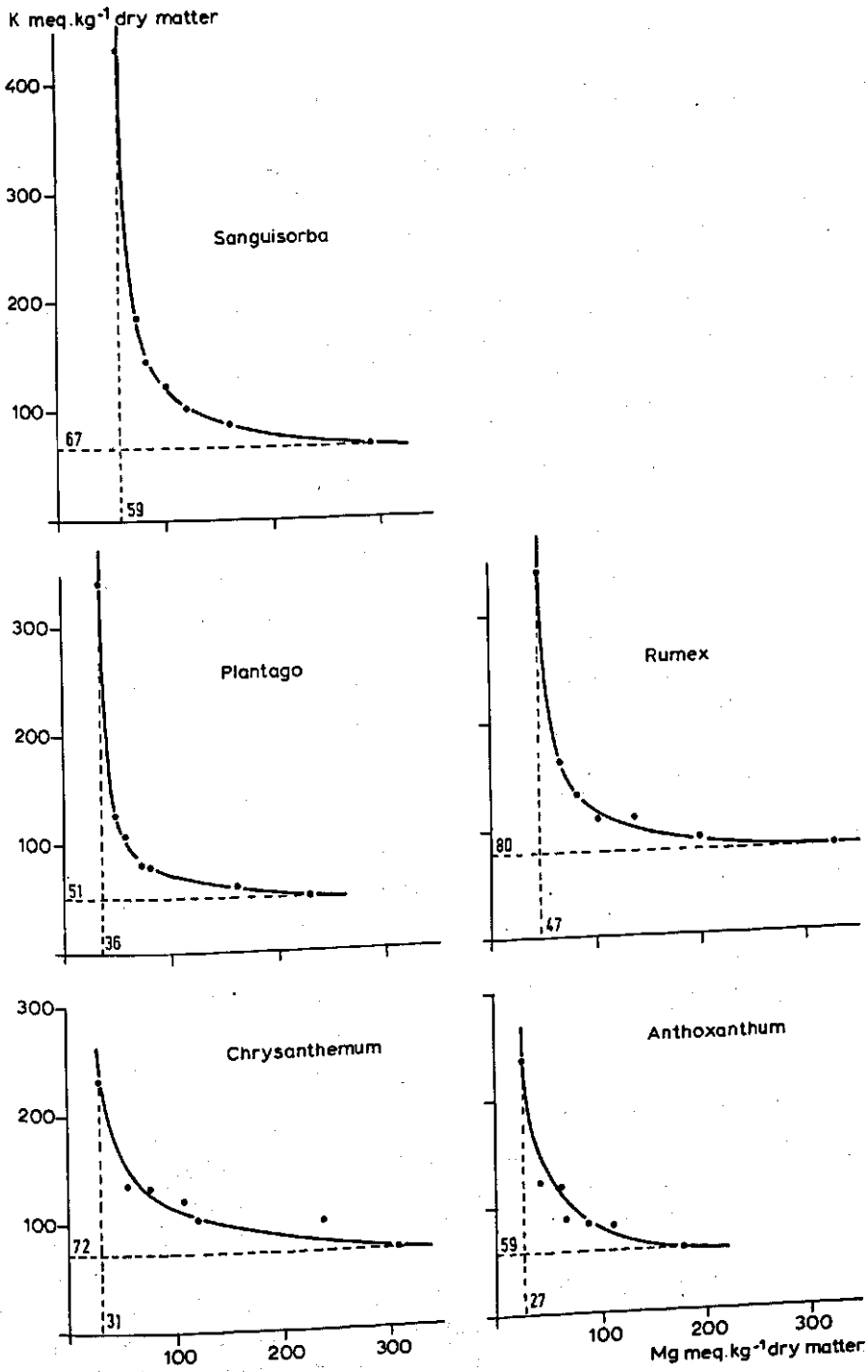


Fig. 52. Internal K and Mg concentrations (meq kg⁻¹ DM) of the species of Experiment V. The minimum concentrations are indicated by auxiliary lines.

of the relative proportions of both nutrients, is most suitable).

Whether the nutrients K and Mg are partly substitutable or the maximum yields were not or not yet attained, can not be decided from our experiment. An experimental design in which the expected yields are equal, assuming perfectly complementary nutrients, may resolve this question. Such a design can only be made when the place of the optimum yield is known. It consists of two series of nutrient solutions in which one or the other nutrient increases, starting from the optimum ratio. Such a 'double addition series' has been applied in Experiment VI, which is discussed in Section 7.7.

For whatever reason, the optimum yields are only half of what was expected from the minimum concentration, assuming complementary nutrients, it still seems possible that the equilibrium conditions of our model are valid, because the optimum nutrient ratio agrees with the ratio of the minimum concentrations.

7.7 EVALUATION OF THE EQUILIBRIUM POSSIBILITIES OF THE SPECIES INVESTIGATED

To find a species combination suitable to evaluate the model of multiple resource competition and its essential conclusion, that differential nutrient limitation permits stable equilibria between plant species in homogeneous environments, we examined whether the possible combinations of the species investigated met the equilibrium condition of the model with K and Mg as limiting nutrients, using the data available from Experiments I to V. Although the third term of the equilibrium condition:

$$1 < (k_{ab}^1/k_{ab}^2) < (1/k_{ab}^2)(m_a^1/m_b^1) < (m_a^1/m_a^2)/(m_b^1/m_b^2) \quad (5.17)$$

cannot be determined, because the relative crowding coefficients are not individually known, we can check already the crucial part by substituting measured values in the double quotients

$$(U_a^1/U_a^2)/(U_b^1/U_b^2) = k_{ab}^1/k_{ab}^2$$

and $(m_a^1/m_a^2)/(m_b^1/m_b^2)$.

Because the uptake ratios of the species (U^1/U^2) as well as their quotients depend on the substrate ratios (see Fig. 48), it is not possible to calculate k_{ab}^1/k_{ab}^2 unconditionally. Table 17 gives the uptake ratios of the four species used in Experiment III as well as Experiment V, measured on the Solutions 3, 9 and 7 in Experiment III. The values lacking are completed by extrapolation. (For *Rumex* a ratio line was drawn through point 9, parallel to the ratio line through points 10 and 8). The relative K and Mg requirements, expressed as the ratio of the minimum concentrations, have been calculated using the lowest concentration in whole plants found in the Experiments I to V. The double quotients of relative requirements and uptake ratios for all the combinations of the four species are also given.

By comparison of these double quotients it can be concluded that none of the species combinations meets the equilibrium conditions. Only for the combinations of *Plantago* and

Table 17. The quotient U^K/U^{Mg} at different K/Mg substrate ratios; the quotient m^K/m^{Mg} (see Table 13) of four grassland species and the double quotients for all combinations of the four species. Extrapolated figures in brackets.

Quotient	U^K/U^{Mg}			m^K/m^{Mg}
	3	9	7	
Solution				
<i>Plantago</i>	0.94	4.46	14.7	1.42
<i>Chrysanthemum</i>	4.67	13.3	(40.)	2.32
<i>Rumex</i>	(0.85)	2.39	(7.)	1.70
<i>Sanguisorba</i>	0.70	1.09	3.00	0.90
Double quotient				
<i>Plant.</i> / <i>Chrys.</i>	0.20	0.34	0.37	0.61
<i>Plant.</i> / <i>Rum.</i>	1.11	1.87	2.10	0.84
<i>Plant.</i> / <i>Sang.</i>	1.34	4.09	4.90	1.58
<i>Chrys.</i> / <i>Rum.</i>	5.49	5.56	5.71	1.36
<i>Chrys.</i> / <i>Sang.</i>	6.67	12.20	12.33	2.58
<i>Rum.</i> / <i>Sang.</i>	1.21	2.19	2.33	1.89

Rumex with *Sanguisorba* do the double quotients of uptake ratios lie between unity and the double quotients of minimum concentrations. However, this only holds for a limited range of substrate conditions with extremely low K/Mg ratios.

From the available data it has to be concluded that it is not possible to evaluate the equilibrium conditions of the model with the species and nutrients investigated. In general the variation in the relative requirement of species appears to be smaller than the variation in the relative uptake ratios.

7.8 COMPETITION FOR K AND Mg BETWEEN PLANTAGO AND SANGUISORBA (EXPERIMENT VI)

Although it had to be concluded in the previous section that an experimental verification of the equilibrium conditions of our model was not possible with the species investigated, we carried out a competition experiment to see whether the model gives a reasonable description of the simultaneous competition for K and Mg. We chose for this experiment the species *Plantago* and *Sanguisorba*.

7.8.1 Experimental technique

Seeds of *Plantago* and *Sanguisorba* were germinated and transplanted as described for Experiment V. The total plant density was 8 plants per six-liter pot. The experiment included five replacement series on different nutrient solutions. A replacement series consisted of 15 pots distributed over 9 plant frequencies as shown below:

Plant ratio (Z_p/Z_s):	0/8	1/7	2/6	3/5	4/4	5/3	6/2	7/1	8/0
number of replicates :	1	3	2	1	1	1	2	3	1

This design was chosen to enable the determination of S-shaped replacement curves and to reduce the effect of plant heterogeneity with a minimum number of pots. The plants on

Table 18. Total amounts of nutrients supplied with the five solutions of Experiment VI (in meq pot⁻¹).

Solution number	I	II	III	IV	V
K	1.0	1.0	1.0	1.5	5.0
Mg	5.0	1.5	1.0	1.0	1.0
Ca	12.0	12.0	12.0	12.0	12.0
Na	11.6	11.5	11.4	11.5	11.6
NO ₃	20.0	17.0	17.0	17.0	20.0
H ₂ PO ₄	4.8	4.5	4.2	4.5	4.8
SO ₄	4.8	4.5	4.2	4.5	4.8

In all solutions: 10 mg Fe l⁻¹ and micro-nutrients as in Table 6.

each pot were grouped per species to reduce the effect of light competition, and to separate the roots.

