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Interactions between plants nad population dynamics

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Interaktionen zwischen Pflanzen können experimentell auf dreierlei Weise untersucht werden, nämlich I. nach dem Additions-Modell, II. nach dem Substitions-Modell und III. nach dem dynamischen Modell. Die Vor- und Nachteile dieser Modelle werden diskutiert.
Eine einfache Methode wurde entwickelt, um festzustellen, ob Arten in derselben Nische oder teilweise in verschiedenen Nischen wachsen. Besonderes Augenmerk wird gerichtet auf den Unterschied zwischen der Populationsdynamik annueller Pflanzen, bei denen der leere Raum jährlich mit Keimlingen wieder zu besetzen ist, und perennierenden Pflanzen, bei denen der besetzte Raum jährlich neu zu verteilen ist.
Abschließend wird die Populationsdynamik einer alten Graslandgesellschaft diskutiert, die 20 Jahre lang beweidet oder gemäht und mit unterschiedlichen Düngern gedüngt worden ist.

Competition, grassland, mathematical model, niche differentiation, population dynamics, replacement experiments, spacing.

1. Introduction

In studying interactions between plants, biologists generally observe individual plants and investigate how populations are controlled, whereas agronomists observe entire crops and prefer parameters based on area units. Why this different approach?

Biologists are more concerned with the vegetation and agronomist with sown annual crops. These two subjects differ in at least three aspects:

I. In the vegetation the environment greatly determines the botanical composition, which is a very long-term process from generation to generation and results in a more or less stable association. In arable land, however, man frequently selects the species for just a year. Within short periods great changes in botanical composition may occur, often leading to dominance of one species.

II. Compared with nature with its complicated biotic and abiotic structure, in cultivated land soil and crop are much more homogenized. It may be assumed that in a heterogeneous environment interactions between plants are less intensive, since the species grow and multiply in their own microsites which are better adapted to their specific requirements.

III. A cultivated crop usually has a much higher production level than the vegetation, because the former can be supplied with minerals ad libitum. In cultivated land encroachment will be more intensive, competition for space being, therefore, of great importance.

For these reasons competition is often less fierce in the vegetation than in cultivated crops and biologists persist in thinking, therefore, in terms of the performance of individual plants instead of space, space being defined by all growth requisites like light, water, nutrients and actual space for which the species compete (WIT 1960).

2. Experimental approaches of competition

Three types of competition experiments will be discussed: additive experiments, replacement (substitution) experiments and experiments designed to simulate competition in time.

2.1 Additive experiments

With these experiments to one population other populations of different size are added. This design may answer the question to what extent the yield of a crop is reduced by different infestations of a weed. The drawback of this design is, however, that there are no adequate mathematical models available to quantify the effects, because of the different plant densities.

2.2 Replacement (substitution) experiments

In replacement experiments all stands have the same density, but the stands differ in their planting frequencies of the species, with as ultimate "mixtures" the monocultures. The competition effects in replacement series can be most adequately quantified by WIT's (1960) model (TRENBATH 1978; SPITTERS 1979). On the other hand the results obtained according to this approach cannot be generalized for other densities.

2.3 Dynamic simulation of competition

The above mentioned drawbacks are avoided with dynamic simulation of competition effects in time. This model developed by BAEUMER, WIT (1968) and improved by SPITTERS (1979) predicts the competitive relations in a mixture at any time on the basis of parameters derived from a spacing experiment with the species grown in monocultures and harvested at intervals.

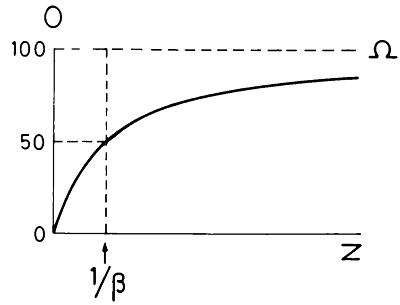


Fig. 1: Relation between yield per unit area (O) and plant density (Z).
The meaning of Ω and β is explained in the text.

