

Coexistence of plant species by niche differentiation

1. INTRODUCTION

For many years biologists have been interested in the frequently observed phenomenon that a large number of species can continue to occur within a relatively small area for a long time. It is only during the last ten years that workers from other disciplines have also been actively engaged in this question, which has been much to the benefit of the developed theories.

GRUBB (1977) very recently wrote a comprehensive review on the mechanisms that may cause species-richness in plant communities, so we can confine ourselves to the following very simple scheme. In trying to explain how species can coexist two main groups of suppositions can be distinguished:

(1) suppositions associated with a heterogeneous environment, and (2) those based on a homogeneous environment.

For the heterogeneous environment a distinction can be made between theories which consider: species that cannot grow in each other's micro-habitat, and species that can grow in each other's micro-habitat but, nevertheless exclude each other because each species has the greatest competitive ability in its own micro-habitat. In essence these "mixtures" consist of many micro-mono-cultures, therefore the term "apparent coexistence" is preferred here. This type of coexistence has attracted much attention already (see HARPER 1961; THOMAS & DALE 1976; HICKMAN 1977; GRUBB 1977; WERNER & PLATT 1977).

For the homogeneous environment, some functional niche differentiation in the sense of ELTON (1927) must be supposed to occur. In this case the theories depend on species being limited by: one or more factors in different periods, and/or different factors simultaneously. In this sort of environment mixtures are involved in which "true coexistence" may occur.

Within the scope of this paper, we shall only treat this functional niche differentiation within a homogeneous environment. In our opinion an ecological stabilizing mechanism must underly the natural species-richness, which makes that an incidental decrease of the population density is followed up by an increase in reproductive rate. It is very unlikely that species-richness is maintained by accidental events, like climatic fluctuations, which cause changes in the competitive relations between the populations.

In experimental research on niche differentiation it may be very

advantageous to grow both monocultures and mixtures under conditions which are exactly the same except for the competitive situation, since this permits determination of the Relative Yield Total (RYT). This parameter, introduced by DE WIT & VAN DEN BERGH (1965) may be used to indicate the degree of niche differentiation.

2. THE RYT CONCEPT

2.1. SPACING

To show the usefulness of the RYT first a spacing experiment will be described. Fig. 1 shows that the individuals of the same plant species begin to interact as soon as yield per unit area is no longer proportional to plant density.

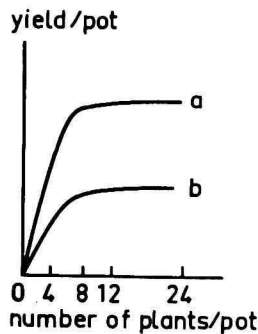


FIG. 1. Spacing curves of species a and b

The dependence of yield on plant density is linear up till 6 plants of species a per pot, which means that the per-plant weights are constant. There is a diminishing effect of density on yield per pot as density increases per-plant weights decrease due to competition. With 8 plants per pot the maximum yield is approached and, at higher densities, any doubling of the number of plants leads to a halving of per-plant weights. The same holds for species b; the only difference is that the per-plant weights of species b are smaller.

2.2. REPLACEMENT SERIES

The interference of individuals of different plant species is often studied in replacement series. In these, the yields of the species in the mixtures are compared with their yields in monoculture, on the understanding that the total sowing density of the mixed and monocultures are equal. In these replacement diagrams the yields of the separate species can be plotted against their planting frequencies.

Assuming that the species do not interfere with each other, the curves in a replacement diagram of a mixture experiment of species a and b at a total density of 24 plants per pot (Fig. 2) will be the same as those of the spacing

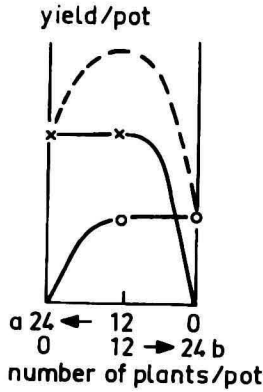


FIG. 2. Replacement diagram of species a and b without interspecific interference (see text)

x yields of species a per pot
 o yields of species b per pot
 --- total yields per pot

experiment of Fig. 1. In this case competition occurs only within the species and the total yield of the 12/12 mixture approaches the sum of the yields of both monocultures. Although the species grow close enough to affect each other, there is no interference, because they grow in entirely different niches.

