J. P. van den Bergh

Institute for Biological and Chemical Research
on Field Crops and Herbage

An analysis of yields of grasses in mixed and pure stands

1968 Centre for Agricultural Publishing and Documentation

Wageningen

The author was awarded the degree of Doctor of Agricultural Sciences, Agricultural University, Wageningen, The Netherlands, on a thesis with the same title and contents.

Acknowledgment

This research was carried out at the Institute for Biological and Chemical Research on Field Crops and Herbage (IBS) Wageningen. The directors, Ir J. Wind and his successor, Prof. Dr Ir G. J. Vervelde, enabled me to do this work by providing all the facilities for my work.

Without Prof. Dr Ir C. T. de Wit's unfailing inspiration and his deep interest, this thesis would never been completed.

Prof. Ir M. L. 't Hart became involved only in the last stages of this work. He has much improved the agricultural aspect of this thesis.

Mr W. Th. Elberse assisted with great intelligence in carrying out the experiments.

Much admiration is due for the diligence of the staff of the Laboratory of Botanical Grassland Research of IBS, when it is realized that thousands of samples were analysed by them.

I also feel obliged to Miss A. H. van Rossem who checked the English text, to Mr G. Beekhof who made the many drawings and to PUDOC for the final layout of the thesis.

Contents

1 Introduction

Farm grasslands may be divided into two groups: old permanent grasslands and sown leys. The grasslands of the first group are usually characterized by a greater number of plant species. These species interfere with each other, which may result in one species reducing another species or even crowding it out. The botanical composition may therefore be considered the resultant of the competitive abilities of the individual species.

The correlative ecological work of de Vries and his school has shown that there is a close correlation between the botanical composition of grassland and environment, which implies that the competitive ability of species is specifically influenced by the environment, in other words the environment is reflected in the botanical composition (Kruijne, de Vries & Mooi, 1967). Botanical grassland survey has turned this to good account; in addition to drawing up a botanical inventory, grassland survey can indicate what complex of factors is limiting optimum grassland management.

Evidently, a quantitative assessment of the influence of a single factor from correlative ecological data only, is impossible. Yet this assessment is essential for a better understanding of the relation between vegetation and environment. If it is planned to change the environment, the effect of this change on the production and composition of the grassland must be known. But our understanding of the manner and the extent to which the single growth factors affect quantity and quality of a grass crop is very limited. In the intensification of grassland management, account should be taken of the effect of high rates of nitrogen on the sward and a greater number of harvests per year. Here too our understanding shows imperfections.

Field investigations on causal ecological relations are very difficult, because environment is changing continuously as a result of weather conditions and seasonal changes. As a consequence the botanical composition also changes continuously, even though the edaphic and anthropogenic effects remain clearly recognizable. In view of the above-mentioned, experiments under controlled conditions should be taken in investigating the causal relations between vegetation and environment.

Grasslands in the second group have developed from sown seed. Here it is possible to choose the species and the ratio between the seed quantities of the species. But this method cannot control the botanical composition of the crop. Already from the very beginning, the mass proportions of the species are affected by environment and competitive interference. The phenomena which occur during the period of emergence, seedling establishment and growth of the first cut will not be discussed in detail, although in treating the effect of pH on botanical composition (section 5.5), some attention will be paid to this aspect. For a detailed analysis of the crop during this period see Baeumer & de Wit (1968).

Often one species will become so dominant that one wonders why a mixture was sown. In addition it is uncertain whether a mixture gives higher dry-matter yields than a monoculture. The specific response of the various species to ever-changing seasonal and climatic conditions is often supposed to ensure an optimum production. But the idea that a mixture of species can exploit the environment better than a monoculture, is not based on experimental results.

For permanent grassland our understanding of the causal relations between botanical composition and single environmental factors should be deepened and for leys the problem should be solved whether a mixture or a monoculture should be preferred.

Based on experiments with oats and barley sown in mixture (van Dobben, 1956), de Wit (1960) developed a model, giving a quantitative description of competition. De Wit & van den Bergh (1965) showed that competition between repeatedly cut perennial grasses in pot experiments under controlled conditions can also be described by this model.

The results of competition experiments with perennial grass species under controlled conditions will be compared with those under field conditions. After this, some competition experiments in which growth-limiting factors occur are discussed. Finally, there is a detailed discussion about the problem whether the result of competition may be deduced from monocultures and whether a mixed culture is to be preferred to a monoculture.

2 Theoretical considerations

To measure competition the performance of a species in one situation should be compared with the performance of the same species in another situation and with the performance of other species. Comparing the performance of one species in situations in which growth took place during the same period, measures like above ground yield, nitrogen uptake, number of tillers, leaf area or carbohydrate reserves may be used, agreeing intuitively that there is twice as much of a species if the yield is twice as large. Because of the high linear correlation between yield measures, it is often immaterial which measure is used for comparison.

However, such a simple approach fails when the species is growing during different time periods: 50 grammes of dry matter of a species harvested after a growing period of 20 days is qualitatively different from 50 grammes of dry matter of the same species harvested after 40 days. Likewise it is impossible to compare the performance of different species in terms of absolute yields: 50 grammes of perennial ryegrass is something completely different from 50 grammes of white clover.

2.1 Relative yield

The difficulty mentioned above may be met by growing the species in mixture as well as in monoculture and comparing their performances on the basis of relative yield, which is defined by

$$r = O/M$$

in which O is the yield of the species in mixture and M the yield of the species in monoculture, grown under the same conditions, except for the competitive situation.

The justification of this procedure lies in the observation that species in a mixture often exclude each other, i.e. the sum of the relative yields of the species or the relative yield total,

$$\mathrm{RYT} = r_a + r_b = O_a/M_a + O_b/M_b, \quad (1)$$

is equal to 1. This is shown in fig. 1, where the observational points, presenting the relation between the yields of the second harvest of perennial ryegrass (L) and sweet vernal grass (A) in various mixtures of the same pot experiment, are scattered around a straight line.

When Harper (1961) stated that "If we neglect for the moment species which reproduce vegetatively and confine attention to those whose density is determined by the number of successful establishments from seed, we eliminate one of the most confusing factors in an ecological analysis", he did not realize that the number of seeds is a yield measure of the same catagory as any other. Just as it is impossible to compare grammes of vegetative dry material of different species, it is impossible to compare numbers of seeds of different species: in both cases reference has to be made to some standard which enables the calculation of a dimensionless measure.

2.2 Relatieve yield total equal to 1

Relative yields enable the relative replacement rate of species a to be defined with respect to species b at the nth harvest with respect to the mth harvest by

$$^{nm}\rho_{ab} = \frac{^{n}r_a / ^{m}r_a}{^{n}r_b / ^{m}r_b} \quad . \tag{2}$$

The species neither gain or loose in the mixture when ϱ is equal to 1. If the nth harvest is later than the mth harvest, species a gains when ϱ is greater than 1 and loses when ϱ is smaller than 1. The relative replacement rate characterizes the competitive interference irrespective of the variable effects of changing growing conditions on the yield of the species in monoculture.

Provided RYT = 1, it follows from equation (1) and (2) that the relative yields at the nth harvest depend on those at the mth harvest according to

$$^{n}r_a = \frac{^{nm}\rho_{ab}\ ^{m}r_a}{^{nm}\rho_{ab}\ ^{m}r_a + ^{m}r_b} \quad \text{and} \quad ^{n}r_b = \frac{^{m}r_b}{^{nm}\rho_{ab}\ ^{m}r_a + ^{m}r_b} \quad . \tag{3}$$

Instead of the relative yields at the mth harvest, the relative planting frequencies or the relative seed rates may be substituted, provided the experiment is set out as a replacement series, i.e. the sum of the relative planting or seed rates is put at 1.

Fig. 2a gives the results of the pot experiment with perennial ryegrass (L) and sweet vernal grass (A). The relative yields of vernal grass (r_A) or ryegrass ($1\text{-}r_A$) at the 2nd harvest are plotted horizontally. These are obtained by the adjustment procedure presented in fig. 1 and described in section 2.5, supposing the relative yield total to be equal to 1. The yields at the 6th harvest are plotted vertically. The curves are drawn according to equation (3). Because the observations are in agreement with these curves, ϱ is independent of the composition of the mixture, which is proportional to the relative yields (fig. 1). Fig. 2b, representing the relative yields, shows that at the 6th harvest RYT is equal to 1 as well.

Analysis of many experiments discussed by de Wit (1960), de Wit & van den Bergh (1965), de Wit, Tow & Ennik (1966), show that the general rule is that when RYT equals 1, ϱ is independent of the composition of the mixture and when ϱ is independent of the compostion of the mixture, RYT equals 1.

2.3 Relative yield total deviating from 1

Of course it has to be verified whether the simple situation as described above is actually present in the experiments under consideration. This is done in the following way. First ${}^{nm}\varrho_{ab}$ is replaced by ${}^{nm}k_{ab}$ in the first equation (3) and by ${}^{nm}k_{ba}$ in the second equation (3):

$$ {}^{n}r_a = \frac{{}^{nm}k_{ab}\ {}^{m}r_a}{{}^{nm}k_{ab}\ {}^{m}r_a + {}^{m}r_b} \quad \text{and} \quad {}^{n}r_b = \frac{{}^{nm}k_{ba}\ {}^{m}r_b}{{}^{nm}k_{ba}\ {}^{m}r_b + {}^{m}r_a} . \qquad (4) $$

The constants k are called the relative crowding coefficients (de Wit, 1960).

The value of one of the constants k may be obtained by adjustment to the yields of one of the species in the mixture and the value of the other k by adjustment to the yields of the other species in the mixture. The equations show that if the product of these k values is equal to 1, RYT will equal 1 too.

In the practice the product of the k values very seldom is exactly 1, due to experimental errors or possible systematic deviations. But a straightforward estimate of the confidence interval of the estimate of the product is not feasible because the two sets of yield data on which the estimates of k are based are not independent: except for monocultures, yields are obtained two by two from the same pot or field.

The product of the k values or RYT is always close to 1 for the first yield after planting, provided planting has been carried out in a replacement series. From that moment RYT may increase or decrease systematically but when this happens, equation (4) with constant k values can no longer be used, as was shown by de Wit, Tow & Ennik (1966) for mixtures of legumes and grasses. This type of interference has not been found in mixtures of grasses and therefore will not be discussed.

However, with grasses the situation occurs in which due to experimental errors or systematic deviations, the product of the k values deviates to some extent from 1, although adjustment of the observational data with equation (4) is still acceptable. Now the question arises what practical importance has to be attached to such deviations.

When equation (4) with constant values for k is used to adjust experimental data and when the product of the k values simultaneously deviates slightly from 1, the extreme value of RYT may be calculated by adding equations (4) and taking the first derivate with respect to r_a:

$$ \frac{d(\text{RYT})}{dr_a} = \frac{k_{ab}}{(k_{ab}r_a + r_b)^2} - \frac{k_{ba}}{(k_{ba}r_b + r_a)^2} . $$

RYT is at its maximum or minimum, if this differential quotient is equal to 0, i.e. if

$$\left(\frac{k_{ab} r_a + r_b}{k_{ba} r_b + r_a}\right)^2 = \frac{k_{ab}}{k_{ba}} . \tag{5}$$

The value of r_a at which this extreme value of RYT is obtained may be calculated by substituting $(1 - r_a)$ for r_b and solving r_a by

$$(r_a | \text{RYT extreme}) = \frac{k_{ba}(\sqrt{k_{ab} k_{ba}} - 1)}{(\sqrt{k_{ab} k_{ba}} + k_{ba})(\sqrt{k_{ab} k_{ba}} - 1)} . \tag{6}$$

The value of $(r_a | \text{RYT extreme})$ is undeterminate for $k_{ab} \times k_{ba} = 1$, RYT being equal to 1 throughout. If $k_{ab} \times k_{ba} \neq 1$,

$$(r_a | \text{RYT extreme}) = \frac{k_{ba}}{\sqrt{k_{ab} k_{ba}} + k_{ba}} . \tag{7}$$

Combining equations (4) and (7) gives

$$\text{RYT extreme} = 2 \, \frac{k_{ab} k_{ba} - \sqrt{k_{ab} k_{ba}}}{k_{ab} k_{ba} - 1} . \tag{8}$$

The maximum or minimum value of RYT therefore only depends on the product of the k values as is presented in graphical form in fig. 3.