The relation between yield (O) per unit area and plant density (Z) is generally represented by a hyperbolic function

$$O = \frac{\beta Z}{\beta Z + 1}\,\Omega$$

in which Ω is the yield when the available space is completely occupied (Fig. 1). The parameter β, which measures the curvature of the density curves, increases with time (Fig. 2) and reflects the space occupied by a single plant growing alone (WIT 1960) and therefore is a measure for its competitive ability. It is found that at first β increases exponentially with time. On a log-scale a straight line

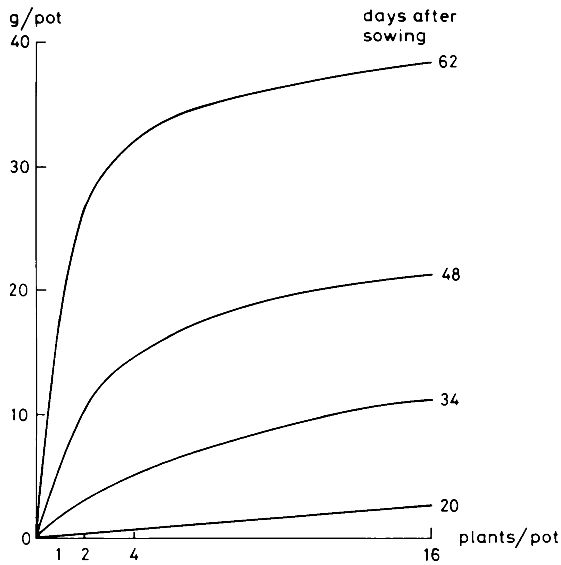


Fig. 2: Density response of *Hordeum vulgare* at four harvest times.
(after ELBERSE, KRUYF 1979).

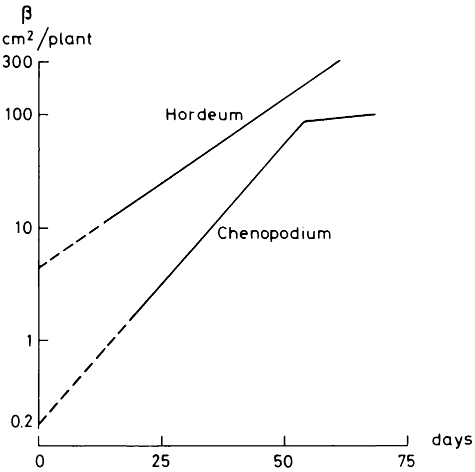


Fig. 3: Time curves of β for *Hordeum vulgare* and *Chenopodium album* with β plotted on a log-scale.
(data from ELBERSE, KRUYF 1979).

is obtained (Fig. 3), which means that the relative "growth" rate of β (the slope of the line) remains constant. Generally at the beginning of flowering the line flattens off rather sharply (barley did not flower during the experimental period), after which β remains constant.

The competitive relations among species can be understood from their β-curves. These curves demonstrate that the competitive ability of a species is greater with a higher initial value of β (great number of plants, early emergence and large seeds (SPITTERS 1979) and with a greater relative growth rate of β. The parameter Ω has no influence on the final result of competition, as it only measures the efficiency with which the species converts the occupied space into biomass. This model was experimentally tested by BAEUMER, WIT (1968); WIT (1970); RERKASEM (1978) and by ELBERSE, KRUYF (1979) and discussed by SPITTERS, BERGH (1981).

3. The RYT-concept

In the previous examples the crops and weeds compete for the same limiting resources, that is to say they occupy the same ecological niche, otherwise the weed is not called a weed (a crop yield depressing species). This is tested by the Relative Yield Total (RYT) in a replacement experiment (WIT, BERGH 1965; BERGH, BRAAKHEKKE 1978):

$$RYT = r_a + r_b = O_a/M_a + O_b/M_b$$

in which the relative yield of species a (r_a) is equal to the quotient of its yield/unit area in mixture (O_a) and its yield/unit area in monoculture (M_a). The species exclude each other (occupy exactly the same niche) when RYT = 1 (Fig. 4d).