The total amounts of nutrients supplied with the different solutions are mentioned in Table 18. These amounts were supplied in dosages during the experiment for three reasons: firstly, to build up deficiencies of K and Mg gradually; secondly to minimize the influence of possible starting difficulties of the species, on the distribution of the nutrients among them; thirdly, to reduce the changes in the relative composition of the nutrient solution due to differential exhaustion of the separate nutrients. Four dosages were supplied at 0, 22, 29 and 36 days after the transplantation, respectively, the first one being twice as great as the other three. On the 43rd day a fifth dosage was supplied without K and Mg.

The nutrient amounts were chosen in such a way that up to the last application the Ca dosage was ten times that of K and Mg in Solution III. The solutions form two series, connected through Solution III, in which the supply of K or Mg increases from 1.0 to 5.0 meq pot⁻¹, while the supply of Mg or K, respectively, was kept constant. The reason for this design was explained in Section 7.6.3. According to the results of the previous experiments the optimum ratio of K and Mg supply should be near Solution III for *Sanguisorba* (ratio 1.14 in Experiment V and 0.9 according to Table 13) and near Solution IV for *Plantago* (ratio 1.42).

The solutions were prepared and replenished with demineralized water. The pots were aerated continuously and placed on mobile frames that were moved daily. The experiment was carried out in a climate room at 18°C, 70% air humidity and 50 W m⁻² illumination with HPL-lamps during 17 hours a day. The plants were harvested on the 35th day when severe deficiency symptoms were found in all pots and little further growth was observed for some days. Dry weights and concentrations of K, Ca, Mg and Na were determined of roots and shoots, separately. Mostly replicates were combined. Some were analyzed separately to see whether deviating yields were caused by errors in the nutrient solutions.

7.8.2 Results and discussion

7.8.2.1 Growth

Before dealing with the competitive processes the influence of the five different nutrient solutions on the species in monocultures will be discussed and compared with the results of Experiment V. The yields of the monocultures are presented in Figure 53 in the form of two concentration series plotted in opposite direction and connected through Solution III. Although the differences are small and probably not significant, *Plantago* produces more than *Sanguisorba* when K is limiting and vice versa when Mg is limiting. This is contrary to what was expected from the results of Experiment V, where the K/Mg requirement ratio of *Plantago* was higher (1.42) than that of *Sanguisorba* (1.14; 0.9 in Table 13). In Experiment VI this is reversed, the ratio of the minimum requirements being 1.14 for *Plantago* and 1.22 for *Sanguisorba* (see Fig. 51). These results show that the minimum concentration is not a reliable parameter of the K and Mg requirement of a species either.

The yields of both species have a minimum on Solution III in which K and Mg were limiting almost to the same extent. When K or Mg was added to this solution, while the supply of the other nutrients remained the same, the yields of both species increased with a factor 1.6 or 1.2 respectively. Consequently, the extra supply of the one nutrient must have relieved the limitation by the other nutrient. Therefore, it has to be concluded that K and Mg are substitutable to some extent. If they had been perfectly complementary, the yields would have been equal on all the solutions. Even when Solution III did not have the optimal K/Mg ratio, this conclusion would stand, because in this case there would have been a gradual transition between two yield levels. The fact that the minimum yield was not found at one of the extremes but in the middle of the series I to V proves that K and Mg are functionally substitutable. In addition to their specific functions in enzyme activation and chlorophyll, these elements must have functions in common, probably

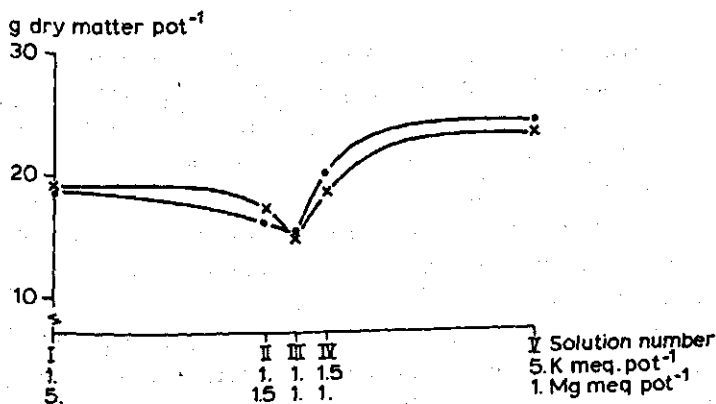


Fig. 53. The effect of increasing K or Mg supply on the yield (g dry matter pot⁻¹) of *Plantago* (x) and *Sanguisorba* (•) growing in monoculture, starting from a situation in which K and Mg are limiting to the same extent (Solution III). (Exp. VI).

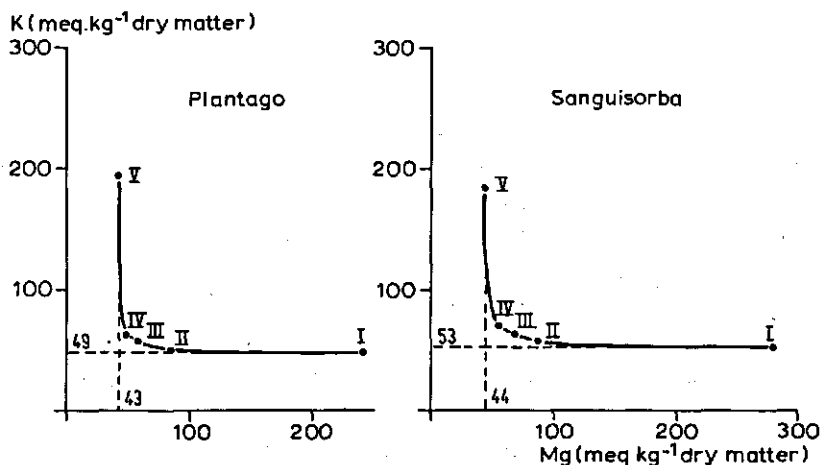


Fig. 54. The internal K and Mg concentrations of *Plantago* and *Sanguisorba* growing in monoculture on the nutrient solutions of Experiment VI. The minimum concentrations are indicated by auxiliary lines.

osmotic and transport functions. That there is a limit to this substitution, is demonstrated by the yields levelling off to the extremes. In drawing the curves it was assumed that they have horizontal asymptotes.

The alternative explanation, suggested in Section 7.6.3, for the rounded yield curves in the K/Mg replacement series of Experiment V, was that the yields in the middle of the replacement series had not yet attained their maximum at the time of harvest. Comparing the minimum concentration curves of Experiment V and VI (Figs. 52 and 54), it becomes evident that this suggestion is also confirmed. The curves could have been much more angular than they were in Experiment V. When the plants in this experiment had continued growth until the curves were congruent to those of Experiment VI, the yields would have been approximately a factor 1.5 higher.

7.8.2.2 Competition

The competitive effects that occurred in Experiment VI and the influence of the nutrient solutions on it will be discussed next. The dry weight of the whole plants are presented in the replacement diagrams of Figure 55a. All the replicates are shown to give an idea of the experimental error. The amounts of K and Mg taken up are shown in the replacement diagrams of Figure 55b and 55c. The K and Mg concentrations in the whole plants are shown in Figure 56. The replacement curves of the nutrient amounts and the yields are fitted in such a way that their quotient, which is the curve in Figure 56, fits as closely as possible to the nutrient concentrations.

The replacement diagrams of Ca and Na uptake are not shown, but the parameters are given in Table 19, together with those of the other diagrams. The replacement curves for roots and shoots are fitted in such a way that their sum fits as closely as possible to the whole plant curve. Strictly, the addition of root and shoot curves with a frequency independent relative crowding coefficient does not result in a whole plant curve with a