For very high values of $k_{ab} \times k_{ba}$, RYT $= 2$. In this case the species do not interfere at all. Furthermore it is understood that with equal yields of the monocultures the advantage of the mixture is at most 10, 20, 30 % ... for RYTextreme $= 1.1, 1.2, 1.3 \ldots$ The extreme value of RYT therefore is a measure for the possible advantage of a mixture over the monoculture. The value of r_a at which this maximum advantage may be attained is calculated with equation (7). Only when the monocultures and the k values of both species are the same will the 1 : 1 mixture be most profitable throughout the experiment.

2.4 The maximum yielding mixture

The situation becomes more complicated in the usual case where the relative crowding coefficients and the yields of the monocultures are not the same. To analyse this situation the extreme value of the yield of mixture $(O_a + O_b)$ is compared with the yield of the higher yielding monoculture.

The sum $(O_a + O_b)$ is extreme when the derivate

$$\frac{d(O_a + O_b)}{d r_a} = 0 ,$$

or according to equations (1) and (5) when

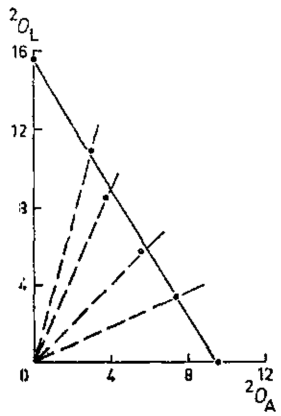

Fig. 1. Dry-matter yields in grammes at the 2nd harvest of *Lolium perenne* (^2O_L) and *Anthoxanthum odoratum* (^2O_A) in mixture and monoculture plotted against each other. The relative yields can be read on the intersections of the dotted lines and the line through the observations.

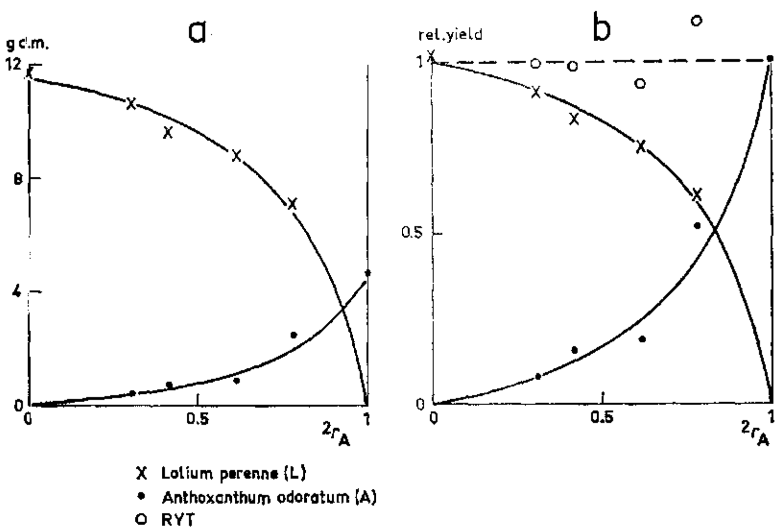

Fig. 2. Replacement diagrams of the same competition experiment as in fig. 1. The relative yields of *Anthoxanthum* at the 2nd harvest (^2r_A) horizontally and the yields (a) or the relative yields (b) of *Lolium* and *Anthoxanthum* at the 6th harvest vertically. The pots were cut every 3 weeks.

$$\left(\frac{k_{ab}\, r_a + r_b}{k_{ba}\, r_b + r_a}\right)^2 = \frac{k_{ab} M_a}{k_{ba} M_b} . \qquad (9)$$

The value of r_a at which this extreme is attained is equal to

$$(r_a | (O_a + O_b) \text{extreme}) = \frac{k_{ba}\sqrt{k_{ab} M_a} - \sqrt{k_{ba} M_b}}{(k_{ab}-1)\sqrt{k_{ba} M_b} + (k_{ba}-1)\sqrt{k_{ab} M_a}} . \qquad (10)$$

If the maximum value of (O_a + O_b) is attained with the monoculture of the higher yielding species a, i.e. at r_a = 1, it follows from equation (10) that

$$k_{ab} \times k_{ba} = M_a / M_b . \qquad (11)$$

Hence, only when $k_{ab} \times k_{ba}$ is larger than M_a/M_b, (O_a + O_b) maximum will be larger than the higher yielding monoculture M_a. In other words, for two species which differ by a factor 2 in the yield of their monocultures, mixtures have an advantage only, if the product of their relative crowding coefficients is greater than 2 and this only in the transient situation in which the r_a proper is achieved.

The maximum value of (O_a + O_b) is obtained by substituting r_a of equation (10) in equation (4),

$$(O_a + O_b)\max = \frac{k_{ab}\, k_{ba}(M_a + M_b) - 2\sqrt{k_{ab}\, k_{ba} M_a\, M_b}}{k_{ab}\, k_{ba} - 1} , \qquad (12)$$

and the maximum advantage of the mixture, only achieved with the value proper of r_a, is equal to

$$\frac{(O_a + O_b)\max}{M_a} = \frac{k_{ab}\, k_{ba}(1 + M_b\, M_a^{-1}) - 2\sqrt{k_{ab}\, k_{ba}\, M_b\, M_a^{-1}}}{k_{ab}\, k_{ba} - 1} . \qquad (13)$$

Equation (10) shows that the value of r_a at which the maximum yield is obtained depends on the quotient M_a/M_b and on the individual values of k_{ab} and k_{ba}. However, according to equation (12) the maximum yield which is obtained at the combination proper of the species depends on M_a/M_b and the product of the k values, rather than on individual values. This enables the maximum advantage of a mixture to be presented in a graph with the values of M_a/M_b and $k_{ab} \times k_{ba}$ along the axis (fig. 4). The first quadrant is discussed first.

Considering equation (11), it is always advantageous to cultivate the higher yielding monoculture when $k_{ab} \times k_{ba}$ is smaller than M_a/M_b, but for $k_{ab} \times k_{ba}$ larger than M_a/M_b there is a mixture yielding more than the higher yielding monoculture. The limit between these two regions is presented by the 45° line. Thus within the region between the vertical axis and this 45° line, the monoculture of species a always yields more, whereas between the 45° line and the horizontal axis there are mixtures which yield more than the higher yielding monoculture M_a.

The maximum yield is shown by the curves calculated with equation (13) and marked with 1.05, 1.10, 1.20 and so on. Hence, it can be seen that for the case M_a/M_b = 2 and $k_{ab} \times k_{ba}$ = 4, the yield of the mixture may be 1.05 times the

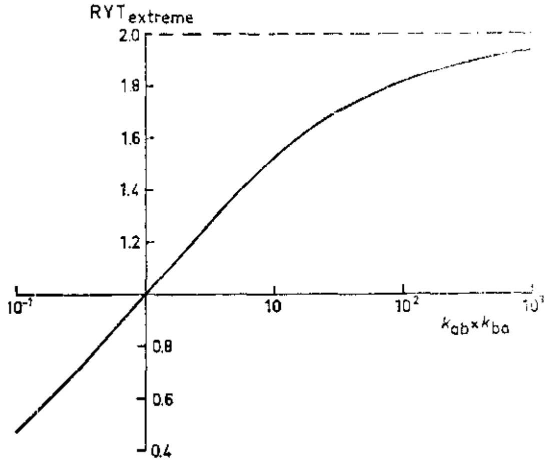

Fig. 3. Relation between the extreme value of the relative yield total and the product of the relative crowding coefficients of species a and b.

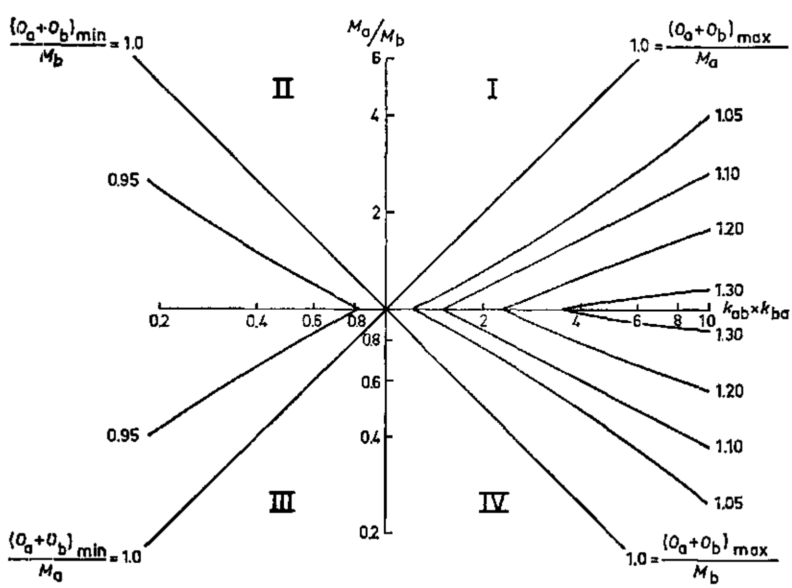

Fig. 4. Relation between the quotient of the yields of monocultures (M_a/M_b) and the product of the relative crowding coefficients ($k_{ab} \times k_{ba}$) at constant quotient values of the extreme value of the yield of the mixture and the higher (quadrant I and IV) or lower (quadrant II and III) yielding monoculture.

higher yielding monoculture. The composition of this mixture also depends on the individual values of k. For $k_{ab} = 1$ and $k_{ba} = 4$, the value of r_a for the maximum yielding mixture is equal to 0.86 and for $k_{ab} = 4$ and $k_{ba} = 1$ this value is equal to 0.61 (equation 10). This has important consequences. For instance, planting is carried out in such a way that $r_a = 0.61$ at the first harvest, because it is known that k_{ab} and k_{ba} will be equal to 4 and 1 at the second harvest. According to equation (13) the yield of the mixture at the second harvest is 5 % higher than of the higher yielding monoculture, M_a/M_b being 2. But it is quite possible that at the third harvest k_{ab} and k_{ba} both equal 2. The mixture yields instead of 5 % only 3 % more, as may be easily verified with equation (4). Moreover, if M_a is not 2 times M_b but 2.5 times M_b, the mixture yields 5 % less than the higher yielding monoculture.

This example shows that, although a somewhat higher yield may be achieved with a proper choice of the relative planting frequencies, in practice this is difficult to achieve. Only if M_a/M_b and $k_{ab} \times k_{ba}$ have such values that the maximum expected yield of the mixture is considerably higher than the higher yielding monoculture (for instance $M_a/M_b = 1.5$ and $k_{ab} \times k_{ba} = 6$), it may be worthwhile to gamble on the mixture. This is for instance so in fig. 5b where the values of M_p/M_g and $k_{pg} \times k_{gp}$ of *Panicum* (grass) and *Glycine* (legume) with *Rhizobium* and N fertilization are shown for successive cuts. However, in these cases situations evolve in which the relative crowding coefficients depend on the composition of the mixture, so that an equilibrium may be approached (de Wit, Tow & Ennik, 1966). These situations are of small importance with grass-legume mixtures in the absence of *Rhizobium* (fig. 5a) or with grass-grass mixtures. With such mixtures the product of the k values is so close to 1, while they change so unsystematically, that the only right choice is cultivation of the higher yielding species.