In the (theoretical) case that the species do not interfere with each other at all, both curves in the replacement diagram will be identical to the known hyperbolic density curves and the maximum RYT-value will be equal to 2 (Fig. 4a). Two species with a different growing period will hardly interfere with each other in a mixture (different spaces in time). Fig. 4 shows a sequence of possiblities in which the effect of interference varies from positive via indifferent to negative. When the relative yield $r_a > 1$, there is a stimulating effect of species b on species a (Fig. 4f), but this need not be reciprocal (supporting plant and climber, parasite and host plant, etc.). In these cases RYT may be even greater than 2 (grass - legume mixtures, RAININKO 1968). Very recently BRAAKHEKKE (1980) published an extensive study on niche differentiation and possibilities for coexistence, especially concerning the uptake of nutrients. RYT < 1 (Fig. 4e) may indicate hampering effects. In this case toxic substances may be excreted or a disease may occur by which the carrier species is not damaged but the neighbouring species is indeed infected (SANDFAER 1970).

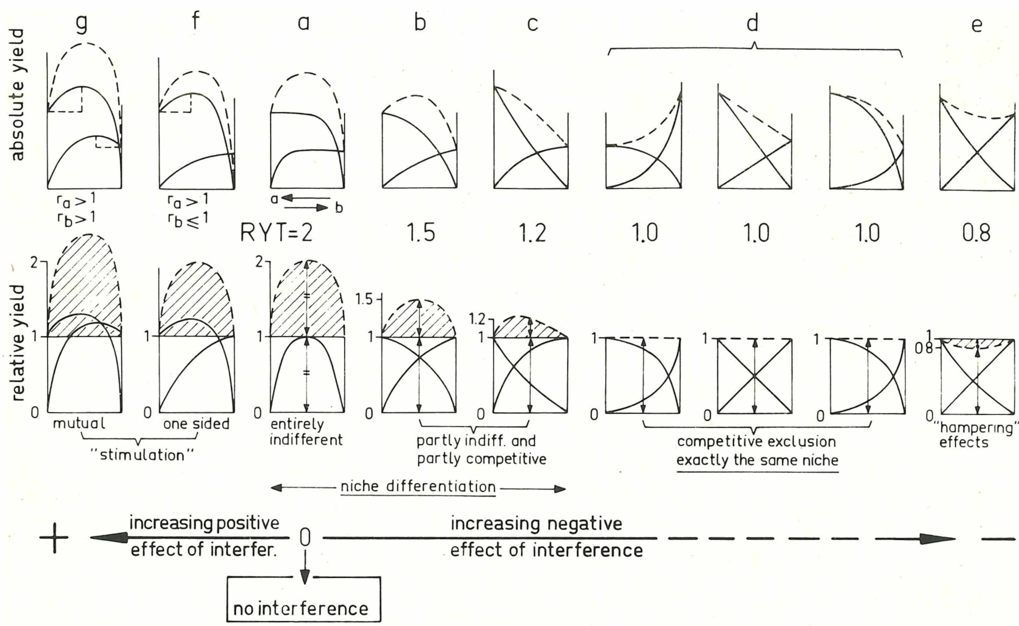


Fig. 4: Ways of interference (for explanation see text).
Dotted lines in the upper series of replacement diagrams represent the absolute total yields and in the lower series the RYT values of the mixtures (after BERGH, BRAAKHEKKE 1978).

4. Annuals versus perennials

An important difference between annuals and perennials with respect to population dynamics from year to year is that the plant parts with which the perennial continues growth in the next year, are the very parts lost by the annual (stubble, underground parts). This implies that with perennials the space already occupied is redistributed every year, whereas with annuals the "empty" space has to be occupied again by seedlings. Therefore with perennials the ratio of the relative spaces occupied by the species (O_a/M_a : O_b/M_b) determines the final result of

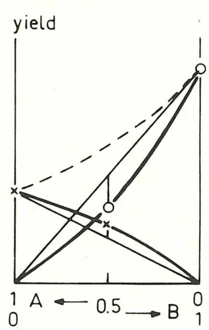


Fig. 5: Replacement diagram of species A and B.
For explanation see text.

competition, whereas with annuals the ratio of the absolute seed yields of the species in the mixture (O_a/O_b) determines this result. Therefore a difference should be made between competitive ability in the vegetative phase and reproduction via seed. This may lead to opposite results. In case species A and B are perennials (yield is expressed in biomass) species A will win (convex curve and O_a/M_a : $O_b/M_b > 1$, Fig. 5). In case species A and B are annuals (yield expressed in number of seeds) species B will win ($O_b/O_a > 1$). In spite of its smaller competitive ability (concave curve) it still wins because of its high generative reproduction ($M_B >> M_A$). This phenomenon was first described by MONTGOMERY (1912).