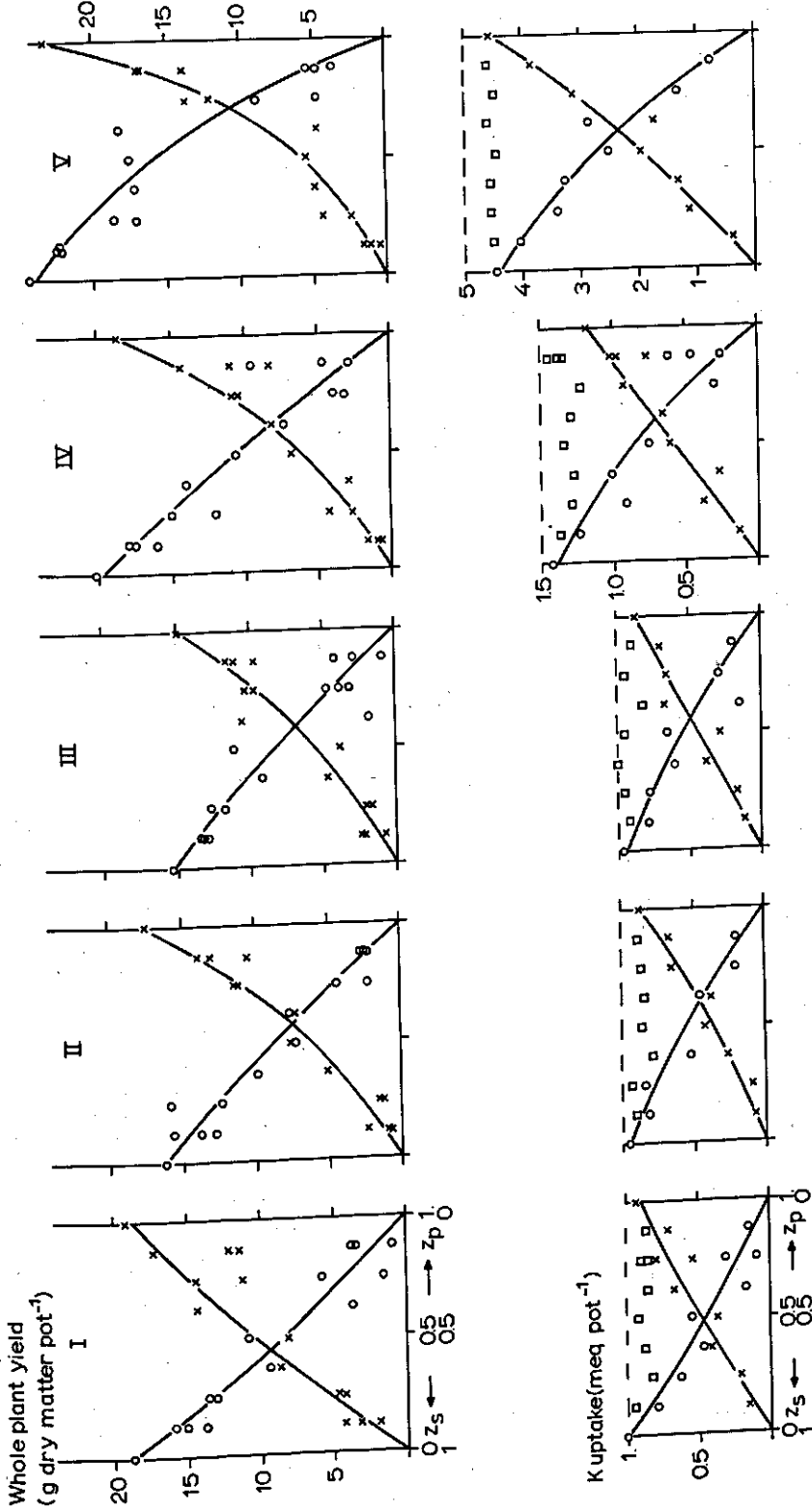


Fig. 55. Replacement diagrams of the whole plant yields (g DM pot⁻¹), the K uptake and the Mg uptake of *Plantago* (x) and *Samolus borba* (o) in competition experiments on five nutrient solutions in which K and Mg are limiting to various extents (Exp. VI). The dosages of K and Mg supplied are indicated by interrupted lines. The combined uptake of both species is indicated by (n). The parameters of the replacement curves are given in Table 19.

Mg uptake (meq pot⁻¹)

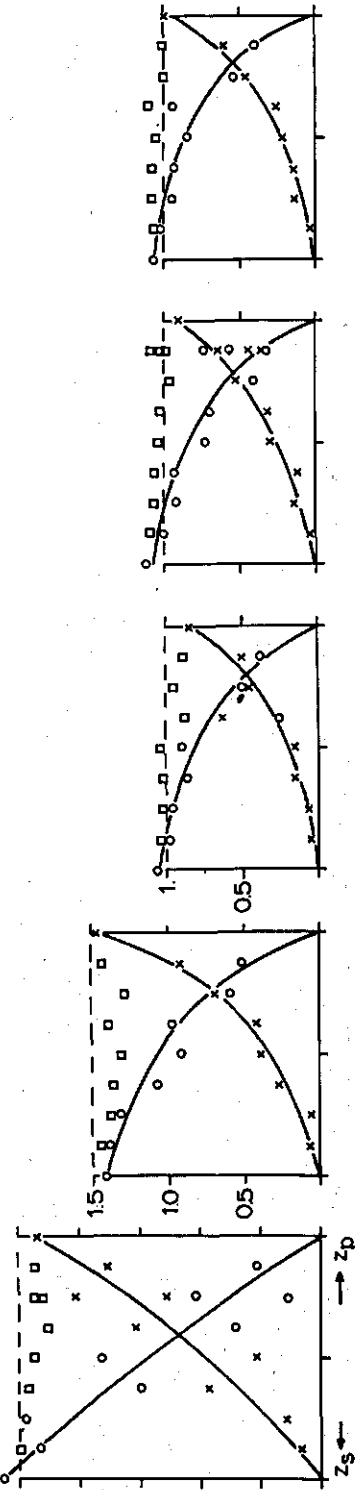


Fig. 55 (continued).

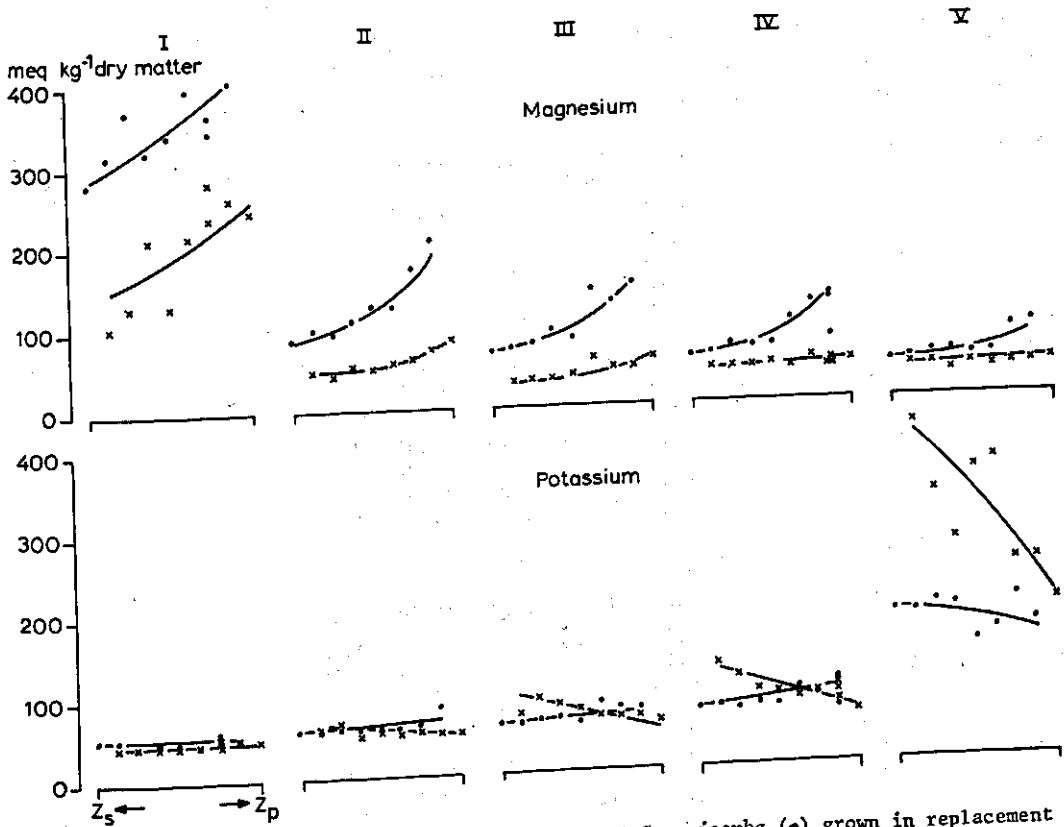


Fig. 56. K and Mg concentrations of *Plantago* (x) and *Sangvisorba* (•) grown in replacement series on five nutrient solutions (I to V) in which K and Mg were limiting to various extents. (Exp. VI). The curves are calculated from the replacement curves in Figure 55.

frequency independent relative crowding coefficient, but this difference was neglected, because it is small compared to the experimental error and the results give no reason to assume frequency dependence.

The replacement diagrams of the yields (Fig. 55a) demonstrate that the competitive relationship depends on the conditions: when K is limiting (Sol. I) *Plantago* wins, though not convincingly; when Mg is limiting (Sol. V) *Sangvisorba* wins. From the replacement diagrams of K and Mg uptake it is seen that the competitive ability of a species for a nutrient also depends on the conditions, but not in the same way as the yields do.

To allow more insight in this matter the relative crowding coefficients are plotted in Figure 57. The k_{ps} values are discussed first because they are easier to interpret. Figure 57a shows that k_{ps}^{IM} is equal to k_{ps}^K when K is limiting, and equal to k_{ps}^{Mg} when Mg is limiting. When K and Mg are limiting to the same extent k_{ps}^{IM} lies between k_{ps}^K and k_{ps}^{Mg} . These results strongly suggest that the competitive ability of *Plantago* is directly determined by its ability to compete for the limiting nutrient. The limiting nutrient may differ from place to place and, consequently, competitive dominance too, since species may differ in their relative uptake rates and use-efficiencies of the limiting nutrients.

Table 19. Parameters of the replacement curves of the yield components and the cation amounts taken up in Experiment VI.

Solution	Yield component	k_{ps}	M_p	k_{sp}	M_s	k_{ps}	k_{sp}
I	shoot	1.33	13.5	0.80	11.00	1.06	
	root	0.85	5.1	0.80	7.70	0.68	
	whole plant	1.25	18.6	0.80	18.70	1.00	
	K	1.22	0.9	0.80	1.00	0.98	
	Na	1.50	12.0	0.60	8.40	0.90	
	Ca	1.90	11.0	0.80	7.9	1.52	
	Mg	0.69	4.7	1.20	5.27	0.83	
II	shoot	0.60	13.20	1.25	9.95	0.75	
	root	0.50	4.20	1.00	6.40	0.50	
	whole plant	0.55	17.40	1.17	16.35	0.64	
	K	0.75	0.86	1.40	0.95	1.05	
	Na	0.88	11.14	0.75	7.94	0.66	
	Ca	0.81	11.10	1.05	12.37	0.86	
	Mg	0.30	1.44	3.18	1.42	0.97	
III	shoot	0.80	11.0	1.30	9.80	1.04	
	root	0.26	3.7	1.10	5.40	0.29	
	whole plant	0.60	14.7	1.20	15.20	0.72	
	K	1.04	0.85	1.40	0.94	1.46	
	Na	0.75	11.00	0.90	8.00	0.68	
	Ca	0.90	11.50	1.60	9.16	1.44	
	Mg	0.30	0.85	3.40	1.04	1.02	
IV	shoot	0.70	13.40	1.32	12.00	0.92	
	root	0.20	5.20	1.03	7.80	0.21	
	whole plant	0.50	18.6	1.17	19.80	0.59	
	K	1.00	1.18	1.60	1.40	1.60	
	Na	0.85	11.57	0.81	9.24	0.69	
	Ca	0.75	10.2	1.50	11.23	1.13	
	Mg	0.40	0.92	3.60	1.07	1.44	
V	shoot	0.48	17.30	2.00	16.50	0.96	
	root	0.13	5.90	2.00	7.50	0.26	
	whole plant	0.35	23.20	2.00	24.00	0.70	
	K	0.77	4.49	1.59	4.42	1.23	
	Na	0.42	13.20	1.28	9.14	0.54	
	Ca	0.74	10.01	1.83	9.73	1.35	
	Mg	0.33	0.94	4.26	1.06	1.39	

On the other hand, there also is an influence of growth on the competitive ability for a nutrient when it is not limiting, since k_{ps}^K and k_{ps}^{Mg} are not constant but seem to be carried along by k_{ps}^{DM} on Solutions V and I, respectively. When a species is strong in the competition for the limiting nutrient, it is also strong in the competition for the other nutrients. Yet k_{ps}^K and k_{ps}^{Mg} are not equal. A difference of a factor 1.8 to 3.5 is maintained between them.