The situation in the 4th quadrant only differs from that in the 1st quadrant by M_b being larger than M_a. The other quadrants represent the situation in which the product of the k values is smaller than one, so that the lowest yielding mixture may yield less than the lower yielding monoculture. This needs no further explanation.

2.5 Treatment of the results

As an example, the yield data will be treated of a pot experiment with perennial ryegrass (L) and sweet vernal grass (A). In fig. 1 the yields of the single species at the 2nd harvest are plotted on the axis. Each point concerns the yields of one pot: the yield of the monoculture of ryegrass on the vertical and the yield of the monoculture of vernal grass on the horizontal axis and the yields of the mixtures intermediate. The observations are scattered around a straight line, so that the RYT values calculated from the single observations do not differ much from 1. The relative yields are calculated as follows:

1. Reading the yields O at the intersections of the solid line through the observations and the broken lines through the origin and each of the observations

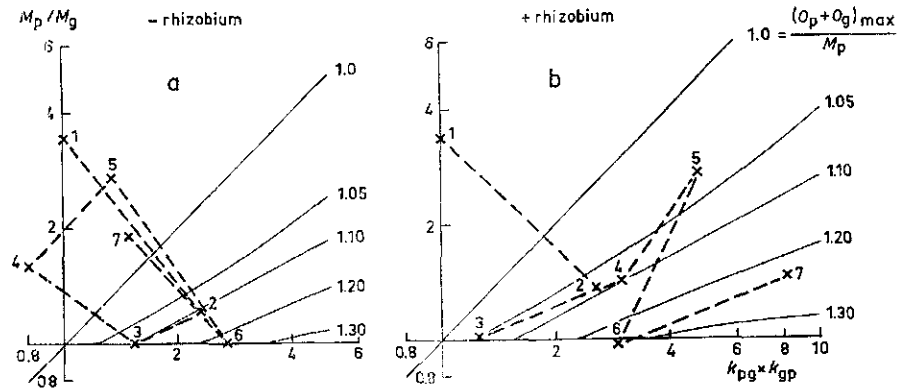

Fig. 5. Quotient of the yields of the monocultures of *Panicum maximum* (p) and *Glycine javanica* (g) plotted against the product of their relative crowding coefficients at 7 successive harvests. Treatments: a) with nitrogen and without *Rhizobium;* b) with nitrogen and with *Rhizobium*. Data from de Wit, Tow & Ennik (1966).

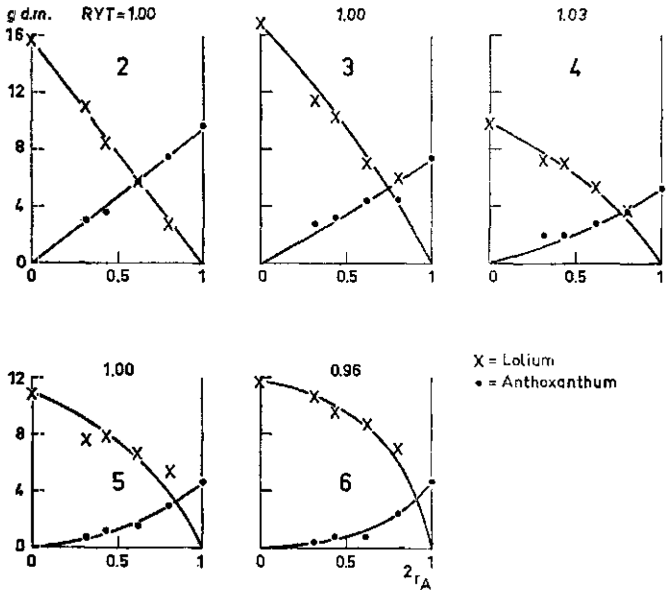

Fig. 6. Replacement diagrams with the calculated relative yields of *Anthoxanthum* at the 2nd harvest (see fig. 1) plotted horizontally and the yields of *Lolium* and *Anthoxanthum* at 5 successive cuts plotted vertically.

2. Reading the yields M at the intersections of the solid line and both axes
3. Calculating the relative yields at the 2nd harvest (reference) from these values.

The choice of the reference harvest is rather arbitrary. In general a harvest is chosen with smallest scattering of observations around a straight line (as in fig. 1).

The next step is plotting the yields of the successive harvests against the relative yields of the reference harvest in replacement diagrams (fig. 6). The k values are obtained by

1. Drawing free-hand curves through the observations which are of a shape dictated by equation (4)
2. Calculating by equation (4) the k values from the smoothed values of the yields of the monocultures and of the mixture at a relative yield of 0.5 of the reference
3. Drawing curves with the calculated k values
4. Verifying whether the curves are in agreement with observations
5. If not, making another estimate of the k values.

As stated in section 2.4, the extreme value of the relative yield total of the various harvests is not achieved at the same relative yield of the reference harvest. To get an idea about the height of the RYT values of an arbitrary mixture during the experiment, RYT is calculated from the smoothed yields of the mixture with $r_A = 0.5$ at the reference harvest. This value is indicated at the top of each replacement diagram.

The relative replacement rates of the successive harvests with respect to the reference harvest ${}^{n2}\varrho_{LA}$ may be calculated also for the mixture with $r_A = 0.5$ at the reference harvest by dividing the relative yields by each other (equation 2). When RYT is about equal to 1, this ϱ value also holds for all other mixtures.

When the ϱ values of successive harvests are plotted on a logarithmic scale against time (fig. 7), course lines are obtained (de Wit & van den Bergh, 1965). The angle of the course line with the horizontal is a measure for the rate at which ryegrass replaced vernal grass. A horizontal course line would indicate that the species match and a downward sloping course line that vernal grass replaced ryegrass. It follows from equation (2) that the same course line may be obtained, when the quotient of the relative yields of the species at successive harvests is plotted in the same graph, this quotient at the reference harvest being equal to 1. Parallel course lines are obtained by plotting the quotients of the relative yields for other relative yields at the reference harvest, ϱ being independent of the composition of the mixture.

When the RYT value of each cut is about 1, this does not necessarily mean that the sum of the yields of all cuts of a mixture may not exceed that of the monocultures. This is illustrated schematically in fig. 8a: the RYT values for the total dry-matter production are greater than 1. However, the RYT values concerning the total dry-matter production for the example in fig. 8b are roughly 1, in spite of considerable changes in the yields for the monocultures. It has been already mentioned here that with all the experiments discussed in this paper, the first example never occurred.

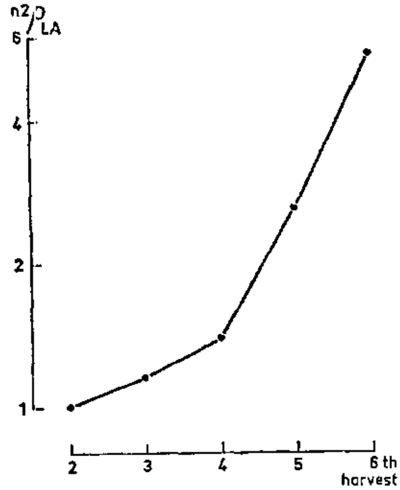

Fig. 7. Relative replacement rates with respect to the 2nd harvest presented as a course line for *Lolium* (L) with respect to *Anthoxanthum* (A) for 5 successive harvests.

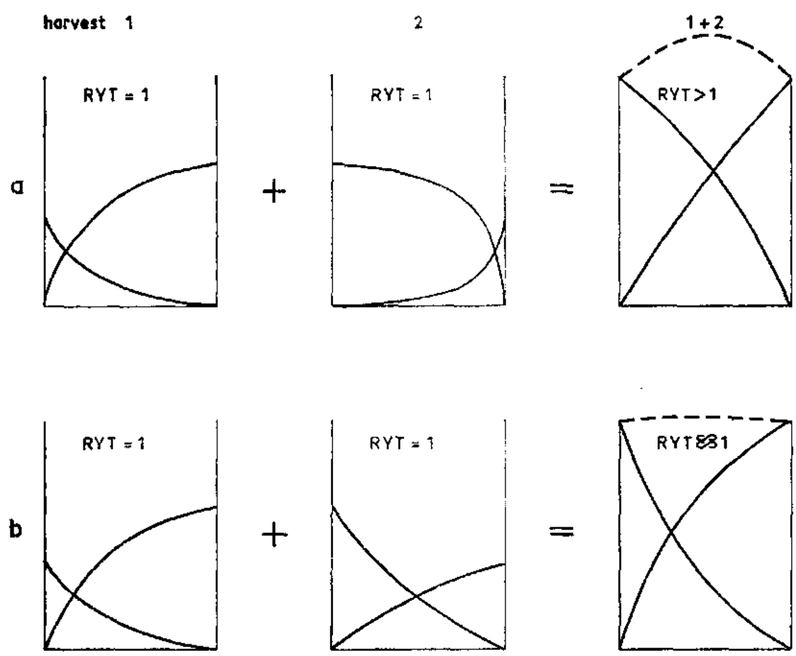

Fig. 8. Scheme of replacement diagrams of dry-matter yields for two successive cuts and of total dry-matter yields.

3 Experimental procedure

Results of outdoor experiments, to be considered in this paper, were derived from literature. The relevant aspects of the experimental procedure will be discussed together with the results.

The indoor experiments were carried out in growth rooms and greenhouses at about 20°C and with a daylength of 17 hours, which prevented flowering. Hence, all experiments were carried out with plants in their vegetative stage. The artificial light in the growth rooms was provided by 400 watt high-pressure mercury-vapour lamps (Philips HPL) giving a light intensity of 5×10^4 ergs cm^{-2} $sec.^{-1}$ at the surface of the pots.

Most of the experiments were started by planting single tillers, obtained from clones, in pots with a diameter of 20 cm and containing about 8 kg of sandy soil with a humus content of 4.5 % and a pH (water) of 5.2.

Each experimental series consisted of pots planted with mixtures of two species or with monocultures. The relative plant frequency was defined by the ratio between the number of planted tillers of a species in a mixture divided by the number of planted tillers in the monoculture. Planting was according to the replacement principle, i.e. the sum of the relative plant frequencies in the mixture is equal to 1. In most experiments the number of tillers in the monoculture was kept the same for both species. In some experiments the species were sown, but this was also done in a replacement series.

Except where stated otherwise, the plants were treated in the following way:

1. They were cut at 3-4 week intervals at a height of 5 cm
2. Sufficient nutrients were applied by watering the pots with a Hoagland solution after cutting
3. Moisture content was kept at about 18 % of the oven-dry weight of the soil by weighing daily
4. Overhanging of the aerial plant parts outside the area of the pots was prevented by placing PVC rings 8 cm high and 20 cm diameter on the pots, one on top of the other according to need.

The yield of the single pots were separated into species, oven-dried, weighed and if necessary analysed. Mineral contents were determined in the laboratory of the Institute.

4 Basic experiments

In this chapter it will be shown that the model used in chapter 2 to describe competition between plants, may be applied to competition experiments with grasses under controlled conditions, outdoors in boxes and in the field.

4.1 In growth rooms

To study the effect of spacing on the relative replacement rate (ϱ), monocultures and mixtures of ryegrass and sweet vernal grass were planted at densities of 12, 24 and 48 tillers per pot. It has already been shown that ϱ is independent of the planting ratio of the grass species in the mixture (section 2.2); it will therefore suffice to study competition with mixtures of 6 ryegrass tillers (L) + 6 vernal grass tillers (A), 12 L + 12 A and 24 L + 24 A, and the monocultures 12 L, 24 L, 48 L and 12 A, 24 A and 48 A. The pots were 8 times harvested at intervals of 3 weeks.