5. Population dynamics

With most competition experiments under controlled conditions in glasshouses and in the field with sown mixtures, after some time one population will dominate. In these cases the populations compete for the same (homogenized) space, the populations exclude each other (RYT = 1, TRENBATH 1974) and there is no stable equilibrium.

On permanent grassland a quite different picture is obtained: many populations are growing together in a (apparent) stable community. Closer observation, however, shows great fluctuations in their frequency of occurrence.

During 20 years a formerly alternate pasture near Wageningen has been partly grazed and partly hayed at the end of June and a second cut has been harvested in October (ELBERSE 1966). The fertilizer treatments of the grazed plots were O, PK, NPK, Ca (40 kg P_2O_5/ha, 60 kg K_2O/ha , 60 kg N/ha, 1000 kg CaO/ha). The treatments of the hayed plots (in duplo) were O, P, K, PK, NPK, Ca (120 kg P_2O_5/ha, 400 kg K_2O/ha, 100 kg N/ha in spring + 60 kg N/ha after haying, 1000 kg CaO/ha). The fertilizers used were superphosphate, potassium sulphate, ammonium nitrate and limestone.

At the start of the experiment the species density was 58 in an area of 0.05 ha. The main species were (in order of decreasing F%): *Festuca rubra, Agrostis (tenuis + stolonifera), Anthoxanthum odoratum, Holcus lanatus, Rumex acetosa, Trisetum flavescens, Alopecurus pratensis* and *Lolium perenne.* The production level during the last 10 years of the hayed plots without fertilizers was about 4.5 ton dry matter/ha and of the hayed NPK-Plots 9 ton dry matter/ha. On the grazed control and the NPK-plot the production was about 7 and 9.5 ton/ha resp. The results of the soil analysis are shown at the top of the diagrams in Fig. 6.

The botanical composition was analysed by the 25 sq. cm-frequency method of VRIES (1937). On each plot 50 samples of 25 sq. cm were taken at random in May and the presence of each species in each sample was recorded. From this a frequency percentage (F%) was calculated.

5.1 Unmanured plots

In Fig. 6 F% of some species are given during a period of more than 20 years. On the grazed plots (Fig. 6a) the F% is more or less constant. On the hayed plots (Fig. 6b), however, fluctuations of the F% are much more pronounced. In the first place the change of alternate pasture to pure hayfield brought about a kind of a shock, which is manifested by great fluctuations during the first 6 years. In the second place besides vegetative reproduction generative reproduction took place on a larger scale than on the grazed plots. Germination and seedling establishment is very sensitive for changing weather conditions, hence this may cause greater fluctuations than on the grazed plots.

5.2 PK-plots

Higher fertility stimulates productive grasses with the result that the less productive grasses like *Agrostis* and *Anthoxanthum* are crowded out (Fig 6c and d). The most obvious difference between the grazed and the hayed PK-plots is the increase of *Lolium* on the former and *Dactylis* on the latter plots.