The difference between the relative crowding coefficients of yield and K uptake causes the K concentration in the plants to be frequency dependent (see Fig. 56). This dependency decreases when the K becomes limiting and starts determining the yield. The concentrations are frequency independent when $k_{ps}^{DM} = k_{ps}^K$. On Solution II, III and IV both

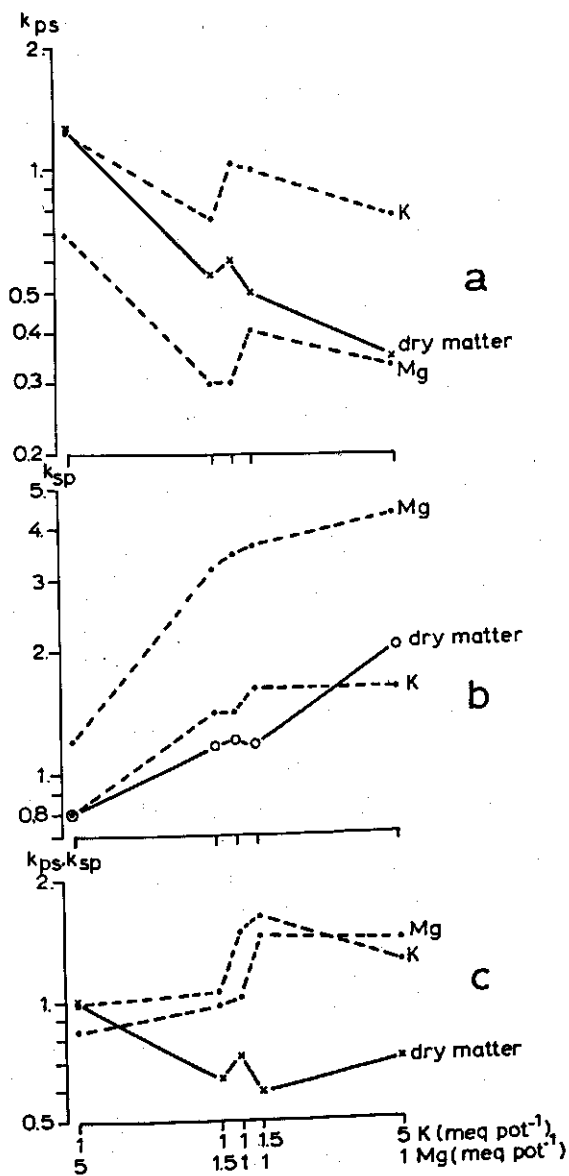


Fig. 57. Relative crowding coefficients of *Plantago* with respect to *Sanguisorba*: k_{ps} (a) and of *Sanguisorba* with respect to *Plantago*: k_{sp} (b) and their product (c) for P_s whole plant yields, K uptake and Mg uptake, in competition experiments on five nutrient solutions (I to V) in which K and Mg are limiting to various extents (Exp. VI).

species use K less efficiently in the mixture than in the monoculture (higher K concentrations in the mixtures), for which we have no explanation.

Looking at the Mg concentrations it is seen that on Solutions II, III and IV *Plantago* uses Mg more efficiently due to the competition of *Sanguisorba*, while *Sanguisorba* itself does not efficiently use the Mg it gained from *Plantago* (high concentrations in the mixtures). Even in Solution V, where Mg is highly limiting, *Sanguisorba* fails to produce in the mixtures until the Mg concentration drops to a minimum. Probably, we were not quite successful in preventing light competition at the end of the experiment, which could have delayed growth of *Sanguisorba* in the mixtures with much *Plantago*, so that its Mg utilization was not yet at a maximum at the time of harvesting. It is not clear why this did not occur where K was limiting. Possibly K deficiency occurred earlier in the experiment, which might have enabled the plants in the mixtures to make up arrears. The time of harvest may be rather critical in this respect.

With this in mind we can better understand Figure 57b. When K is limiting k_{sp}^{DM} is equal to k_{sp}^K as was expected. When Mg is the limiting factor k_{sp}^{DM} falls behind k_{sp}^{Mg} , because growth of *Sanguisorba* in the mixtures was not yet stopped. Therefore k_{sp}^{DM} is smaller than unity (Fig. 57c). Perhaps, if we had harvested few days later, k_{sp}^{DM} would have been approximately equal to k_{sp}^{Mg} and Figure 57b would have shown the same pattern as Figure 57a.

The estimation of relative crowding coefficients always involves the presupposition that the competitive formulas are valid. Moreover the accuracy often is low. Basing conclusions on differences between relative crowding coefficients therefore is tricky. However, the primary observation of the nutrient concentrations in the plants (Fig. 56) provides a check on the above conclusions, independently of any presupposition. The frequency independent K concentrations on Solution I show that for both species their competitive abilities measured for K uptake and DM yield are the same. When K ceases to be limiting a difference grows, so that its concentration becomes frequency dependent. The same comparison can be made between the Mg uptake and DM yield.

The K/Mg ratio in the plants provides a similar check for the inferred differences between the relative crowding coefficients for K and Mg uptake. Figure 58a shows that in the monocultures K and Mg are taken up almost exactly in the ratio in which they are supplied (interrupted line; on Solution V some K is left or missing otherwise, compare Figure 55b). In the mixtures the species change each others uptake ratio, in opposite directions, away from the substrate ratio. In conformity with their preferences *Sanguisorba* takes away Mg from *Plantago* and *Plantago* takes away K from *Sanguisorba*. This effect is of course the greatest when one plant of a species is surrounded by many plants of the other species. The result is a difference in the K/Mg uptake ratio of the species growing in the same pot. This difference, expressed by the double quotient $(U_p^K/U_p^{Mg})/(U_s^K/U_s^{Mg})$, is not frequency dependent (Fig. 58b).

According to the model this double quotient is mathematically identical to quotients k_{ps}^K/k_{ps}^{Mg} and k_{sp}^{Mg}/k_{sp}^K . Though differing somewhat from each other, the mean of the quotients indeed equals the double quotient of U values. The double quotient varies from about 1.6 on Solution I, to 3.0 on Solution IV. This lies within the range of Experiment III, where

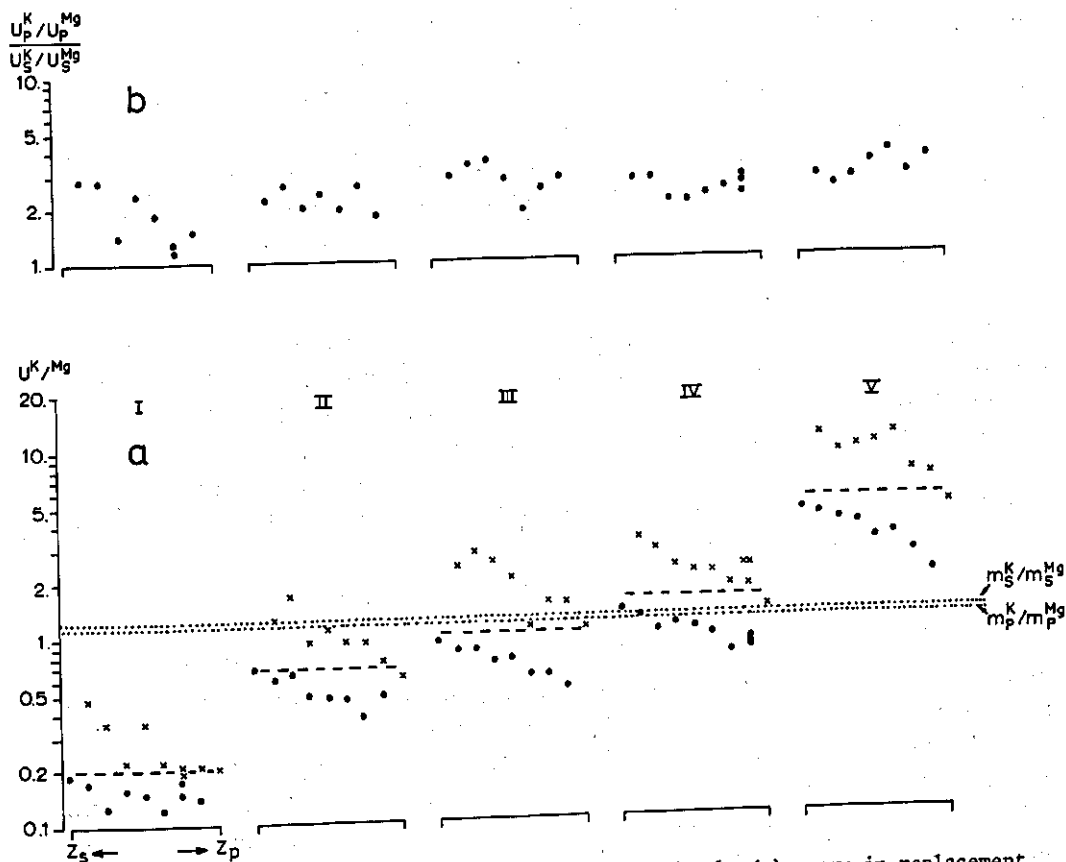


Fig. 58. (a) K/Mg uptake ratio of *Plantago* (x) and *Sanguisorba* (•) grown in replacement series on five nutrient solutions in which K and Mg are limiting to various extents. (Exp. VI). The K/Mg substrate ratios are indicated by interrupted lines. The optimum K/Mg ratio of *Plantago* and *Sanguisorba* as measured by the ratio of their minimum concentrations in the monocultures (Fig. 54), are indicated by the dotted lines. (b) Quotient of the K/Mg uptake ratios of *Plantago* and *Sanguisorba*.

values of 1.34, 4.09 and 4.90 were found on Solutions 3, 9 and 7 respectively (see Table 17). The range of K/Mg substrate ratios was much greater in Experiment III, namely 0.01 to 100 compared to 0.2 to 5 in Experiment VI.