In fig. 9 the yields of the 5th harvest of ryegrass and vernal grass are plotted against each other. At all densities the observations are scattered around a straight line, which means that the species exclude each other. Taking this harvest as a reference, the 8 successive harvests are presented in replacement diagrams in fig. 10. The *k* values of the curves in all these diagrams are reciprocal, so the species excluded each other also during the whole experimental period. These diagrams show that at the time of the 8th harvest vernal grass is almost replaced by ryegrass at all densities.

The relative replacement rates with respect to the 5th harvest were obtained by calculating the quotient of the relative yields of each harvest of the mixture with $r_A = 0.5$ at the 5th harvest (section 2.5), and plotted as course lines in fig. 11. It has already been mentioned that the slope of these lines presents the rate of replacement.

The high degree of parallelism in these course lines at the 3 densities implies that density hardly affects the rate of replacement and the final result of competition. It should be realized that with very steep course lines, the difference in vertical direction means only some days retardation or acceleration in the process of replacement.

Before the 3rd cut, vernal grass replaces ryegrass to a small extent. During establishment, when the monocultures have not yet achieved their maximum production (fig. 10), vernal grass obviously developed somewhat more rapidly than

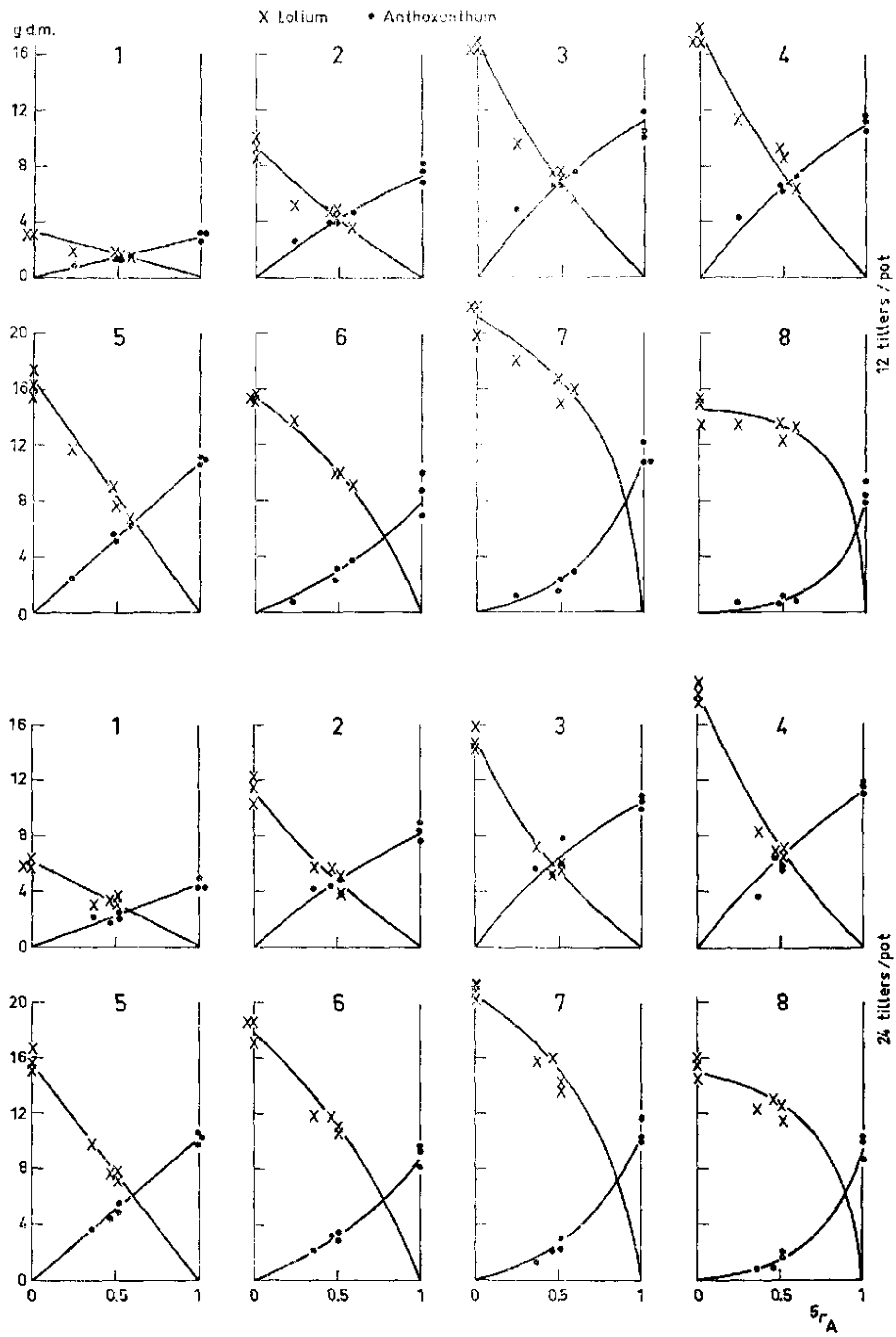

Fig. 10. Continued →

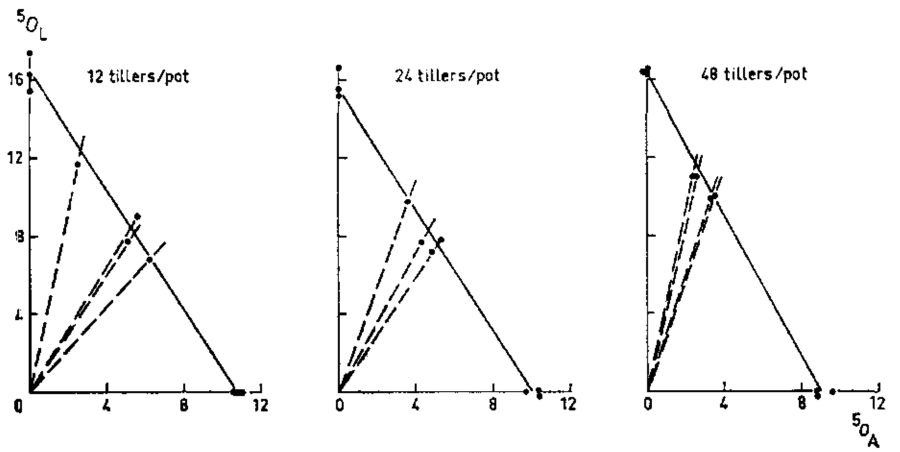

Fig. 9. Dry-matter yields in grammes at the 5th harvest of a pot experiment with *Lolium* (^5O_L) and *Anthoxanthum* (^5O_A) in mixture and monoculture at 3 densities plotted against each other.

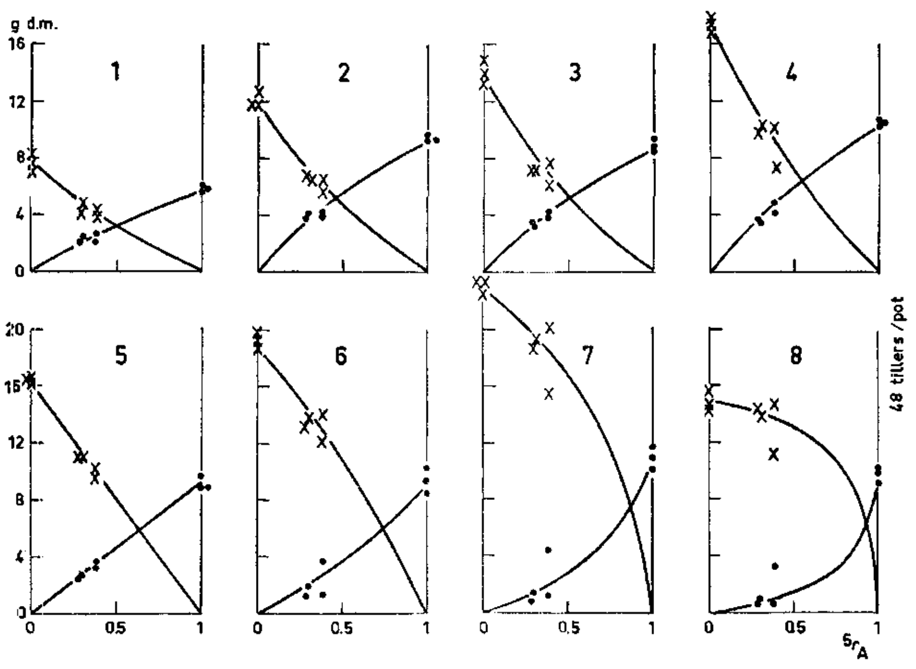

Fig. 10. Replacement diagrams with the calculated relative yields of *Anthoxanthum* at the 5th harvest (see fig. 9) on the horizontal axis and the yields of 8 successive harvests (1-8) on the vertical axis (continued on opposite page).

ryegrass. However, with 48 tillers per pot, vernal grass hardly gains on ryegrass. In other experiments with high densities ryegrass started immediately to replace vernal grass. Probably lack of space prevented the expansion of vernal grass. In other words, as long as the yields increase with increasing planting density, as in the first two cuts (fig. 10), density will influence the value of ϱ. This effect will disappear in the course of time.

After the 3rd cut ryegrass replaces vernal grass at an increasing rate and the number of living tillers of vernal grass in the mixtures decreases steadily. After the 8th harvest the last living tillers also die (de Wit & van den Bergh, 1965). In this case vernal grass was entirely crowded out by ryegrass. Other experiments under controlled conditions in which the species remain associated, are discussed in section 4.4.

To compare the total yields of the mixtures and monocultures during a longer period, the RYT values concerning the total dry-matter production during the 8 periods of 3 weeks have been calculated. These values proved to be about 1 (fig. 12), which means that the mixtures do not have the advantage of the highest yielding monoculture, corresponding with the example given in fig. 8b.

4.2 Outdoors in boxes

Under controlled conditions without generative development, grass species exclude each other (section 4.1). However, it remains to be shown whether this also occurs under natural conditions with generative development and the difference in response between species to the ever-changing conditions.

England (1965) studied competition between an early and a late flowering variety of perennial ryegrass and two varieties of cocksfoot in the open air in boxes (43.2 × 43.2 cm and 9.5 cm deep) at densities of 16 and 64 seedlings per box. In the year of planting, the crop remained vegetative, but in the second year normal generative development took place. A series of combinations of 2 varieties consisted of mixtures and monocultures in duplicate; altogether 6 boxes. England only reported the dry-matter yields in the second year, during which the crop was harvested 5 times.