5.3 Ca-plots

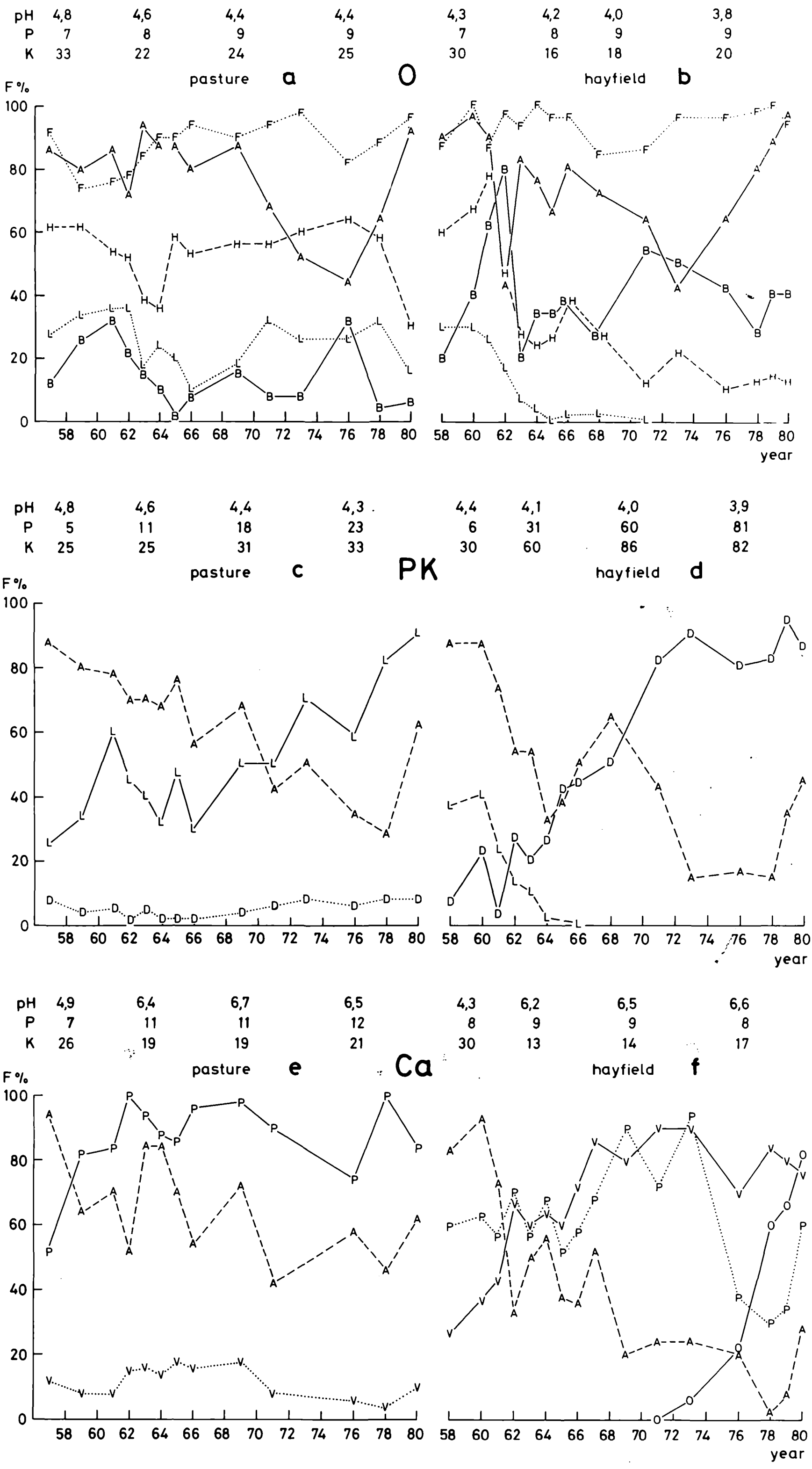
With all the other treatments pH went down with about half a unit, except on the Ca-plots on which the pH increased 1.5 to 2 units to about 6.5. While *Poa trivialis* decreased on the other plots (not shown in the figures), it maintained a high F% on the Ca-plots (Fig. 6e and f) and on the grazed NPK-plot (Fig. 6g). Another remarkable fact is the very clear response of *Poa pratensis* on the hayed Ca-plots (see also the hayed NPK-plots, Fig. 6h and i).

5.4 NPK-plots

A highly dynamic picture is obtained from the NPK-plots, especially from the hayed ones, because of the strongly increased fertility.

The grazed NPK-plot is much alike the grazed PK-plot, except for *Poa trivialis* which stays on a high level, though strongly fluctuating (Fig. 6g).