It may be concluded that the difference in cation selectivity was directly responsible for the difference in the ability to compete for K and Mg and for the resulting difference in overall competitive ability on substrate differing in K/Mg ratio. Though their ratio is fixed, the absolute values of the relative crowding coefficients for K and Mg may be various, depending on time and on conditions. The complete reversal of the competitive dominance in this experiment, which makes the results more spectacular, may have been a stroke of luck. However, also when there was no reversal, but only a change from slightly dominant to very dominant, our conclusions would stand.

The changes observed in uptake ratio due to competition are the very effects on which on RYT > 1 and a stable equilibrium may be based, provided that for both species

the change is in the direction of the optimum ratio, so that luxury consumption is reduced. The latter is obviously not the case in our experiment, since the optimum K/Mg ratio of *Plantago* and *Sanguisorba* as measured by the ratio of the minimum concentrations in the monocultures are nearly the same (Fig. 58a). On Solution III and IV the competition effect moves the uptake ratio of both species away from their optimum, thus increasing luxury consumption, which will have contributed to the low product of $k_{ps}^{DM} k_{sp}^{DM}$.

7.8.2.3 Conclusions

Summarizing we may conclude that this experiment substantiates our model of multiple resource competition in some aspects and disproves it in other aspects. It has shown that the simultaneous competition for K and Mg may be described by the De Wit-competition equations. It has disproved convincingly that the individual relative crowding coefficients k_{ps}^K and k_{ps}^{Mg} are independent of the substrate composition. The quotient k_{ps}^K / k_{ps}^{Mg} , however, is reasonably constant, and can be estimated from the uptake ratios of the species in monoculture.

The experiment has shown that K and Mg are functionally substitutable to some extent, so that the optimum K/Mg uptake ratio of the species is not sharply defined and the maximum yield at the optimum uptake ratio is lower than expected. It has revealed difficulties in the prediction of the optimum K/Mg uptake ratio from the minimum K and Mg concentrations determined in exhaustion experiments.

Notwithstanding the difficulties in parameter estimation, the model may give a reasonable description of multiple-resource competition in some cases. When the mutual substitutability of the resources is too great, or when they are not taken up completely or are not redistributed internally, the model has to be adapted.

The competitive performance of the species is determined by their ability to compete for a limiting nutrient. Differences in selectivity cause differences in the ability to compete for separate nutrients. The outcome of competition therefore depends on which nutrient is limiting. Our experiment confirms this and proves therefore that a unified concept of competitive ability (Grime, 1977; 1979, p. 16) is essentially incorrect.

The results justify a moderate optimism about the possibilities of a stable equilibrium due to differential nutrient limitation. Because of the difference in selectivity the species may influence each others nutrient uptake ratio in a competitive situation. Due to each others presence they change their 'diet', causing a difference between them where there would have been none when they were growing separately. With substitutable resources this would result in reduced competition, which might permit coexistence. With complementary resources coexistence depends also on the relative requirements of both species. The change in diet may lead to increased luxury consumption of both species when their uptake ratios move away from the optimum ratio. $RYT < 1$ is the result and no stable coexistence is possible. When the optimum ratios of the species are widely different, it is possible that luxury consumption is decreased in the mixture as compared to the monocultures. This would happen when the ratio of the nutrients in the substrate lies between the optimum ratios of the species. It results in $RYT > 1$ and offers possibilities for stable coexistence.

8 Final remarks

The study of the 'balance of nature' is both challenging and discouraging. It is challenging because many of the problems man is facing nowadays result from his disturbing influence on the ecosystem he is part of. Insight into the functioning of natural communities and the maintenance of their steady state is needed to understand how disturbances act and may be avoided or counteracted.

Studying the balance of nature is discouraging, because of its sometimes hidden existence, its complexity and its fragility. The striking fluctuations in the densities of many natural populations (Van den Bergh, 1979) suggest the absence of any equilibrium and have led some ecologists to deny the existence of a 'balance of nature' (Ehrlich & Birch, 1967). Others have accepted the concept of a balance of nature and have stressed the necessity of regulatory mechanisms compensating for the continual perturbations (Slobodkin et al., 1967). Evidently I have adopted the latter standpoint and made a case for the existence of many equilibrium mechanisms (Chapter 3). None the less, the dynamic behaviour of natural populations makes it sometimes difficult to believe that equilibrium is not a fiction.

Dealing with complexity is one of the greatest difficulties in studying natural ecosystems. There are two strategies to cope with it: (1) neglecting it, by conceiving a community as a simple system (the approach of May, 1974) or by considering it as a 'black box' (Van Leeuwen, 1966); (2) reducing it, by isolating a few components and studying their characteristics in enough detail to explain their interactions, as we have tried.

These strategies are complementary, attacking the problem at opposite ends, but they are still far from 'meeting in the middle'. Neither strategy can do complete justice to the complexity of the ecosystem. This is not always a disadvantage, since we may be interested in other aspects of the system. However, when we are studying the diversity of a community and try to understand how it is maintained, we are essentially interested in complexity and the disabilities of our methods are more seriously felt.

The fragile and fugitive character of natural equilibria makes them difficult to approach experimentally. One is never sure whether a vegetation stand is in equilibrium. Stochastic effects and unintended influences of the investigator may disturb it. Theoretical arguments and practical experience set down in this report lead to the conclusion that efforts to create equilibria artificially, will succeed only under strict conditions and may fail for many reasons.

The difficulties just mentioned have left their marks on the present study. The discrepancy between the possibilities to explain equilibrium theoretically and the possibilities to provide experimental proof for the explanations is evident when one

compares the two parts of this report.

In the first part possible explanations for the species richness of grassland vegetation are reviewed and categorized (Chapter 3). Suggestions for the analysis of some equilibrium mechanisms are given (Section 4.9) and one suggestion is worked out in detail (Chapter 5).

In the second part two approaches have been followed:

It was investigated which of the mechanisms summed up in Chapter 3 was responsible for a specific stabilizing effect that was observed in a previous experiment. Attempts were made to provide experimental proof of the equilibria based on differential nutrient limitation analysed in Chapter 5.

Neither approach has led to clear-cut conclusions. With respect to the first approach it was concluded in Section 6.5 that a difference in growth rhythm occurred, which might have been responsible for part of the stabilizing effect. Autotoxic activities and differential use of nitrogen and phosphorus are suggested to explain the rest of the effect. Other causes were considered less likely but could not be excluded.

With respect to the second approach it was concluded in Section 7.8 that plant species differ in their relative uptake and relative requirement of nutrients, which is one essential condition for equilibria based on differential nutrient limitation. However, the plant species investigated did not differ in the correct way, so that the equilibrium could not be exemplified. The results suggest that species in general differ more in their uptake ratio than in their minimum requirements. This would reduce the chance that a species combination meets the equilibrium conditions, since these conditions (Eqn 5.17) require the reverse.

Assuming that the model of Chapter 5 gives a reasonable description of the simultaneous competition for two nutrients, the above would make it improbable that differential nutrient limitation plays an important role in maintaining the species richness of grassland vegetation. This is not necessarily true, however, as the improbable may become common, provided that it maintains itself whenever it occurs, which is an essential property of stable species equilibria and of life in general.

Even if the model should prove not to give a suitable description of reality, which is all but unlikely, it is still possible that differential nutrient limitation may give rise to stable equilibria. The experiments with algae (Titman, 1976) have demonstrated this. Evidence of this principle working also with terrestrial plants could not be given as yet.

Notwithstanding these 'mitigating circumstances' and optimistic remarks, the situation remains that our experiments give no clear answer to the basic question about the causes of diversity and stability in grassland vegetation. They would have fitted better to other questions. They demonstrated, for example, that potassium and magnesium are to some extent functionally substitutable (Exp. V and VI). They also gave a good picture of the characteristic cation uptake patterns of different species on waterculture of constant composition (Exp. III), which patterns broadly agreed with information from the field. They demonstrated that differences in cation selectivity between species are reflected in their uptake pattern, when they are competing in an exhaustion experiment (Exp. VI). They gave a clear and positive answer to the question whether competitive ability depends

on environmental conditions or not (Exp. VI).

Yet we have decided to keep to the original objective and present the experiments in their connections with the theoretical considerations about coexistence. This is done for the sake of veracity and to place this subject of research in the spotlight, because of its importance for understanding the functioning of grassland communities.

Evidently, there is need for a better understanding of the relation between nutrient uptake and growth of a plant. The physiology of different species must be better known before we can understand the interactions between them. The central question in this connection is how the different limiting nutrients interact. Limitation by deficiency of a single nutrient was used in our model for the sake of simplicity. Most probably, however, specific deficiencies are of subordinate importance in our grasslands. Rather the entire ion balance and the regulation of internal pH and osmotic value will be involved. Interaction with other limiting factors such as light and water will be important too, not to speak of grazing and diseases.