With the 4th harvest of the second year as a reference harvest the replacement diagrams of the varieties Ayrshire perennial ryegrass (A) and Daeno II cocksfoot (C) at both densities are shown in fig. 13. The RYT values are about 1. This means that these varieties indeed excluded each other during the entire growing season. From fig. 13 it may be calculated that the average yield of the monocultures of ryegrass on 21 July was 17 % of that on the preceding cutting date, 18 June, whereas the monoculture of cocksfoot only decreased to 34 % in this period. In spite of these distinct specific responses on seasonal or climatic changes, the RYT values concerning the total dry-matter production during the year proved to be 1. Not only indoors (section 4.1) but also in this outdoor experiment a mixture had no advantage. This conclusion holds for all other combinations of

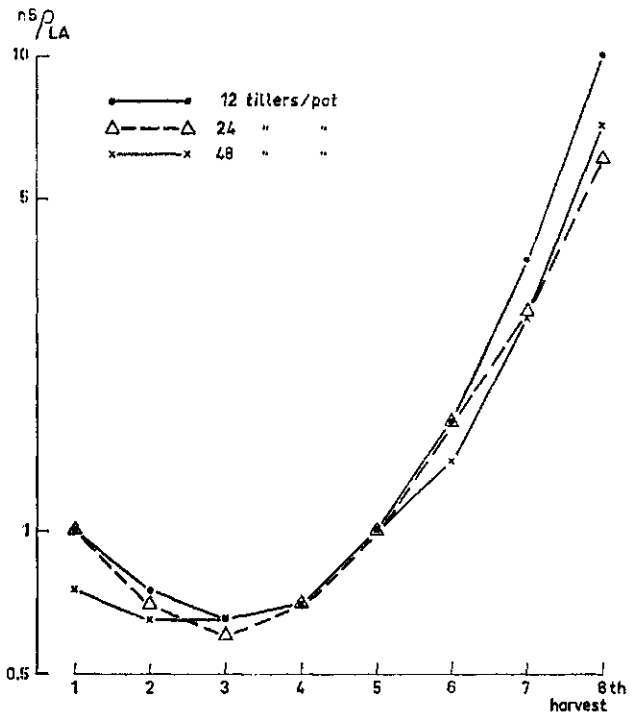

Fig. 11. Relative replacement rates with respect to the 5th harvest presented as course lines for *Lolium* (L) with respect to *Anthoxanthum* (A) at 3 densities for 8 successive harvests (n = 1, 2 . . . 8).

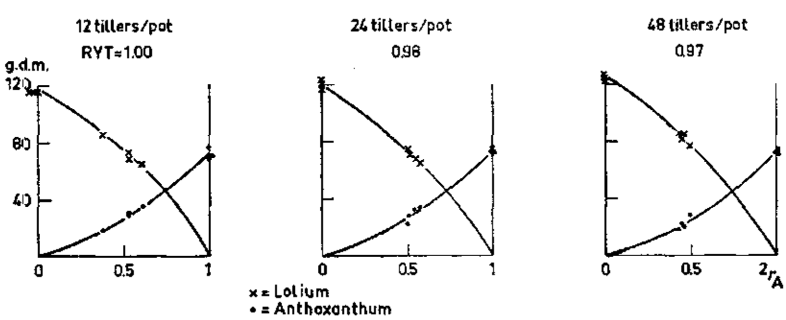

Fig. 12. Total dry-matter production of *Lolium* and *Anthoxanthum* for eight periods of 3 weeks plotted against the relative yields of *Anthoxanthum* at the 2nd harvest.

these 4 varieties.

From May to August the curves of cocksfoot variety C show an increasingly upward trend and those of ryegrass variety A a downward one, hence cocksfoot gains. This process is much better illustrated by the course lines in fig. 14. Ryegrass variety A is replaced at a much higher rate by cocksfoot variety C (fig. 14a) than ryegrass variety B (fig. 14b). From the parallelism of the course lines concerning the same combinations of varieties, but different densities, it may be concluded that density did not affect competition during the 2nd year. The effect of density on competition, if any, already disappeared in the 1st year, the composition of the mixtures at both densities being about the same (compare fig. 13a with 13b).

The course lines of all possible combinations of the four varieties at the highest density are presented in fig. 15 and symbolized by ×———×. If there were no specific interaction of variety A and B, the course line of variety A with respect to variety B could be derived also from the series in which A competes with C and B competes with C, since ${}^{n4}\varrho_{AC}/{}^{n4}\varrho_{BC} = {}^{n4}\varrho_{AB}$. The results are given in fig. 15a by o———o. The same was done by taking variety D as a reference species instead of C. The results are presented by •———•. Thus, 3 course lines for all combinations are presented in fig. 15. The course lines corcerning the same combination are very similar and this proves that the competitive ability of these varieties is independent of their associates.

This independence enables the observations to be treated as replicates. Average ϱ values were obtained by taking logarithmic means of the values at each harvest. These are presented in fig. 16. The slopes of the lines show that ryegrass variety A is by far the least vigorous competitor and cocksfoot variety C the most vigorous, although the difference between the two cocksfoot varieties is very small. Great changes in the mixtures of ryegrass and cocksfoot occur only during the summer months, coinciding with drastic yield reductions in the monocultures of the ryegrass varieties (see also fig. 13). Essential differences in behaviour are not observed at low densities.

It is of great practical importance that the competitive ability is independent of the associates. Firstly experiments with mixtures of more than 2 species will not yield more information than experiments in which one of the species is combined with the other species in bicultures (see also next section). Secondly it is possible now to study competition between two varieties, strains or ecotypes, morphologically the same, by competition experiments between each of the varieties and a third species.

Besides a treatment with the first cut on 2 May discussed above, England included a treatment with a first cut 18 days later on 20 May. Thereafter the time between the cutting dates was gradually diminished.

The influence of the time of the 1st cut on the composition of the mixture is illustrated by the average relative yields in table 1. Only a slight influence, if any, is found when the two varieties of ryegrass (A and B) or the two varieties of cocksfoot (C and D) compete with each other, the relative yields on 2 May and

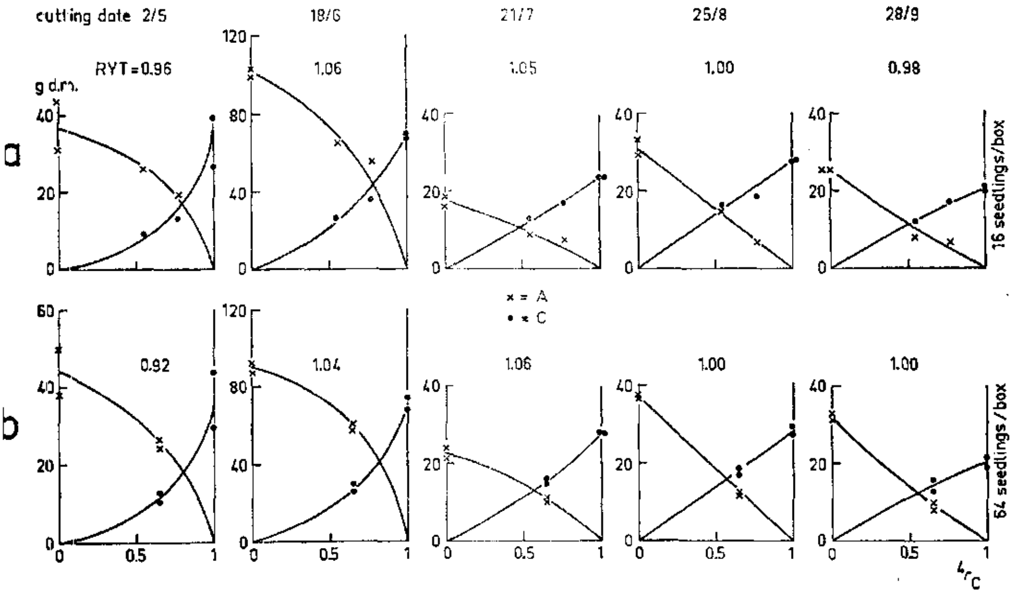

Fig. 13. Replacement diagrams with the calculated relative yields of *Dactylis* var. C at the 4th harvest of the 2nd year at 2 planting densities on the horizontal axis and the yields of *Lolium* var. A and *Dactylis* var. C at 5 successive harvests on the vertical axis.

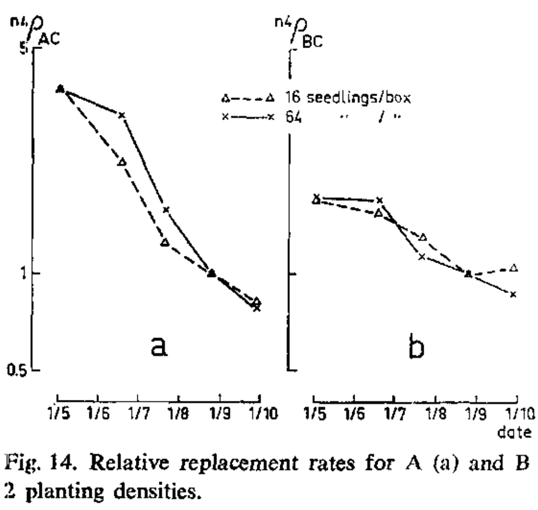

Fig. 14. Relative replacement rates for A (a) and B (b) with respect to C in the 2nd year at 2 planting densities.

Table 1. Average relative yields of the duplicates on 2 May (early cut) and on 20 May (late cut). A and B are ryegrass varieties and C and D are cocksfoot varieties.

cutting date	mixture AB	AC	AD	BC	BD	CD
	r_B	r_C	r_D	r_C	r_D	r_D
2 May	0.46	0.35	0.28	0.37	0.33	0.49
20 May	0.48	0.48	0.44	0.51	0.38	0.48

20 May being almost the same. However, when ryegrass competes with cocksfoot, the relative yields of the cocksfoot strains are always higher on the late cutting date. This means that in competition with ryegrass, cocksfoot profits by the late cut.

The trend in competition after the first cut is shown in fig. 17. The ϱ values of the early-cut group are very close to the course lines of the late-cut treatment, which means that competition with these varieties is independent of the cutting scheme.

4.3 Under field conditions

The experiment described in the previous section was outdoors in boxes. It will now be shown that grasses also exclude each other under field conditions.

Lampeter (1960) studied competition of several grass species on plots of 1 square metre for two years in which the crop was harvested in June and August. The monocultures were replicated 5 times and the mixtures 5 or 10 times. As the data of the single observations could not be obtained the following calculations had to be based on the average yields of 5 plots. In the first year fresh weights and in the second year dry weights were reported only but, assuming proportionality between dry and fresh weights in the monocultures and in the mixtures for each species, this is immaterial because the relative replacement rate is based on relative yields.

Table 2 shows that the RYT values do not in general differ systematically from 1 and that in 43 cases out of 60 the yields of the mixtures are lower than the higher yielding monoculture. These differences are very great, even with RYT values about 1, if the yields of the monocultures differ considerably. At the last harvest, 20 Aug. 1958, with the combinations cocksfoot with tall oatgrass and timothy with meadow grass only RYT values greater than 1 resulted in an advantage of more than 10 % for the mixture over the higher yielding monoculture. But this advantage was neutralized by the lower yields of the mixtures than of monocultures at previous harvests, illustrating the remark in section 2.4 that it is impossible to maintain such a mixture at the most advantageous composition. On the other hand with the combination timothy with meadow grass the value

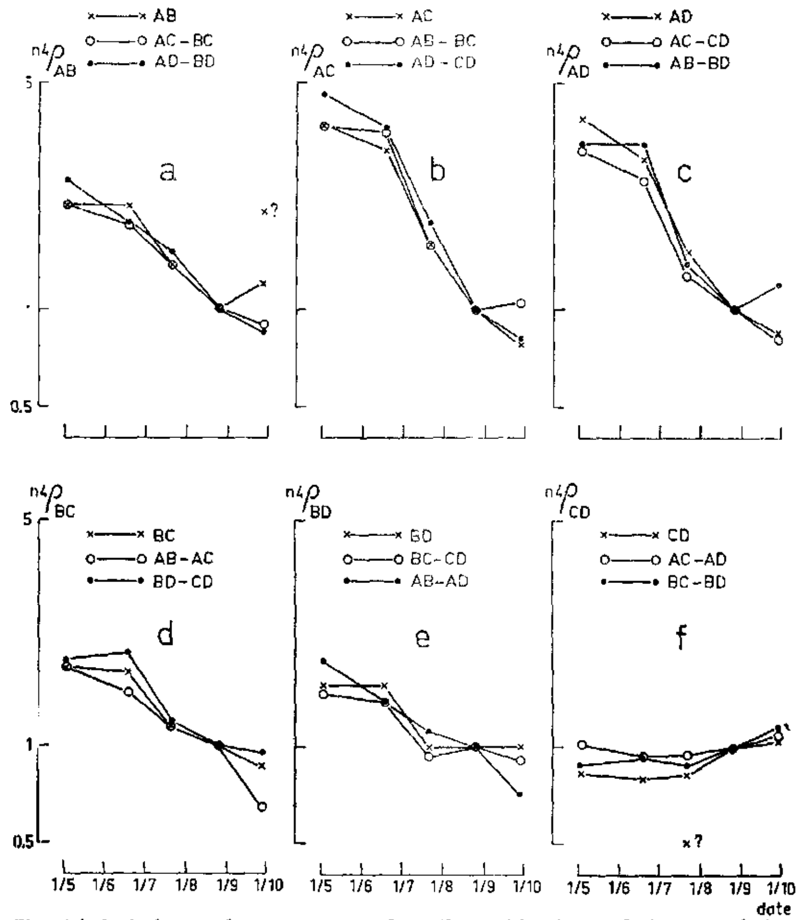

Fig. 15. Relative replacement rates for all combinations of the 4 varieties at high density. Of the two crosses with a ? one replicate is obviously wrong; instead the other replicate is used in constructing the course lines.