2.3. RELATIVE YIELDS AND RELATIVE YIELD TOTAL (RYT)

For a better indication of the degree of overlap of the niches of the species, the absolute yields can be converted into dimensionless relative yields. The relative yield (r) of a species is the quotient of its yield in the mixture (O) and of its yield in the monoculture (M).

In Fig. 3a the relative yields of the 1/1 mixture are both approaching 1 and the sum of the relative yields (Relative Yield Total = RYT) approaches 2. The growth processes leading to these curves in this diagram are completely independent. Going from diagram a to d, however, the growth processes represented by the curves become more and more dependent on the interference between the species. In diagram b both curves are still convex, but to a less extent than in the preceding case. In diagram c the convex curve is partly compensated for by a concave curve and finally in diagram d, the one curve is convex to the same extent as the other is concave. In this order the niches in which the species grow overlap more and more; this is also shown by the RYT value

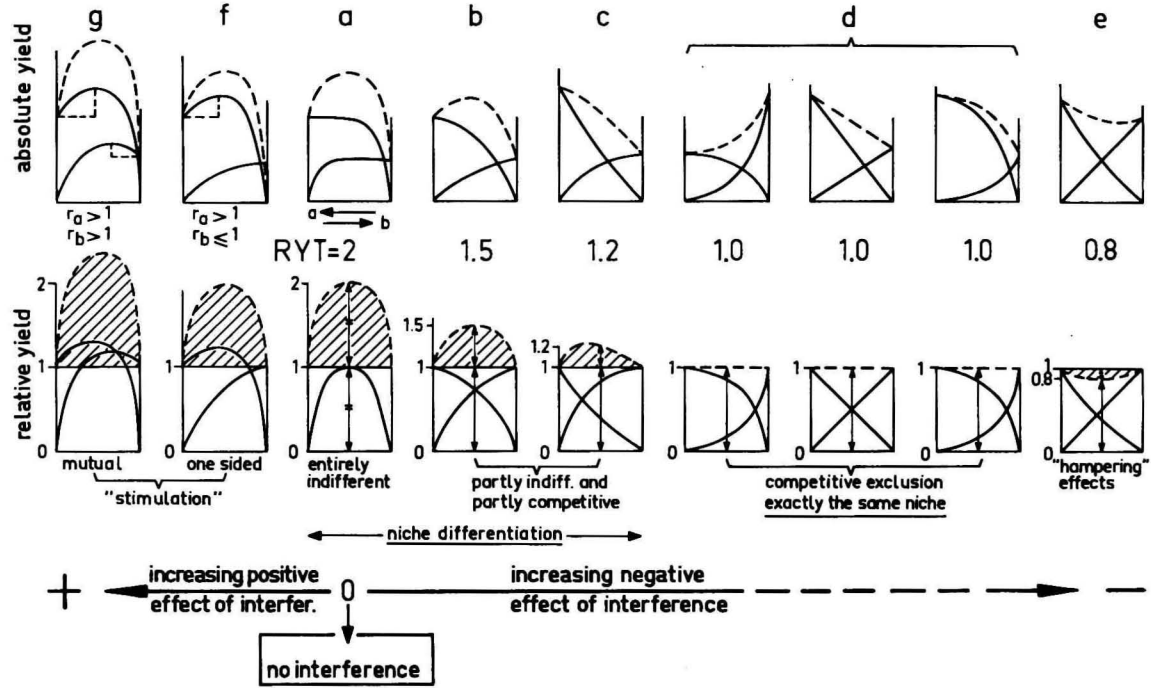


FIG. 3. Ways of interference (for explanation see text)

decreasing from 2 to 1. When $RYT = 1$ the species occupy exactly the same niche (diagram d). Ultimately the less aggressive species will be crowded out by the more aggressive species in the mixture. Where $RYT > 1$, on the other hand, the species are occupying partly different niches and coexistence may occur.