In short: we need more quantitative and comparative research on the functioning of plants under various suboptimal conditions. Obviously, this is important for many purposes besides the study of natural equilibria. In this connection it is worth noting that for the understanding of species interactions it is important to know the influence of the environment on the plant, as well as the influence of a plant on the environment. Too little attention has been paid to the latter aspect.

A model of the relation between uptake and growth should permit us to evaluate the information chemical analysis of plant material gives about the kind and the degree of nutrient limitation. Diagnosis of the relative importance of limiting factors for different species living in the same vegetation is needed to get an impression of the role of differential nutrient limitation in maintaining the species richness of grasslands.

About this role, it is our expectation that it will prove to be real, though perhaps not as important as differentiation in micro-habitat, in time, or in rooting depth. This is inherent to the autotrophic and sessile character of plants.

Summary

This report deals with the functioning of plant communities in grasslands. It tries to explain phenomena like diversity and stability of the species composition by processes affecting the individual and the population. In stable and diverse grassland, individuals of many species live in close contact. Since vegetation as a whole is considered to be limited by resources, competition seems inevitable. Apparently, competition is reduced or regulated in such a way that species do not exclude each other.

The main question was: How can competitive exclusion be avoided? A second question was: How can one explain the apparent failure to avoid competitive exclusion in so many floristically poor grasslands, such as intensively farmed grassland?

In Part I terms and concepts used are explained, such as equilibrium, diversity, coexistence, competition, stability and niche (Chapter 2).

'Niche differentiation' is defined as a functional difference between species that may lead to stable coexistence in a homogeneous environment. The term 'habitat differentiation' is used when species differences result in spatial separation.

A survey is given of mechanisms that may contribute to the species diversity and stability of grassland vegetation (Chapter 3). One important mechanism is microhabitat differentiation, which depends on environmental heterogeneity. Since it does not result in true coexistence, this was described as 'non-coexistence equilibrium'. Species may occur in each others microhabitat in a 'non-equilibrium coexistence' when a continuous immigration and extinction takes place. Non-equilibrium coexistence is also possible when competitive exclusion is interrupted frequently by environmental fluctuations. This, however, cannot prevent extinction in the long run in a homogeneous environment without an additional mechanism that reduces the chance of extinction.

Mechanisms depending on functional differences between species enable true coexistence also in a homogeneous environment. Differential use of resources is one of them. The ability to use different resources is limited for plants. Limitation by different nutrients resulting from quantitative differences in the uptake and requirement of the same nutrients may, however, also result in stable coexistence. Other means exist when the species use the same resource at different places or times or with different efficiencies and rates. Differences in other regulating factors, such as predators, may also allow coexistence. In addition, coexistence resulting from some other mechanisms is discussed.

It is concluded that together these mechanisms may explain high species densities. Though environmental heterogeneity is considered as an important source of diversity, functional differentiation must be involved too, when the species are growing as intensely intermingled as they do in most grasslands. A high number of potentially limiting

factors may therefore conduce to high species densities.

In addition to a general lack of adapted species, this may be an explanation for the low diversity under extreme conditions in which one factor is of predominant importance for most species. Not stress as such, but the one-sidedness is adverse to coexistence. Attention is drawn to the complexity of the growth regulation of species in the field, and to the need of diagnosis of factors limiting different species in the same vegetation, through analysis and experiments. More quantitative and comparative research on growth under combinations of suboptimal conditions is necessary.

In Chapter 4 the competition theory of De Wit is introduced, emphasizing equilibria. The frequency dependency of the Relative Replacement Rate, and the Relative Yield Total exceeding unity are considered important indications for equilibrium possibilities. The demonstration of an equilibrium ratio in a ratio diagram is better evidence, but it depends more on the conditions. The discrepancy between the apparently widespread occurrence of coexistence in the field and the lack of indications for equilibrium in experiments is due to the simplicity of the experimental conditions, which reduces the chance of niche and habitat differentiation to come to expression.

A number of suggestions is made for the analyses of competition in more complicated situations. They are based on separate formulation of different competitive and non-competitive processes and analyses of the effect of their simultaneous operations. Four complicating effects are described with models which are closely related, viz.: environmental heterogeneity, generative and vegetative reproduction, multiple resource competition and resource refuges. The distinction between complementary resources, that are typically used by autotrophic organisms, and substitutable resources typical for heterotrophic organisms is found to be important to the analysis of multiple resource competition. Other complicated cases considered are seasonal changes in competitive dominance, seed immigration, supra-optimal densities, allelopathic and beneficial effects. Several of these analyses provide alternative explanations for the existence of frequency dependent competitive ability.

In Chapter 5 multiple resource competition for complementary resources is considered in more detail and the conditions for equilibria through differential resource limitation are derived. It is concluded that species may coexist in a stable equilibrium in a homogeneous environment when their nutrient requirements and uptakes meet certain conditions. They have to differ more in their relative requirements than in their relative uptake ratios. In addition the environmental conditions, e.g. the amounts present of the nutrients, have to be within a certain range which is determined by the species characteristics. RYT exceeding as well as smaller than unity is possible; the first indicates that one part of the equilibrium conditions is met. In the second case the distribution of the nutrients among the species is more nearly to the optimum when they are growing in monocultures compared to a mixture.

The model explains complex processes and patterns in vegetations, in terms of interactions and physiological differences between species. It predicts low diversity in heavily fertilized grasslands and the existence of contrasting vague and sharp vegetation transitions, known as 'limes divergens' and 'limes convergens', along environmental gradients under conditions which are favourable or adverse to the mainte-

nance of species equilibria, respectively.

Experiments with phytoplankton species by Tilman (1977) have already exemplified equilibria within a range of environmental conditions, predicted by a model similar to ours. The complexity of higher plants and terrestrial environments will make it more difficult to obtain this result with grassland species.

In the experimental part of the report two approaches are followed. First, two field trials are presented, which were carried out to reproduce and explain an observation of RYT exceeding unity in multi-species mixtures in which *Plantago lanceolata* and *Chrysanthemum leucanthemum* were dominating (Chapter 6). Secondly, it was tried to exemplify under controlled conditions the equilibrium possibilities resulting from differential resource limitation, using some suitable combination of grassland species (Chapter 7).

Field Trial I was continued for four years. It included seven plant ratios of *Plantago* and *Chrysanthemum* (including monocultures) and two harvest series (in the first year only). Frequency-dependent competitive ability was not observed. The RYT values in the subsequent years were 1.06, 0.94, 1.17 and 1.52. A change in dominance was observed in the first year indicating seasonal differentiation between the species, which may have caused the small deviation of the RYT in this year. The extremely dry summer of the second year will have made functional differentiation impossible.

The seasonable differentiation was investigated in detail in Field Trial II. Growth of *Plantago* and *Chrysanthemum* was followed during one season in monoculture and in mixture, using the non-destructive point-quadrat measurements. The difference in growth rhythm was confirmed, but it could not account for all of the increase in RYT, which came up to 0.4 in May and June. Observations on root distribution of the species showed that possible differentiation was prevented by a gravel bank at a depth of 40 cm.

In the last two years of Field Trial I a sharp reduction in the productivity of *Plantago* occurred in the mixtures as well as in the monocultures. This was caused by senescence of the original plants, which was not compensated for by seedling establishment, possibly due to self-inhibition. *Chrysanthemum* plants in the mixtures evidently profited by this spontaneous retreat, which resulted in the high RYT values. The ratio diagram and the course lines clearly showed a frequency dependent RRR, but no equilibrium point was present. It is suggested that the occurrence of *Plantago* in grasslands depends on continual establishment on new sites.

The first two experiments under controlled conditions were carried out to investigate the possibility of stable coexistence of *Plantago* and *Chrysanthemum* through differential nutrient limitation. Because the species were known to differ with respect to their K and Ca nutrition these cations were chosen as limiting nutrients. The K and Ca requirements of the species were investigated in a nutrient replacement experiment (Exp. I). The relative uptake abilities were investigated in competition experiments on three nutrient solutions with different K and Ca concentrations (Exp. II). It turned out that this combination of species and nutrients did not meet the equilibrium conditions, because the species differed more in their relative K/Ca uptake ratios than in

their relative K/Ca requirements (with a factor 2.3 and 1.5, respectively), whereas the reverse is required.

Chrysanthemum was unable to take up Ca from concentrations $< 0.1 \text{ meq l}^{-1}$, leaving a Ca-refuge for *Plantago*. As *Plantago* was already the stronger competitor, this did not result in an equilibrium either.

In search for a more suitable species-nutrients combination the K, Ca and Mg requirements and uptake abilities were investigated of a number of grassland species which were pre-selected because of their contrasting cation composition while co-occurring in the field. Beside *Plantago* and *Chrysanthemum*, *Anthyllis vulneraria*, *Cerastium holosteoides*, *Rumex acetosa* and *Sanguisorba minor* were chosen.

The relative uptake abilities of these species were studied by growing them together on nutrient solutions with different K, Ca and Mg concentrations which were kept constant (Exp. III). To represent the relation between the substrate composition and the K, Ca and Mg uptake of the plants a triaxial ratio diagram was devised. The species differences in cation selectivity agreed broadly with the differences observed in the field. *Chrysanthemum* took up much K, *Sanguisorba* took up relatively much Mg. *Rumex* and *Cerastium* were characterised by their low Ca uptake, *Plantago* and *Anthyllis* by a lack of selectivity between Ca and Mg.

The K, Ca and Mg requirements of these species were investigated by growing them together on three nutrient solutions with a limited supply of K, Ca or Mg (Exp. IV). The differences in cation selectivity were reflected in the relative amounts taken up by the species. It was concluded that the model of multiple resource competition is not applicable when Ca is a limiting nutrient.

The K and Mg requirements of *Plantago*, *Chrysanthemum*, *Rumex*, *Sanguisorba* and of *Anthoxanthum odoratum* were determined more precisely in a K-Mg replacement experiment (Exp. V). The results suggested that K and Mg are mutually substitutable to some extent, contrary to the assumptions of the model. From a comparison of the quotient of the K and Mg minimum concentrations and the K/Mg uptake ratios found in Experiment III, it was concluded that none of the possible species combinations met the equilibrium conditions of the model. In general, the variation in relative requirement appears to be smaller than the variation in relative uptake of nutrients.