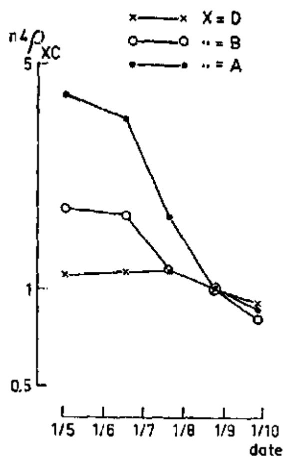

Fig. 16. Average relative replacement rates for 3 varieties with respect to variety C.

Table 2. RYT values and the yield of the mixtures in percentages of the higher yielding monoculture of 15 combinations of 7 grass species on 4 cutting dates. Data of Lampeter (1960). The figures are for mixtures with a relative yield equal to 0.5 at the reference harvest.

	1957				1958			
	13/6		13/8		13/6		20/8	
mixture	RYT	%	RYT	%	RYT	%	RYT	%
D - Ar	1.00	87	1.08	95	1.03	101	1.19	115
Fp	1.00	88	1.02	97	0.89	85	0.90	85
Fr	1.10	97	1.00	97	0.88	85	1.03	95
Ph	0.88	79	1.00	82	1.01	96	1.13	109
Bi	1.06	103	1.14	105	1.00	80	1.10	103
Pp	1.00	66	1.02	91	0.76	74	1.06	102
Ar - Fp	1.12	109	1.04	93	1.00	98	1.05	92
Fr	1.32	104	1.19	97	0.96	91	1.00	97
Ph	1.01	97	1.06	99	1.09	108	1.00	84
Bi	1.06	94	1.00	92	1.08	100	0.96	88
Fp - Fr	1.00	79	0.92	84	0.90	89	1.07	89
Ph	1.00	93	0.93	83	1.06	102	1.11	107
Pp	0.90	41	0.98	62	1.08	96	1.00	98
Fr - Pp	1.00	49	1.13	83	—	—	0.85	75
Ph - Pp	1.00	61	1.16	93	1.13	105	1.21	116

D = *Dactylis glomerata*
Ar = *Arrhenatherum elatius*
Fp = *Festuca pratensis*
Fr = *Festuca rubra*
Ph = *Phleum pratense*
Bi = *Bromus inermis*
Pp = *Poa pratensis*

$(O_{Ph} + O_{Pp})\max/M_{Ph}$ gradually increased with time, as illustrated in fig. 18. A longer experimental period might have shown whether this advantage would continue to increase or would disappear as in fig. 5a.

Although it cannot be proved, it seems reasonable to assume that most deviations of RYT from 1 are due to random variations in yields on these small plots.

Cocksfoot being the only species with which all the other species actually compete, it may serve as a reference species in calculating the result of competition between two other species (section 4.2). In fig. 19 two course lines are given for each combination: the solid course lines have been calculated directly and the broken ones have been calculated with cocksfoot as a reference. Since the yield of some species at the first cut was still very low, the second cut has been taken as reference. The similarity in the course lines proves again (section 4.2) that the results of an experiment, in which the species compete with each other in all possible combinations, do not differ much from those of an experiment in which

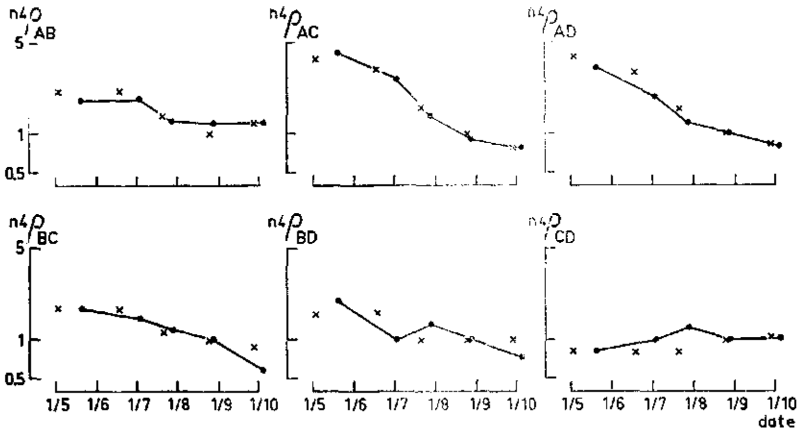

Fig. 17. Course lines for the late-cut treatment. The crosses are ϱ values of the early-cut treatment.

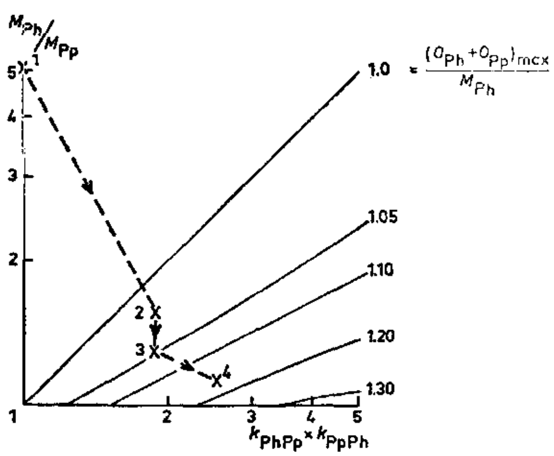

Fig. 18. Quotient of the yields of the monocultures of timothy (Ph) and meadow grass (Pp) plotted against the product of their relative crowding coefficients at 4 successive harvests.

each species competes with one reference species only. If so the number of combinations could be reduced from 21 to 6 and as a reference cocksfoot could be chosen, which is persistent and easy to distinguish from the other species.

The RYT value of the total annual production is about 1. Here again as in sections 4.1 and 4.2, a monoculture of the higher yielding species produces more dry matter per year than a mixture with a lower yielding species.

4.4 Subsisting species

In the examples in the previous sections the species excluded each other and it was shown in section 2.2 that the relative replacement rate is a constant function of the relative yields of the reference harvest. Under constant environmental conditions this will lead to the entire disappearance of one of the species. Generally plants in pot cultures did not persist much longer than 6 months, as reflected in decreasing yields of one or both monocultures. In these cases the species disappear of themselves and not for reasons of competition.

However, in an experiment with a clone of perennial ryegrass (L) and a clone of Yorkshire fog (H_1) this complication did not occur within 12 × 3 weeks. Fig. 20 shows that up to the 9th cut the species behave like those previously discussed, the curves through the observations being calculated with almost reciprocal k values (RYT $\approx$ 1). After the 9th cut the yields of ryegrass in the mixtures are as high as in the monocultures, while Yorkshire fog, though in small quantities, is still present in the mixture. Evidently, Yorkshire fog subsists for a long period, irrespective of the yield of ryegrass. Fig. 21 shows that up to the 8th cut a mixture has no advantage over the higher yielding monoculture. At the 9th cut the maximum advantage of a mixture is 10 %. After the 9th cut $k_{LH_1} \rightarrow \infty$ (see fig. 20), hence the advantage is equal to the dry matter produced by Yorkshire fog in the mixture.

Comparing the structure of the sods of the monocultures showed that ryegrass had an open sod with leafless brown stubbles, whereas Yorkshire fog had a much denser sod. Now it is quite well imaginable, that during the short period after clipping in which the crop surface of the monoculture of ryegrass is not yet closed, the sod of the mixture is able to utilize the light more efficiently. Of course, these mixtures are advantageous only if the monoculture of the species with the open sod produces as much or more than the monoculture of the species with the denser sod.

The experiment just discussed was carried out with clonal material originating from the same fertile pasture. At the same time this clone of ryegrass competed with a clone of Yorkshire fog originating from a very poor pasture. The course lines for both combinations in fig. 22 show that during the first 7 cuts ryegrass replaces Yorkshire fog originating from the poor site (H_2) at a somewhat faster rate than that from the fertile site (H_1). After the 8th and 9th cut, respectively, ϱ is no longer independent of the relative yields and an equilibrium may be established (de Wit, 1960).

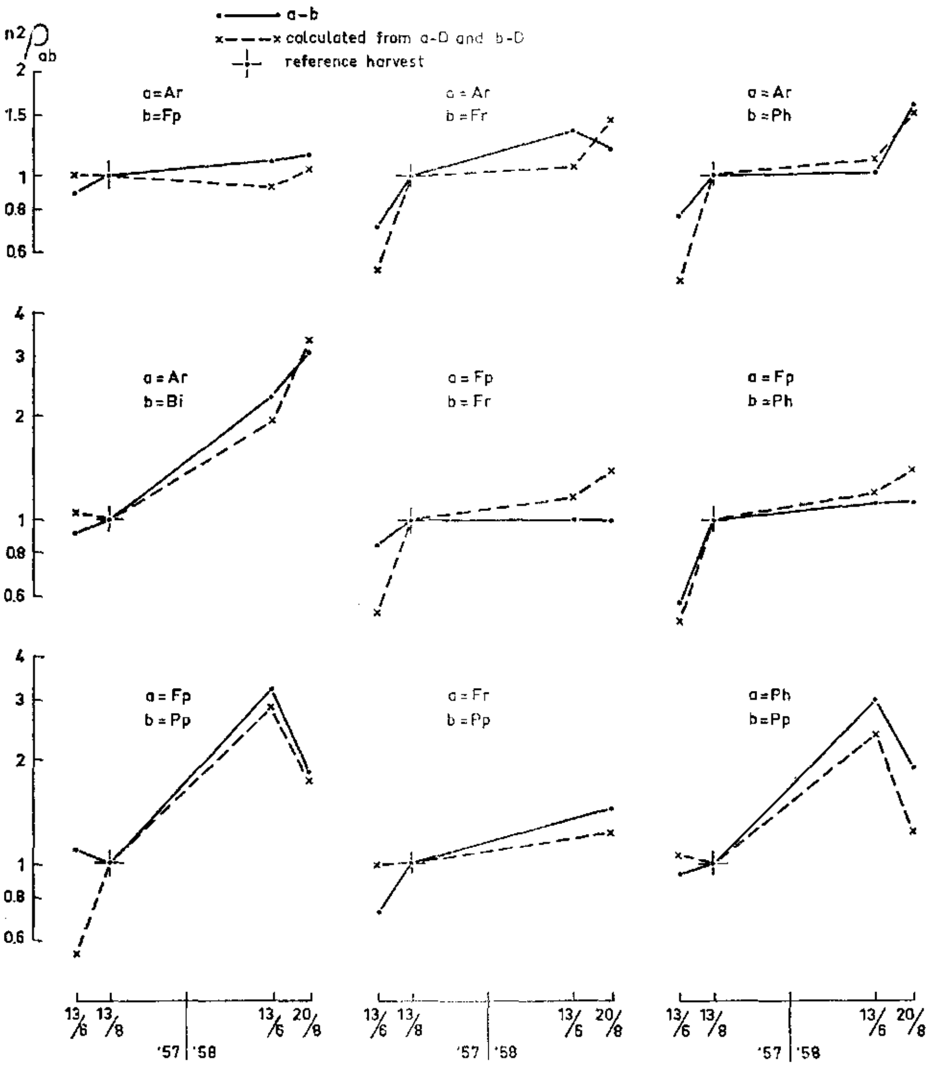

Fig. 19. Relative replacement rates with respect to the 2nd harvest presented as course lines for the mixtures without cocksfoot (solid lines). The ϱ values connected by a broken line were calculated from two mixtures with cocksfoot in common. Symbols for the species are as in table 2.