On the hayed NPK-plots the various populations of tall growing grasses successively show distinct rise-and-fall curves (Fig. 6h and i). First of all the F% of *Alopecurus pratensis* rises within 5 years to the maximum value of 100, staying there for the next 10 years. In the meanwhile *Poa pratensis* shows a rise-and-fall curve, followed up by *Dactylis glomerata.* But from then onwards the replicates


pH 4,8 4,6 4,4 4,4 4,3 4,2 4,0 3,8
P 7 8 9 9 7 8 9 9
K 33 22 24 25 30 16 18 20
pasture a
O
hayfield b
F %
100
80
60
40
20
0
58 60 62 64 66 68 70 72 74 76 78 80
year
pH 4,8 4,6 4,4 4,3 4,4 4,1 4,0 3,9
P 5 11 18 23 6 31 60 81
K 25 25 31 33 30 60 86 82
pasture c
PK
hayfield d
pH 4,9 6,4 6,7 6,5 4,3 6,2 6,5 6,6
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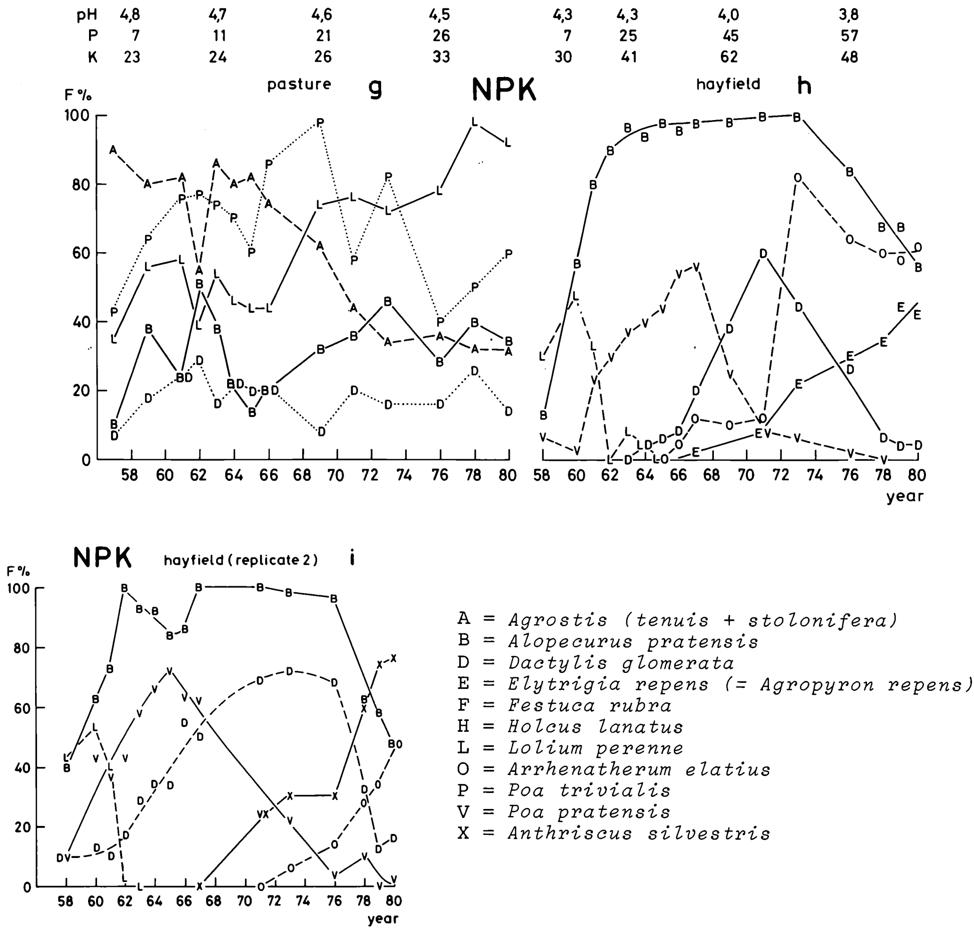

Fig. 6: Frequency percentages of some grass species on different plots of the experiment at Wageningen (see text) plotted against time.
At the top of the diagrams some soil characteristics in the concerning years: pH = pH-KCl, P = mg P_2O_5/100 g soil, K = mg K_2O/100 g soil.

behave entirely different. On one replicate *Arrhenatherum elatius* "explodes" within two years (Fig. 6h), whereas on the other replicate *Anthriscus silvestris* increases dramatically (Fig. 6i). The latest trend is formed by the gradual development of a monoculture of *Elytrigia repens* on one replicate and an increase of *Arrhenatherum* on the other.