Finally, a competition experiment was carried out with *Plantago* and *Sanguisorba* on five nutrient solutions with different K/Mg ratios (Exp. VI) to see whether the model gives a good description of the simultaneous competition for K and Mg. The concentrations of these cations were chosen such as to enable a conclusion about their functional relationship. The results demonstrate that K and Mg are mutually substitutable to a limited extent.

In agreement with the differences in K-Mg selectivity *Plantago* competed better for K and *Sanguisorba* better for Mg. The yields of the species in monoculture were almost equal. Their competitive ability in the mixtures was dependent on the substrate conditions. *Plantago* was the stronger competitor when K was limiting and *Sanguisorba* when Mg was limiting. This change in competitive dominance was determined by the difference in K-Mg selectivity between the species. The concentrations of K and Mg in the plants were frequency dependent when they were not limiting: the species changed each others uptake

ratios. This could, however, not result in an $RYT > 1$, because the relative requirements of the species were almost the same, so that a more efficient partition of K and Mg in the mixtures, compared to the monocultures, was not possible.

It is concluded that, notwithstanding difficulties with parameter estimation, the model may give a reasonable description of multiple resource competition. With other species, differing more in their requirements, $RYT > 1$ and equilibria will be possible. It is argued that our difficulties in obtaining experimental evidence are not representative for the chance that differential nutrient limitation plays a role in the maintenance of species diversity in grasslands.

Samenvatting

Dit verslag handelt over het functioneren van plantengemeenschappen in graslanden. Voor een goed beheer van vegetaties, voor welk doel dan ook, is inzicht nodig in de relaties tussen de aanwezige plantesoorten en de invloed van de omstandigheden daarbij. Deze relaties zijn bepalend voor de soortenrijkdom en de stabiliteit van de betreffende vegetaties. In stabiele en soortenrijke graslanden leven de individuen van verschillende soorten voortdurend in nauw contact met elkaar. Concurrentie lijkt daarbij nauwelijks te vermijden, aangezien verschillende plantesoorten grotendeels dezelfde voedingsstoffen nodig hebben en de groei van de vegetatie als geheel verondersteld wordt door voedsel beperkt te zijn. Experimenten met grassen hebben geleerd dat concurrentie doorgaans leidt tot wederzijdse verdringing en dus tot soortenarmoede. Klaarblijkelijk is in soortenrijke graslanden de concurrentie verzacht of op zodanige wijze gereguleerd dat de soorten elkaar niet wegconcurreren.

De hoofdvraag in dit verslag was nu: Hoe zien de soorten in een soortenrijk grasland kans om wederzijdse uitsluiting te voorkomen? Een tweede vraag was: Waarom is dit niet mogelijk in soortenarme graslanden, zoals de zwaar bemeste cultuurgraslanden?

In deel I wordt een toelichting gegeven bij enkele gebruikte termen en begrippen, zoals evenwicht, diversiteit, coëxistentie, concurrentie, stabiliteit, niche en habitat. Van nichedifferentiatie wordt alleen gesproken als soorten zodanig verschillend functioneren, dat ze onder dezelfde omstandigheden door verschillende factoren in hun uitbreiding worden beperkt, zodat ze evenwichtig naast elkaar kunnen blijven voortbestaan in een homogeen milieu. De term habitatdifferentiatie blijft gereserveerd voor gevallen waarin soortverschillen fungeren als specialisaties op verschillende omstandigheden, zodat ze resulteren in een ruimtelijke scheiding van de soorten.

Vervolgens wordt een overzicht gegeven van mechanismen die kunnen bijdragen tot de soortenrijkdom van graslandvegetaties (hoofdstuk 3). Belangrijk is de habitatdifferentiatie op micro-niveau, welke slechts kan bestaan bij de gratie van micro-milieuheterogeniteit. Hierbij hebben de soorten hun eigen specifieke plekje, waarvan ze de andere soorten kunnen wegconcurreren. Omdat het niet leidt tot samenleven in strikte zin is dit omschreven als 'evenwichtig niet-samenleven'.

Als voortdurend exemplaren van andere soorten de micro-habitat van een soort binnendringen, om daarna geleidelijk te worden doodgeconcurrerd, kunnen we toch de verschillende soorten steeds naast elkaar aantreffen. Dit is omschreven als 'niet-evenwichtig samenleven'. Een voorwaarde hiervoor is dat de binnendringende soorten in de buurt een eigen plekje hebben, vanwaar steeds nieuwe exemplaren worden aangevoerd. 'Niet-evenwichtige samenleving' is ook mogelijk als de wederzijdse verdringing regelmatig wordt onderbroken en de concurrentieverhouding omgekeerd, door veranderingen in de omstandig-

heden. Op de lange duur vindt de verdringing echter toch plaats, tenzij de kans op totale verdringing op één of andere manier is verkleind.

Evenwichtig samenleven, zonder de noodzaak van milieuheterogeniteit of -variabiliteit, is mogelijk wanneer soorten bepaalde functionele verschillen vertonen, zoals bijvoorbeeld verschillende voedselspecialisaties. De mogelijkheid tot voedselspecialisatie is voor planten slechts beperkt omdat ze grotendeels dezelfde basisbehoeften hebben en er weinig variatie is in de vorm waarin de voedingsstoffen worden aangeboden. Kwantitatieve verschillen in de opname en behoefte van dezelfde voedingsstoffen kunnen echter leiden tot een verschil in de beperkende factor, wat onder bepaalde voorwaarden evenwichtig samenleven mogelijk maakt. Dit is ook mogelijk als soorten een zelfde voedingsstof bemachtigen op verschillende worteldieptes of met een verschillende efficiëntie en snelheid. Verschillende andere regulerende factoren, zoals begrazing en ziektes, kunnen ook leiden tot samenleven van soorten die elkaar zonder deze factoren zouden wegconcurreren.

Alles tezamen zijn er theoretisch voldoende mogelijkheden om zeer hoge soortenrijkdom in grasland te verklaren. Hoewel habitatdifferentiatie vermoedelijk de belangrijkste oorzaak van soortenrijkdom is, moet ook nichedifferentiatie een rol spelen waar de soorten zo intens verstrengeld door elkaar groeien als in veel graslanden. De aanwezigheid van veel potentieel beperkende factoren op één plaats zal daarom bijdragen tot een hoge soortenrijkdom. In extreme milieus is vaak één factor van overwegend belang voor de meeste soorten. Dit kan, naast het geringe aanbod van aangepaste soorten, een verklaring zijn voor de lage soortenrijkdom in zulke milieus. Voor het samenleven is niet de 'stress' als zodanig, maar de eenzijdigheid nadelig.

De factoren die de afzonderlijke soorten in een vegetatie beperken, kunnen worden onderzocht door middel van gewasanalyses en experimentele ingrepen. De regulatie van de groei van soorten in het veld is echter zeer complex. Er is daarom behoefte aan meer kwantitatief en vergelijkend onderzoek naar de groei van plantesoorten onder velerlei combinaties van beperkende omstandigheden.

In hoofdstuk 4 wordt de concurrentietheorie van De Wit besproken, waarbij de nadruk wordt gelegd op het constateren van evenwichten. Frequentie-afhankelijkheid van de relatieve vervangingsnelheid (RRR) en een som van de relatieve opbrengsten (RYT) die groter is dan één worden als belangrijke aanwijzingen beschouwd voor het bestaan van evenwichtsmogelijkheden. Een beter bewijs is het aantonen van een evenwichtsverhouding in een ratio-diagram, maar het bestaan hiervan hangt sterk af van de omstandigheden. De tegenstrijdigheid van het veelvuldig voorkomen van coëxistentie in het veld enerzijds en de zeer spaarzame aanwijzingen voor evenwichten in experimenten anderzijds, is te wijten aan de eenvoudigheid van de experimentele omstandigheden, waardoor de kans op nichedifferentiatie sterk wordt verkleind.

Er wordt een aantal suggesties gedaan voor de analyse van meer gecompliceerde vormen van concurrentie. Zij berusten op afzonderlijke formulering van verschillende concurrentieprocessen en het analyseren van hun gezamenlijke werking. De concurrentie in vier gecompliceerde gevallen kan worden beschreven met sterk op elkaar gelijkende modellen. Dit betreft concurrentie in heterogene milieus, concurrentie tussen soorten met generatieve en vegetatieve reproductie, concurrentie om meer nutriënten tegelijk en concurrentie tussen soorten waarvan één of beide over een refugium beschikt. Het onderscheid tussen

onderling wel- en niet-vervangbare nutriënten blijkt van groot belang te zijn voor de analyse van concurrentie om meer nutriënten. Andere gecompliceerde gevallen die de revue passeren zijn: wisselende concurrentiekracht binnen een groeiperiode, zaadimmigratie, supra-optimale dichtheden, allelopatische effecten en afhankelijkheidsbetrekkingen. Verschillende van deze analyses leveren alternatieve verklaringen voor het bestaan van frequentie-afhankelijke concurrentiekracht.

In hoofdstuk 5 wordt het model van de gelijktijdige voedselconcurrentie om onderling onvervangbare nutriënten verder uitgewerkt en de voorwaarden voor evenwichten gebaseerd op een verschil in de beperkende factor worden afgeleid. Het blijkt dat soorten evenwichtig kunnen samenleven in een homogeen milieu wanneer hun nutriëntenbehoefte en opnamesnelheid aan bepaalde voorwaarden voldoen. De soorten moeten meer verschillen in hun relatieve behoefte dan in hun relatieve opname van de nutriënten. Daarnaast moeten de milieu-omstandigheden, d.w.z. de verhouding van de nutriënten in het milieu, tussen bepaalde grenzen liggen die weer door de eigenschappen van de soorten worden bepaald. De nutriëntenbehoefte is hierbij gedefinieerd als het minimumgehalte in de plant. Dit wordt bereikt als de hoogst mogelijke opbrengst met een bepaalde hoeveelheid van het betreffende nutriënt is geproduceerd.