4.5 Discussion

It has been shown that the model of competition developed in chapter 2 applies to perennial grasses growing in pots under controlled conditions and to grasses growing out of doors. In both cases the species exclude each other. This means that with each separate cut the yield of the mixture will not be higher than the higher yielding monoculture. The RYT values calculated by Raininko (1968) and Cowling & Lockyer (1968) for grass mixtures are in good agreement with this result, since their values are about 1.

Moreover, it has been found that this also holds for the total yields of all successive cuts together. In spite of the specific responses of the species on changing weather and seasonal conditions, a mixture had no advantage over the higher yielding monoculture. This does not seem to accord with the conclusions of England (1965) and Lampeter (1960). These authors, however, compared the yield of the mixtures with the average of the yields of both monocultures, which is only sensible if the yields of the monocultures are the same.

It has also been shown that in mixtures with very small quantities of one species, the species need not exclude each other. In these cases the RYT value of the mixture is greater than 1, so that an equilibrium may be established. The advantage of this mixture is only small. But the subsistence of a species may be important from another aspect.

In a study of the ecology or herbage plants, de Vries (1949) determined frequency percentages (F%) and weight percentages (W%). Weight percentages represent a mass proportion, whereas frequency percentages yield information about the distribution of the species. In fig. 23 W% and F% are given for all species in a sample of an arbitrary grassland (file data of de Vries, Institute for Biological and Chemical Research on Field Crops and Herbage (IBS), Wageningen). A species not or hardly represented in the sample by a measurable mass, may still subsist with a high F%. This species so to say is waiting for a change in the environmental conditions, weakening the dominant species. When the dominant species collapses for some reason or another (frost, drought, diseases), the subsisting species may fill up the gaps and temporarily yield more than a monoculture of the dominant species. But if the subsisting species yields less than the otherwise dominant species, yield losses will probably result, because the original species may re-establish slower in the presence of the subsisting species than in its absence.

The problem of invading species will be discussed in section 6.2.5.

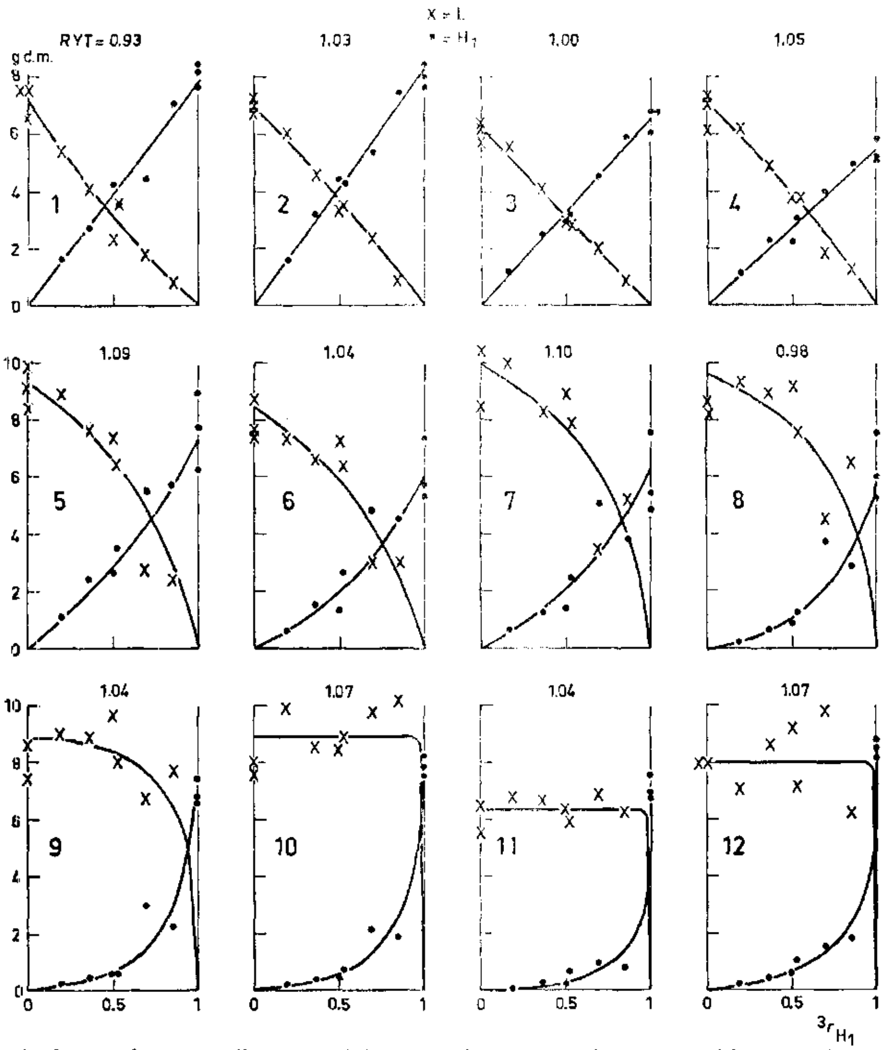

Fig. 20. Replacement diagrams of 12 successive harvests in a competition experiment with a clone of *Holcus lanatus* (H_1), both from the same fertile pasture.

5 Applications

Many surveys have analysed the relation between botanical composition, and climatic and edaphic factors under field conditions. The classical work by de Vries showed that such relations could be found, but that a causal interpretation was difficult, because of the complexity of the problem. In field experiments one factor may be varied and interpreted by the approach discussed in this paper. Such experiments are laborious and difficult because of their size and duration, neither is it simple to find suitable sites for them. However, it has been shown in the previous section that the competitive interference between species in the field and under controlled conditions in pots is similar and it was therefore considered worthwhile first to analyse the influence of some main variants in the greenhouse and growth room.

Attention has been paid to the cutting regime, the nutrient supply and the pH of the soil. As for the cutting regime the influence of carbohydrates in the stubble and the photosynthetic capacity of the stubble has been studied. The nutrient supply has been studied by varying the NPK level, the K:Ca and K:Na ratios of fertilizers.

The influence of soil pH has been investigated during and after establishment of sown species under growth room and field conditions.

5.1 Cutting regime

Differences in the morphology of the stubble may be important in competition between frequently cut grasses. The stubble of cocksfoot consists of robust, green tillers, whereas the tillers of ryegrass are tiny and enclosed by dead brown leaf sheaths. Thus the regrowth of ryegrass just after cutting is not supported by assimilating tissue, whereas cocksfoot can assimilate immediately after cutting. Especially, when the herbage is cut at short intervals, the competitive ability of ryegrass is supposed to be more affected than that of cocksfoot.

To investigate this supposition, monocultures and mixtures were planted with 24 tillers per pot; all the mixtures consisted of 12 tillers of ryegrass (L) and 12 tillers of cocksfoot (D). All the pots were cut at 3 week intervals (normal treatment). From the 4th harvest onwards about half the number of pots was clipped again, two days after harvesting (exhaustion treatment).

In fig. 24 the observations of the 3rd harvest are scattered around a straight line: the RYT value is about 1. Since all the mixtures were planted at the same

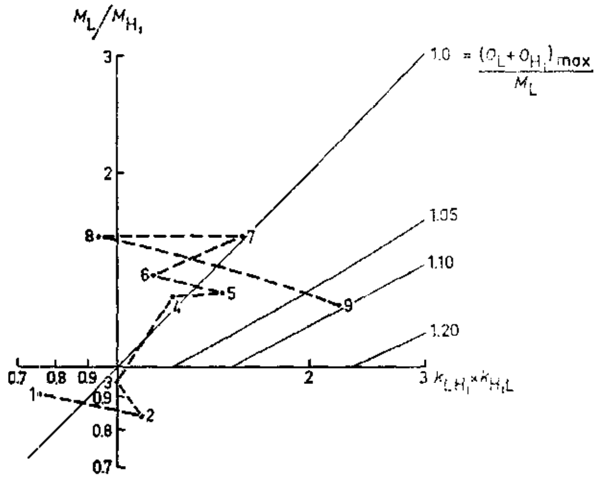

Fig. 21. The quotient of the yields of the monocultures of *Lolium* (L) and *Holcus* (H_1) plotted against the product of their relative crowding coefficients at 9 successive harvests.

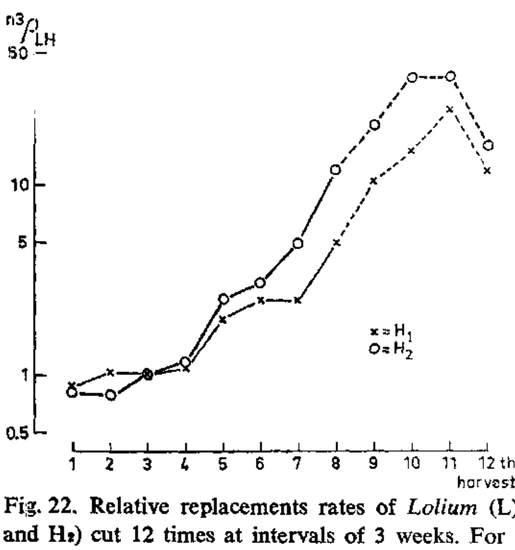

Fig. 22. Relative replacements rates of *Lolium* (L) with respect to two clones of *Holcus* (H_1 and H_2) cut 12 times at intervals of 3 weeks. For the dotted part of the course lines see text.

tiller ratio the relative yields of the mixtures were about the same, so that the average relative yield could be calculated. This value ($^{3}r_D = 0.33$) is plotted on the horizontal axis of the replacement diagrams in fig. 25.

The effect of the intermediate cut on the result of competition is clearly visualized by the course lines in fig. 26. During the first four harvests ϱ_{LD} remains constant but thereafter ϱ_{LD} of the normal treatment increases rapidly and ϱ_{LD} of the exhaustion treatment does not change very much. Thus ryegrass in competition with cocksfoot is less aggressive with this additional cut after two days. This is in accordance with the supposition mentioned above.

The RYT values of the successive cuts in the normal treatment (fig. 25a and b) do not differ systematically from 1 but those of the exhaustion treatment (fig. 25c) increase gradually from 1.03 at the 5th cut to 1.11 at the 8th cut. The sod of the mixture is much denser than the sod of the monoculture of ryegrass (the higher yielding species), which may result in better utilization of the light by the mixture as long as the crop surface is not closed. This period is longer with more cuts and low yields. Hence, the RYT values of the exhaustion treatment only are greater than 1, and the more so as yields decrease (fig. 25). Agriculturally this possible advantage of a mixture is unimportant, since it may occur only when yields are low.

5.2 NPK levels

It has been shown in section 4.4 that there are slight differences in competitive ability between two clones of Yorkshire fog collected from a fertile and a poor site. On the other hand, it may be of interest to know how NPK supply affects competition between two species often occurring on fertile soils.