When the relative yield of species a (r_a) is greater than 1, there is a stimulating effect of species b on a (Fig. 3f, for example supporting plant and climber, host plant and parasite, legume and non-legume, etc.) and when $r_b > 1$ also, the stimulating effect is mutual (Fig. 3g). In all these cases the RYT values may be even greater than 2 (RAININKO 1968).

Finally $RYT < 1$ (Fig. 3e) may indicate hampering effects. This low RYT value may be caused by excretion of toxic substances or by a disease by which the carrier species is not damaged, but the neighbouring species is affected (SANDFAER 1970).

3. CONDITIONS FOR EQUILIBRIUM

The curves in the replacement diagrams of many competition experiments may be described by the hyperbolic functions generated by the model of DE WIT (1960):

$$O_a = \frac{k_{ab} \cdot z_a}{k_{ab} \cdot z_a + z_b} M_a \quad \text{and} \quad O_b = \frac{k_{ba} \cdot z_b}{k_{ba} \cdot z_b + z_a} M_b$$

O_a and M_a represent the yields of species a in mixture and monoculture respectively, z_a and z_b the relative planting frequencies, and k_{ab} and k_{ba} the relative crowding coefficients of species a with respect to species b and vice versa. In the model the k -values determine the degree of curvature of the curves: $k > 1$ results in a convex curve, $k = 1$ gives a straight line and $k < 1$ a concave curve. If k_{ab} is the reciprocal of k_{ba} and therefore their product is equal to 1, the species are supposed to occupy the same niche ("crowd for the same space" in DE WIT's terms), whereas with niche differentiation the product of the k -values is expected to be greater than 1 (which also implies a $RYT > 1$). $RYT > 1$ indicates niche differentiation between two species, but does not guarantee that the species will attain a stable equilibrium.

To study the changes in botanical composition of mixtures through time the relative reproductive rate α has been introduced, i.e. the quotient of the proportions in which the species are represented in the mixture at time (t+1) and time t.

$$\alpha_{ab} = \frac{(O_a/O_b)_{t+1}}{(O_a/O_b)_t} \quad \text{or} \quad \log (O_a/O_b)_{t+1} = \log (O_a/O_b)_t + \log \alpha_{ab}$$

By plotting the log's of these proportions for different mixtures in a ratio diagram (Fig. 4), it is shown in some experiments that α varies with planting frequency.

According to the model, if $k_{ab} \times k_{ba} > 1$ α indeed depends on planting frequency (DE WIT 1960). With increasing frequencies of species a, α decreases, which means that species a is becoming less aggressive with respect to species b.