5.5 Rise-and-fall curves of some herbs

On some plots (independent of the fertilizer treatment, because it did not occur on the replicate, or it did occur on various treatments) some species show distinct rise-and-fall curves (Fig. 7). The reason why is unknown, although many theories are available.

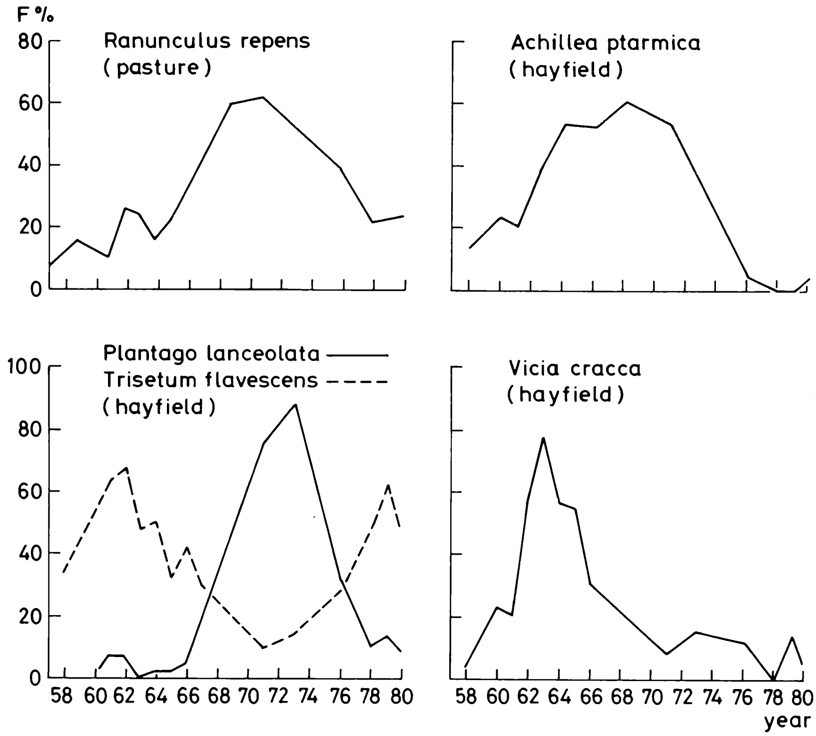

Fig. 7: Rise-and-fall curves of the frequency percentages of some species on different plots of the experiment at Wageningen.

6. Concluding remarks

It is shown that competition experiments with sown or planted mixtures and monocultures are very useful to get more insight in the way populations interfere. This is of importance with regard to:

I. weed control measurements (a monoculture of a crop is desired);

II. mixed cropping (simultaneously grown crops are supposed to exploit the space more efficient)

III. the vegetation in which many populations are growing together.

In particular with annuals dynamic simulation of competition effects by sowing spacing experiments with the species grown in monocultures and harvested at intervals, opens new perspectives in the study of weed control.

The advantage of mixed cropping, if this should be the case, is most conveniently demonstrated by replacement series. By calculating the RYT a measure is obtained for niche differentiaion, which may cause a higher production of the mixture.

The dynamics of populations in old perennial communities is of a very complex nature. The examples presented have shown that in addition to very rapid fluctuations (from year to year), long lasting fluctuations (about 10 years) and very slow trends (over 20 years) may occur in grassland communities. For management of the vegetation it is important to know whether these fluctuations and trends are due to cyclic processes or to permanent changes. To gain insight on this aspect, it is necessary to make observations on, e.g. periodicity in the extent of flowering, seed production, germination and establishment, mortality etc. Besides these endogenous cyclic processes, of course, external cyclic processes may affect the populations, like diseases and pests, fluctuations in the amount of litter, etc. When these processes are better understood permanent changes can be distinguished and counter measures may be taken.

I would like to thank Mr. J. Engelsman for the excellent drawings.

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