Het model verklaart complexe zaken als patronen en processen in vegetaties in termen van interacties en fysiologische verschillen tussen soorten. Het voorspelt de soortenarmoede van zwaar bemeste graslanden en het optreden van vage en scherpe vegetatiegrenzen, bekend als 'limes divergens' en 'limes convergens', langs milieugradiënten onder omstandigheden die respectievelijk gunstig en ongunstig zijn voor het handhaven van evenwichten tussen soorten.

Experimenten van Tilman (1977) tonen aan dat coëxistentie van fytoplanktonsoorten mogelijk is binnen een reeks van milieu-omstandigheden die op dezelfde manier is geformuleerd als de evenwichtsvoorwaarde van het hier gepresenteerde model. De complexiteit inherent aan hogere planten en terrestrische omstandigheden zullen het echter moeilijk maken dit resultaat ook met graslandplanten te boeken.

In het experimentele deel (Deel II) van dit verslag worden eerst twee veldproeven beschreven welke zijn uitgevoerd om een bevestiging en een verklaring te vinden van een RYT-waarde groter dan één die eerder was waargenomen in een soortenmengsel waarin *Plantago lanceolata* en *Chrysanthemum leucanthemum* de overhand hadden (hoofdstuk 6). Daarna worden de pogingen beschreven om onder geconditioneerde omstandigheden met een daartoe geschikte soortencombinatie de evenwichtsmogelijkheden te toetsen die volgens het model bestaan als de soorten door verschillende nutriënten worden beperkt (hoofdstuk 7).

In veldproef I, die vier jaar geduurd heeft, zijn *Plantago* en *Chrysanthemum* in zeven mengverhoudingen ingeplant (inclusief monocultures). De concurrentiekracht was niet frequentie-afhankelijk. De RYT-waarden in de opeenvolgende jaren waren 1,06; 0,94; 1,17; 1,52. In het eerste jaar werd op twee tijden geoogst. Een wisseling van de concurrentieverhouding in dit jaar wees op een verschil in groeiritme tussen de soorten, wat de kleine positieve afwijking van de RYT kon verklaren. De extreme droogte in de zomer van het tweede jaar (1976) heeft hoogst waarschijnlijk elke differentiatie onmogelijk gemaakt.

De mogelijkheid van een verschil in groeiritme is nader onderzocht in veldproef II. Een seizoen lang is de groei van *Plantago* en *Chrysanthemum* in mono- en mengcultuur gevolgd met behulp van de niet-destructieve 'point quadrat'-metingen. Een verschil in groeiritme werd inderdaad gevonden, maar dit kon de sterke stijging van de RYT, met 0,4 in mei en juni, niet volledig verklaren. Waarnemingen toonden aan dat ook een mogelijk verschil in worteldiepte geen verklaring bood, aangezien differentiatie werd verhinderd door een grindbank op 40 cm diepte.

In de laatste twee jaar van veldproef I liep de opbrengst van *Plantago* sterk terug, zowel in mono- als in mengcultuur. Dit werd veroorzaakt door veroudering van de oorspronkelijke planten, terwijl vestiging van jonge planten niet of nauwelijks plaatsvond, vermoedelijk door zelf-remming. In de mengsels profiteerden de *Chrysanthemum*-planten van deze spontane teruggang, hetgeen resulteerde in de hoge RYT-waarden. Het radiodiagram en de koerslijnen toonden duidelijk een frequentie-afhankelijke RRR, maar er was geen evenwichtspunt. We veronderstellen daarom dat het voorkomen van *Plantago* in graslanden afhankelijk is van een regelmatige vestiging op nieuwe plaatsen.

De eerste twee experimenten onder geconditioneerde omstandigheden zijn uitgevoerd om na te gaan of evenwicht tussen *Plantago* en *Chrysanthemum* mogelijk is door verschil in de beperkende factor. Omdat het bekend was dat deze soorten nogal verschillen in hun K- en Ca-opname, zijn deze cationen als beperkende nutriënten uitgekozen. De K- en Ca-behoefte van deze soorten is onderzocht in een K-Ca-ervangingsreeks van voedingsoplossingen (Exp. I). De relatieve opname is onderzocht in een concurrentie-experiment op drie voedingsoplossingen met verschillende K- en Ca-concentraties (Exp. II). Het bleek dat deze combinatie van soorten en nutriënten niet aan de evenwichtsvoorwaarden voldoet, want de soorten verschilden meer in hun K/Ca-opnameverhouding dan in hun K/Ca-behoefteverhouding (met een factor 2,3 en 1,5 respectievelijk) terwijl het omgekeerde is vereist. *Chrysanthemum* was niet in staat Ca op te nemen bij concentraties van minder dan $0,1 \text{ meq l}^{-1}$, zodat een soort Ca-refugium voor *Plantago* overbleef. Dit leverde echter ook geen evenwichtsmogelijkheden op, omdat *Plantago* reeds de sterkste concurrent was.

Op zoek naar een meer geschikte combinatie van soorten en nutriënten is de K-, Ca- en Mg-opname en -behoefte onderzocht van een reeks grasland planten die waren voorge-selecteerd op grond van hun contrasterende cationensamenstelling onder gelijke omstandigheden in het veld. Naast *Plantago* en *Chrysanthemum* waren dit *Anthyllis vulneraria*, *Cerastium holosteoides*, *Rumex acetosa* en *Sanguisorba minor*.

De relatieve opname van deze soorten is bestudeerd door ze tezamen te kweken op een reeks voedingsoplossingen met verschillende K-, Ca- en Mg-concentraties, welke constant werden gehouden (Exp. III). Om de relatie tussen de K-, Ca- en Mg-opname van de planten en de substraatsamenstelling overzichtelijk weer te geven is een drie-assig verhoudingsdiagram ontworpen.

De verschillen in de cationeselectiviteit van de soorten kwamen overeen met de verschillen die in het veld waren geconstateerd. *Chrysanthemum* nam relatief veel K op, *Sanguisorba* veel Mg, *Rumex* en *Cerastium* namen weinig Ca op en *Plantago* en *Anthyllis* werden gekenmerkt door hun geringe Ca-Mg-selectiviteit.

De K-, Ca- en Mg-behoefte van deze soorten werd onderzocht door ze gezamenlijk te

kweken op drie voedingsoplossingen met een beperkte K-, Ca- en Mg-voorziening (Exp. IV). De reeds geconstateerde verschillen in de cationselectiviteit werden opnieuw teruggevonden, nu in de relatieve hoeveelheden die door de soorten werden opgenomen. Het bleek verder dat ons model niet van toepassing is als Ca één van de beperkende factoren is, omdat planten hun Ca-gehalte niet eerst tot een minimumgehalte verlagen, maar vrijwel onmiddellijk ophouden te groeien wanneer Ca-gebrek optreedt.

De K- en Mg-behoefte van *Plantago*, *Chrysanthemum*, *Rumex*, *Sanguisorba* en van *Anthoxanthum odoratum* werd nauwkeuriger onderzocht in een K-Mg-vervangingsexperiment (Exp. V). De resultaten suggereerden dat K en Mg functioneel enigermate onderling vervangbaar zijn, in tegenstelling tot wat in het model is aangenomen. Uit een vergelijking van de K/Mg-behoefteverhouding met de K/Mg-opnameverhouding, gevonden in Experiment III, moest worden geconcludeerd dat geen van de soortencombinaties aan de evenwichtsvoorwaarden voldeed. In het algemeen lijkt de variatie in de relatieve minimumbehoefte geringer te zijn dan de variatie in de relatieve opname van nutriënten.

Tot slot is een concurrentie-experiment uitgevoerd met *Plantago* en *Sanguisorba* op vijf voedingsoplossingen met verschillende K/Mg-verhoudingen (Exp. VI), om na te gaan of het model een bevredigende beschrijving geeft van de gelijktijdige concurrentie om K en Mg. De concentraties van deze cationen waren zo gekozen dat de resultaten tevens uitsluitend zouden geven over hun onderlinge vervangbaarheid. Het bleek dat zij inderdaad in beperkte mate onderling vervangbaar zijn.

In overeenstemming met het verschil in K-Mg-selectiviteit concurreerde *Plantago* beter om K en *Sanguisorba* beter om Mg. In monocultuur verschilden de opbrengsten van beide soorten nauwelijks. De concurrentieverhouding in de mengcultures hing echter af van de omstandigheden: *Plantago* won waar K beperkend was en *Sanguisorba* won waar Mg beperkend was. Deze verschuiving in concurrentieverhouding was terug te voeren op het verschil in de K-Mg-selectiviteit van de soorten. De concentraties van K en Mg in de planten bleken frequentie-afhankelijk te zijn, behalve wanneer ze beperkend waren, waaruit volgt dat de soorten elkaars opnameverhouding beïnvloeden. In ons geval kon dit niet leiden tot een $R_{YT} > 1$, omdat de soorten bijna dezelfde behoefteverhouding hadden, zodat een meer efficiënte verdeling van K en Mg tussen de soorten in mengcultuur (vergeleken met de monocultuur) niet mogelijk was.

We concluderen dat het model een redelijke beschrijving kan geven van de concurrentie om meer nutriënten tegelijk, ook al zijn sommige parameters moeilijk te bepalen omdat ze van de omstandigheden afhangen. Met andere soorten, die meer verschillen in hun relatieve nutriëntenbehoefte, moet een $R_{YT} > 1$ en evenwicht mogelijk zijn. Met nadruk wordt gesteld dat de problemen met het verkrijgen van een experimentele bevestiging niet maatgevend zijn voor de kans dat differentiatie ten aanzien van beperkende factoren een rol speelt bij de handhaving van de soortenrijkdom van graslanden.

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