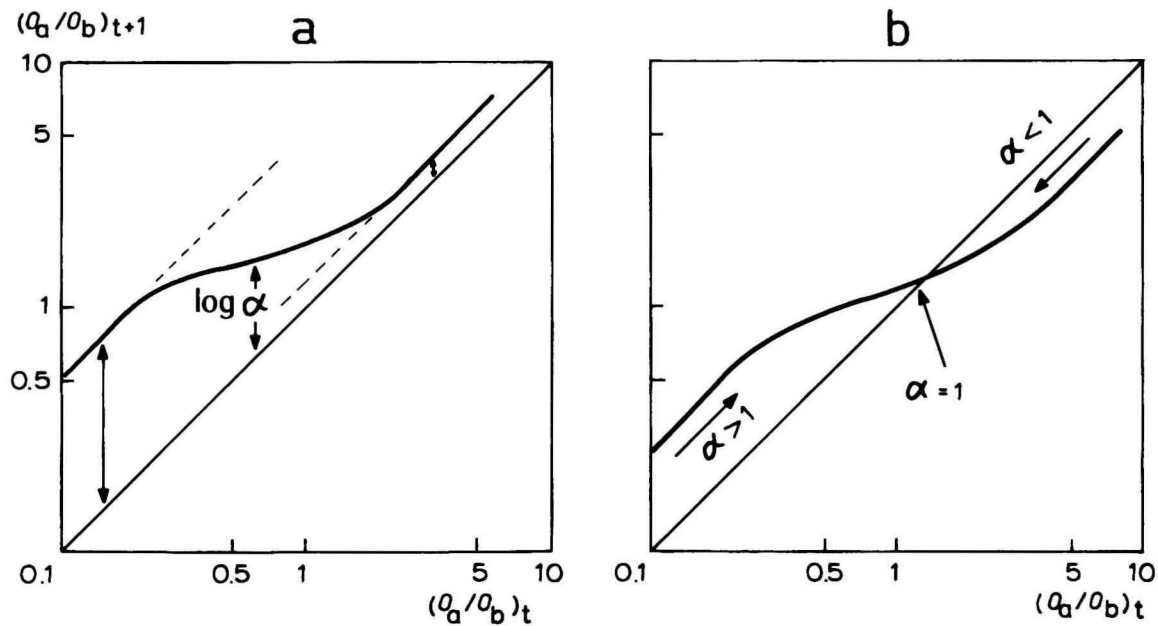


FIG. 4. Ratio diagrams in which the ratio of the yields of species a and b in a mixture at time $(t+1)$ is plotted against this ratio at time t .
 (a) species a replaces species b at all frequencies;
 (b) at high frequencies of species b, species a replaces species b; at high frequencies of species a, species b replaces species a; a stable equilibrium is reached at the intersection with the diagonal ($\alpha = 1$)

However, in the example of Fig. 4a, α remains greater than 1, hence finally species b will be crowded out by species a, in spite of the frequency dependence of α .

In Fig. 4b also the aggressiveness of species a with respect to species b decreases with increasing frequency of species a in the mixture, but in this example the curve intersects the diagonal. This means that to the left of this intersection species a wins and to the right species b wins but that at the intersection the species are in a stable equilibrium ($\alpha = 1$). BRAAKHEKKE (in preparation) has shown that the quotient of the monoculture yields determines whether the diagonal is intersected and, therefore, whether a stable equilibrium is possible. This condition is formulated by the following equation:

$$k_{ba} > M_a/M_b > 1/k_{ab}$$

4. A FIELD EXPERIMENT WITH MULTI SPECIES MIXTURES

The seeds of 13 species were collected on an old extensively grazed pasture: 7 grass species and 6 herbs. 3.5 m² plots were sown as monocultures as well as mixtures according to the replacement principle, with a total density of 1600 viable seeds/m². An area of 90 x 90 cm² was harvested in each plot once a year and the botanical composition analysed and dry weight determined.

Table 1 shows the relative yields of the species in the first and the second year in the various mixtures. 100/0 means that the mixture consists of grass species only; 75/25 means that 75% of the number of seeds were from grasses and 25% were from herbs etc.; 0/100 means that the mixture consists of herbs only. Two herbs *Prunella vulgaris* and *Ranunculus repens* disappeared already in the first year, due to very slow establishment. *Lolium perenne* was by far the most aggressive species with very high relative yields.

When looking at the sum of the relative yields, we see that the RYT value of the mixture involving grass species only is about equal to 1, which means that the species occupy the same niche. With the introduction of herbs in the mixtures the RYT values are greater than 1. 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 of no fertilizers were given (compare also the total absolute yields of the mixtures at the bottom of Table 1). 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 when going 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, namely 1.26. Hence, these two species show remarkable evidence of niche differentiation and therefore we chose them for further experimentation.

TABLE 1. Relative yields, RYT and absolute yields of different mixtures in a field experiment in the first and second year (for explanation see text)

Seed ratio grasses/herbs	1e year					2e year				
	100/0	75/25	50/50	25/75	0/100	100/0	75/25	50/50	25/75	0/100
<i>Lolium perenne</i>	0.68	0.77	0.64	0.39		0.05	0.01	0.02	0.01	
<i>Agrostis tenuis</i>	0.12	0.13	0.18	0.17		0.64	0.38	0.34	0.45	
<i>Anthoxanthum odoratum</i>	0.05	0.05	0.06	0.05		0.18	0.13	0.15	0.11	
<i>Trisetum flavescens</i>	0.04	0.05	0.06	0.05		0.04	0.06	0.04	0.01	
<i>Hordeum secalinum</i>	0.11	0.07	0.11	0.05		-	-	-	-	
<i>Festuca rubra</i>	0.01	0.01	0.02	0.03		0.01	†	0.02	0.04	
<i>Cynosurus cristatus</i>	0.01	0.01	0.01	0.02		0.01	0.02	0.01	†	
<i>Chrysanthemum leucanthemum</i>		0.03	0.06	0.10	0.40		0.29	0.22	0.18	0.82
<i>Plantago lanceolata</i>		0.06	0.13	0.20	0.45		0.22	0.28	0.31	0.44
<i>Rumex acetosa</i>		0.06	0.09	0.25	0.53		0.03	0.06	0.07	0.19
<i>Centaurea 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.d.m./0.8 m ²)	245	301	345	316	434	73	93	87	94	114

5. GROWTH LIMITED BY COMPETITION FOR LIGHT

First of all a possible niche differentiation with regard to light interception has been investigated. Competition experiments between *Chrysanthemum leucanthemum* and *Plantago lanceolata* have been carried out by BERENDSE (in preparation) in a growthroom under optimum nutrient conditions and at two light intensities. Light was regarded to be the only factor which could limit growth of the species.

The RYT values at both light intensities were systematically somewhat greater than 1 (1.05 and 1.08), which points to a slight degree of niche differentiation. The taller *Plantago lanceolata* leaves were erect and the leaves of the shorter *Chrysanthemum leucanthemum* plants were prostrate. Simulations of daily photosynthesis carried out by TRENBATH (1974) showed that the RYT values which may be expected from this favourable leaf arrangement are only about 1.09.

It may be concluded that in grassland vegetation niche differentiation with respect to the light factor is of little importance.

6. GROWTH LIMITED BY COMPETITION FOR MINERALS

The question now arises whether differences in underground behaviour of *Chrysanthemum leucanthemum* and *Plantago lanceolata* may cause niche differentiation. In the field experiment no differences between rooting depths of these species could be observed, hence the occupation of different soil volumes is unlikely. On the other hand it is wellknown that the behaviour of plant species with regard to minerals may vary considerably.

HARPER (1961) already pointed out that two species can coexist only when they are controlled by different factors. This author mentioned the difference in nitrogen source between legumes and grasses. BRADSHAW (1969) argued that not only qualitative but also quantitative differences in mineral requirements can enable species to coexist. In 1970 LEVIN gave this suggestion a theoretical basis.

Recently this possibility has caught the attention of some phytoplankton research workers (STEWART & LEVIN 1973; PETERSEN 1975; TITMAN 1976). As far as we know no studies have been devoted to the possibility of differential limitation by minerals in relation to terrestrial plants. GRUBB (1977) passed it off with only a few words.

It is easy to see that a mixture can produce more than monocultures in the fictitious case that each monoculture does not take up the very nutrient that limits the other monoculture. Consequently $RYT > 1$ and an equilibrium may be possible. This argument has been worked out in a more sophisticated manner by BRAAKHEKKE (in preparation). He has considered two double quotients: that of the minimum concentration (m) of two minerals 1 and 2 in two species a and b and that of the amounts of these minerals taken up (U). The minimum concentration of nutrient 1 in species a is reached at the moment that growth stops because of deficiency of this nutrient, everything else being not limiting. The uptake rates are not considered explicitly in the model but instead the results of the uptake processes; U_a^1 means the amount of nutrient 1 taken up by species a grown in a mixture. Under conditions of limited supply of these nutrients the RYT can be greater than 1, if the following equation holds:

$$\frac{m_a^1/m_a^2}{m_b^1/m_b^2} > \frac{U_a^1/U_a^2}{U_b^1/U_b^2} > 1$$

In addition another condition must be fulfilled. The ratio of the limiting nutrients in the substrate has to be in between certain limits. These depend on the minimum contents in the plants, the uptake abilities and the planting frequency (BRAAKHEKKE, in preparation).

In an attempt to test whether the *Plantago* (P) and *Chrysanthemum* (C) species referred to earlier fulfil the first condition, two experiments were performed using K and Ca, because it was known that these species often differ to some extent with respect to the contents of these nutrients.

In the first experiment, to determine the minimum K and Ca contents, the two species were separately grown on a series of 10 nutrient solutions with an increasing K and a decreasing Ca concentration (Table 2); the other nutrients

TABLE 2. *K and Ca concentrations (me/pot) of nutrient solutions in an experiment with Plantago lanceolata and Chrysanthemum leucanthemum. The other nutrients were added according to $\frac{1}{2}$ Hoagland solution*

Solutions	I	II	III	IV	V	VI	VII	VIII	IX	X
KNO_3	0.10	0.15	0.20	0.25	0.30	0.35	0.40	0.45	0.50	0.55
$Ca(NO_3)_2$	0.50	0.45	0.40	0.35	0.30	0.25	0.20	0.15	0.10	0.05

were abundant. The solutions were not renewed and the plants were harvested when the growth ceased on most of the solutions due to K or Ca deficiency.

Fig. 5 shows the relation between K and Ca concentration in the whole plants. On solution X a minimum concentration of Ca is reached in the plants whereas K is accumulated and on solution I a minimum concentration of K is reached with

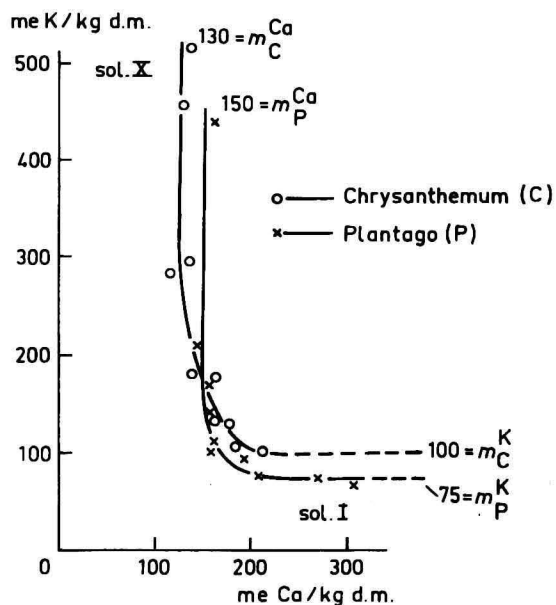


FIG. 5. *The K concentrations of Chrysanthemum leucanthemum and Plantago lanceolata plotted against their Ca contents when grown in a culture experiment with 10 combinations of K and Ca*

Ca accumulated to a less extent. The two curves show that the species differ in their minimum contents. These values may be used in the first part of the above-mentioned equation:

$$\frac{m_P^{Ca} / m_P^K}{m_C^{Ca} / m_C^K} = \frac{150/75}{130/100} = 1.5$$

According to this result a RYT value > 1 for *Chrysanthemum leucanthemum* and *Plantago lanceolata* may occur.

In the second experiment, to determine the double quotients of the amounts of these nutrients taken up by the plants growing in mixture, the two species were grown together in replacement series at low K or low Ca levels, and at low levels of both nutrients.

The value of this double quotient varied between 2 and 3, and hence does not lay in the narrow range between 1 and the value of the double quotient of the minimum contents 1.5. This means that the other part of our first condition is not satisfied.

The RYT values of this experiment appeared to vary between 1.00 and 1.23, which suggests some niche differentiation, that is still unexplained. Anyhow these values are too small to explain the result of the field experiment. It has still to be evaluated if other combinations of nutrient shortages may do better.

7. SOME CONCLUDING REMARKS

In spite of the above-mentioned result, the model just discussed may help us to understand equilibria of plant species in environments which are supposed to be homogeneous. For every plant combination the ratio's of the nutrient concentrations in the substrate have to meet specific requirements to allow this kind of equilibrium. When the substrate is changed for example by fertilizing, the frequencies of the species at equilibrium will change, provided the change of the substrate is within certain limits mentioned above. Larger changes in the substrate destroy the possibility of an equilibrium; they are followed by the extinction of one species.

Raising the concentrations in the substrate without changing the ratio between the nutrients, will disturb the equilibrium also, because the limiting effect of the nutrients disappears and other factors such as light become decisive.

To what extent fluctuations of the nutrient concentrations in the substrate may disturb the equilibrium, depends on the amplitude and the period of the fluctuation in relation to the rate of change of the frequency ratio between the species. This offers a way to describe the rather vague concept of environmental dynamics and to indicate how it affects the species richness of the vegetation. Models like this one can deepen our insight into the relation between diversity and stability and into the problem of eutrophication.

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9. REFERENCES

- BERENDSE, F. - Competition for light between populations of *Plantago lanceolata* L. and *Chrysanthemum leucanthemum* L. (in preparation).
- BERGH, J.P. VAN DEN & W.Th. ELBERSE, 1975 - Degree of interference between species in complicated mixtures. XII. Intern. Bot. Congr., Leningrad, Abstr., Vol. 1, p. 138.
- BRADSHAW, A.D., 1969 - An ecologist's viewpoint. In: I.H. RORISON (Editor), *Ecological aspects of the mineral nutrition of plants*. Blackwell, Oxford, p. 415-427.
- ELTON, C.S., 1927 - *Animal ecology*. Sidgwich & Jackson, London, 209 p.
- GRUBB, P.J., 1977 - The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biol. Rev.*, 52, 107-145.
- HALL, R.L., 1974 - Analysis of the nature of interference between plants of different species. II. Nutrient relations in a Nandi *Setaria* and Greenleaf *Desmodium* Association with particular reference to potassium. *Austr. J. agric. Res.*, 25, 749-756.
- HARPER, J.L., 1961 - Approaches to the study of plant competition. In: F.L. MILTHORPE (Editor), *Mechanisms in biological competition*. University Press, Cambridge, p. 1-39.
- HICKMAN, J.C., 1977 - Energy allocation and niche differentiation in four co-existing annual species of *Polygonum* in Western North America. *J. Ecol.*, 65, 317-326.
- LEVIN, S.A., 1970 - Community equilibria and stability, and an extension of the competitive exclusion principle. *Amer. Natur.*, 104, No. 939, 413-423.
- PETERSEN, R., 1975 - The paradox of the plankton: an equilibrium hypothesis. *Amer. Natur.*, 109, No. 965, 35-49.
- RAININKO, K., 1968 - The effects of nitrogen fertilization, irrigation and number of harvestings upon leys established with various seed mixtures. *Suom. maatal. Seur. Julk.*, 112, 1-137.
- SANDBAER, J., 1970 - An analysis of competition between some Barley varieties. *Danish Atomic Energy Comm., Risø Rep.*, 230, 1-114.
- STEWART, T.M. & B.R. LEVIN, 1973 - Partitioning of resources and the outcome of interspecific competition: a model and some general considerations. *Amer. Natur.*, 107, No. 171, 171-198.
- THOMAS, A.G. & H.M. DALE, 1976 - Cohabitation of three *Hieracium* species in relation to the spatial heterogeneity in an old pasture. *Can. J. Bot.*, 54, 2517-2529.
- TITMAN, D., 1976 - Ecological competition between algae: experimental confirmation of resource-based competition theory. *Science*, 192, No. 4238, 463-465.
- TRENBATH, B.R., 1974 - Biomass productivity of mixtures. *Adv. Agron.*, 26, 177-210.
- WERNER, P.A. & W.J. PLATT, 1976 - Ecological relationships of co-occurring goldenrods (*Solidago: Compositae*). *Amer. Natur.*, 110, No. 976, 959-971.
- WIT, C.T. DE, 1960 - On competition. *Versl. Landbouwk. Onderz.*, 66.8.
- WIT, C.T. DE & J.P. VAN DEN BERGH, 1965 - Competition between herbage plants. *Neth. J. agric. Sci.*, 13, 212-221.

10. DISCUSSION

WHITE (Dublin): How does RYT vary with the biomass production? The production of the mixtures with herbs only in the first year is four times higher than in the second year, and still in both years RYT is about equal to 1.4.

VAN DEN BERGH: There is, I suppose, no direct relationship between RYT and biomass production. In general, one could say that with high production levels under optimal conditions, the RYT tends to be equal to 1, because only light is growth limiting and there are few possibilities for niche differentiation in light use. With low production levels, say less than $6 \text{ ton ha}^{-1} \text{ year}^{-1}$, the possibilities of niche differentiation seem to be far greater, because many factors may limit different species in their growth. All the yields in this experiment, including those of the first year, were less than $6 \text{ ton ha}^{-1} \text{ year}^{-1}$.

HARPER (Bangor): One interesting consequence of this model counting for diversity within an otherwise homogeneous environment is that the various species that are persisting together will each of them be suffering from deficiency of a different nutrient component. This might enable us to detect this happening in the field by studying deficiency symptoms in wild plants. This would be an enormously interesting field operation, because one just tended historically to regard a habitat as a potash deficient one or a nitrogen deficient one, but on your interpretation a habitat will be deficient in something different for each of the species in equilibrium. I wonder whether there is field evidence yet that might suggest this sort of effect?

VAN DEN BERGH: This is a very important aspect of our research. Deficiency symptoms in fast-growing crops are well known, but under marginal condition with slowly growing vegetation the same deficiency might have an entirely different appearance. This means that we do not even know what symptoms to look for. Besides discolourings, deviating growth forms might be of greater importance for the detection of the kind of deficiency that occurs in natural communities.

GRIME (Sheffield): I think there is a danger in work of this kind when one moves on to a question of mechanism. The idea that different plants require different quantities of particular elements may be true, but it may surely also be a question of the spending of the nutrient when it is got actually into the plant. Don't you think that in one case the plant is almost immediately investing the nutrient in growth and in the other case we have what I would like to call a stress tolerator, which is accumulating the nutrient perhaps for future occasions?

VAN DEN BERGH: It is hard to translate your question into our observations. You are talking about total quantities taken up, whereas our determinations concern the minimum content, that is the content in the plant when growth ceases due to lack of a particular mineral. On the other hand, and that is a real problem for us, the various ions differ in their mobility within the

plant. For example, in case of shortage, potash can be redistributed from the old leaves to the young ones, whereas calcium remains in the old tissues. Hence, the Ca content of the different parts of the plant may vary considerably.

CAVERS (Ontario): I am curious to know whether there is a relationship between plant form and the nutrient availability. Is it possible that a plant might grow in a certain way because it has a certain supply of nutrients?

VAN DEN BERGH: As I mentioned in my answer to Professor Harper, we don't know yet. We have to start to study the symptomatology of nutrient deficiencies in natural communities.