Pots were planted with tillers of ryegrass and couchgrass *(Elytrigia repens,* syn. *Agropyron repens)* and after the third monthly cut 4 series of 12 pots were fertilized according to table 3. At each subsequent cut the same dressing was repeated. As is illustrated in fig. 27 the species exclude each other at the 3rd cut. The same holds for the following cuts at all NPK levels: the RYT values do not differ systematically from 1 (fig. 28). According to production of dry matter in the monocultures, the response of couchgrass to the fertilizer treatment is greater than the response of ryegrass (fig. 29). This advantage of couchgrass at high NPK levels is observed also in the mixtures, as illustrated by the course lines in fig. 30.

Table 3. Nutrient salts in me. per pot applied after each cut from the 3rd cut onwards.

	KNO_3	$Ca(NO_3)_2$	$MgSO_4$	$NH_4H_2PO_4$
series I	2.5	2.5	2.5	0.3
series II	5	5	5	0.6
series III	10	10	10	1.2
series IV	20	20	20	2.5

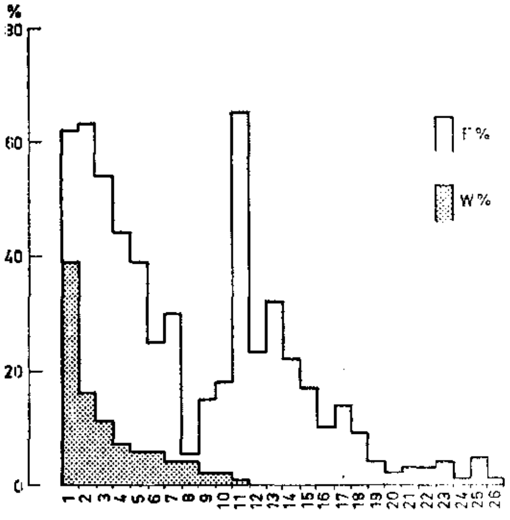

Fig. 23. Frequency (F) and weight (W) percentages of all the species in a herbage sample from a pasture (file data of D. M. de Vries, IBS, Wageningen).

1 *Agrostis stolonifera*
2 *Lolium perenne*
3 *Trifolium repens*
4 *Holcus lanatus*
5 *Poa pratensis*
6 *Ranunculus repens*
7 *Anthoxanthum odoratum*
8 *Cerastium caespitosum*
9 *Festuca rubra*
10 *Ranunculus acer*
11 *Poa trivialis*
12 *Festuca pratensis*
13 *Alopecurus geniculatus*
14 *Glyceria fluitans*
15 *Elytrigia repens*
16 *Agrostis canina*
17 *Rumex acetosa*
18 *Taraxacum officinale*
19 *Phleum pratense*
20 *Cynosurus cristatus*
21 *Bellis perennis*
22 *Cardamine pratensis*
23 *Leontodon autumnalis*
24 *Plantago major*
25 *Potentilla anserina*
26 *Sagina procumbens*

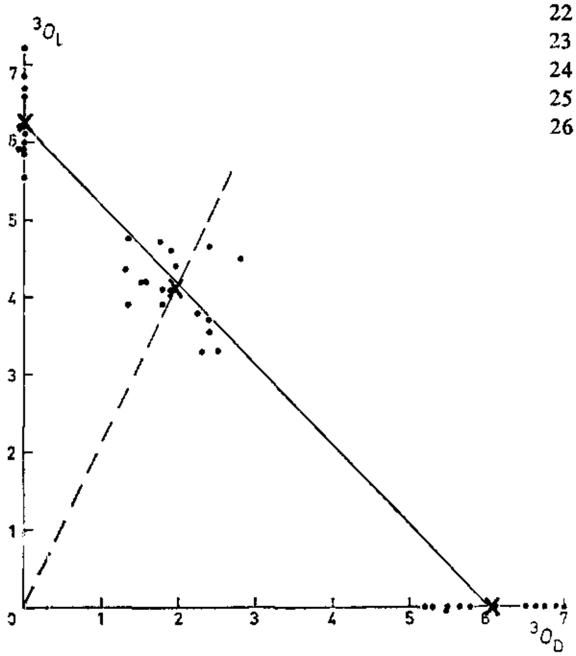

Fig. 24. Dry-matter yields in grammes of the 3rd harvest of *Lolium* (^3O_L) and *Dactylis* (^3O_D) plotted against each other. X indicates the average value of the mixtures and monocultures.

Ryegrass replaces couchgrass at all NPK levels but the higher the NPK level the smaller the relative replacement rates.

After the 6th cut on September 16 the shortening days were lengthened by high-pressure mercury lamps of 400 watt. In contrast to couchgrass, ryegrass did not take advantage of this extra energy: compare the monocultures of the 6th and 7th cut in fig. 28 and notice the sudden change in direction of the course lines in fig. 30.

5.3 K-Ca replacement

Dijkshoorn (1956) and Said (1959) showed that cocksfoot is able to accumulate more potassium and less calcium than ryegrass from the same substrate. Therefore competition between these species was studied at widely different K:Ca ratios in the soil. To ensure a low cation content of the soil, NH_4NO_3 was applied only during the first 2 months of the experiment. After the second cut, 5 series of 12 pots were fertilized by the K-Ca replacement scheme given in table 4. The 3rd and the 4th cut followed after 1 and 2 months. The yields of the 2nd harvest, presented in fig. 31 are scattered around a straight line: the species exclude each other. Since all the mixtures were planted at the same ratio (7 tillers of ryegrass and 7 tillers of cocksfoot), the average relative yield could be calculated from the average yields of the monocultures and mixtures. The replacement diagrams of the 3rd and 4th cut with the 2nd cut as a reference harvest (fig. 32) show a yield increase of the monocultures of both species with increasing potassium but no effect of the treatment on the curvature of the lines through the observations. This is also illustrated by the course lines in fig. 33: independent of the treatment, neither of the species replaces the other.

The cation contents in the dry material of the mixtures at the 4th cut are determined for each species separately (fig 34). With both species potassium is partly replaced by calcium at decreasing K:Ca ratio of the application. In the experiment the K content of both species was the same, whereas the Ca content in cocksfoot was a bit lower than in ryegrass. The ratio diagram (fig. 35) clearly illustrates that the K:Ca ratio in ryegrass increases proportionally to that in cocksfoot with increasing K:Ca ratio in the fertilizer.

Table 4. Nutrient salts in me. per pot applied after the 2nd cut.

	KNO_3	$Ca(NO_3)_2$	$MgSO_4$	$NH_4H_2PO_4$ 0.5N
series I	0	40	10	2.5
series II	5	35	10	2.5
series III	14	26	10	2.5
series IV	26	14	10	2.5
series V	40	0	10	2.5

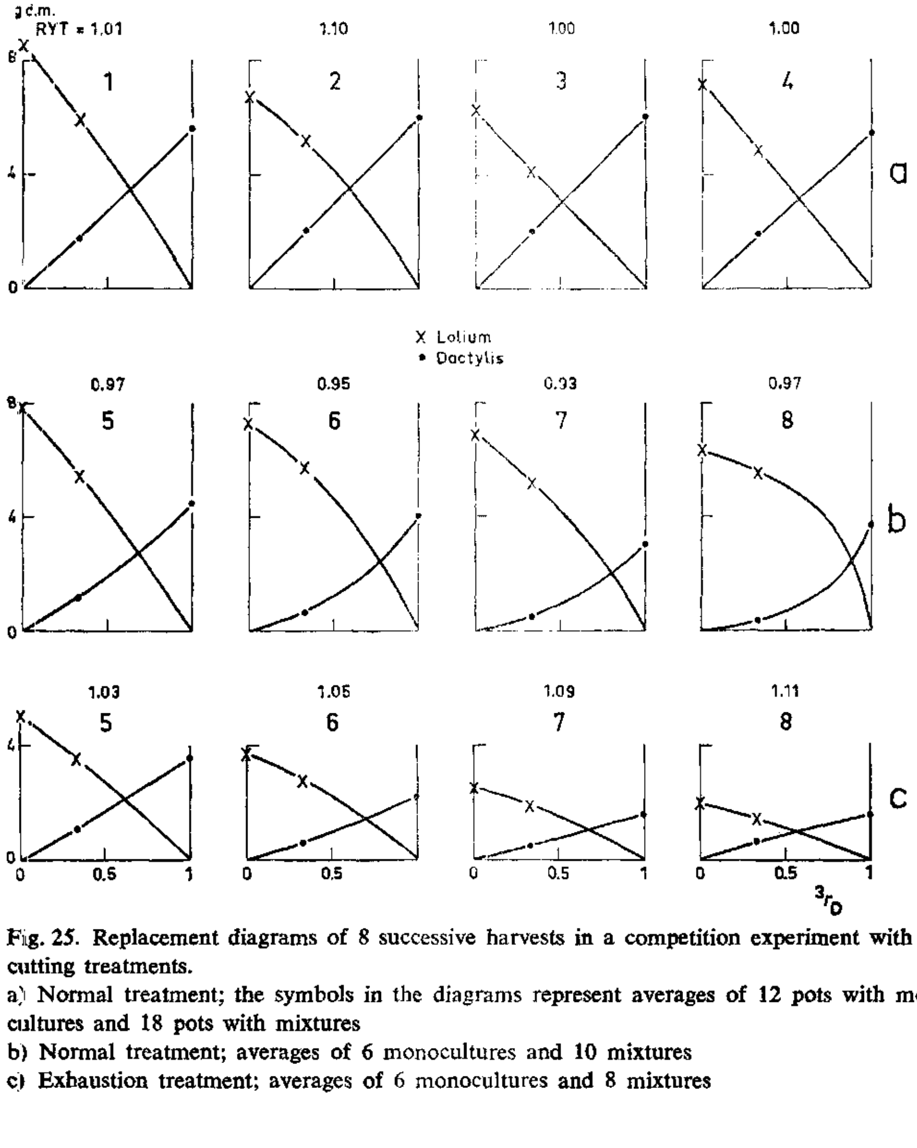

Fig. 25. Replacement diagrams of 8 successive harvests in a competition experiment with two cutting treatments.

a) Normal treatment; the symbols in the diagrams represent averages of 12 pots with monocultures and 18 pots with mixtures

b) Normal treatment; averages of 6 monocultures and 10 mixtures

c) Exhaustion treatment; averages of 6 monocultures and 8 mixtures

5.4 K-Na replacement

Meadow foxtail *(Alopecurus pratensis)* contained much less sodium than other grasses collected from the same spot in the field (personel communication of de Vries, IBS, Wageningen). This difference led to a competition experiment with ryegrass and foxtail at different K:Na ratios in the soil. During the first 2 months of the experiment only calcium and magnesium nitrates were applied. After the second cut 4 series of 6 pots were fertilized according to the K-Na replacement scheme in table 5. The 3rd and 4th cut followed 1 and 2 months later. During this period only 33 me. $Ca(NO_3)_2$ was applied per pot.

According to fig. 36 the species exclude each other at the time of the 2nd harvest. An average relative yield of foxtail of 0.5 was calculated for all the series.

The RYT values at the 3rd and the 4th harvest (fig. 37) did not differ much from 1, except for series I at the 3rd harvest, which cannot be explained. The production of dry matter per pot was not affected, so long as potassium is supplied; without potassium the production of the ryegrass monoculture will drop at the 4th harvest to the half and that of foxtail to a third. Nevertheless in competition foxtail will take the advantage, as more potassium is replaced by sodium (fig. 38). As the course line slopes downward in the (0 K + 40 Na) series, foxtail with a production of less than half that of ryegrass (compare the monocultures in fig. 37) even replaced ryegrass.

Chemical analyses of the 3rd cut of the mixtures show a remarkable difference in Na and K uptake between the two species (fig. 39). With foxtail potassium is not replaced by sodium, so long as potassium is supplied and in the (0 K + 40 Na) series only a small quantity of potassium is replaced by sodium. On the contrary, with ryegrass potassium is readily replaced by sodium with decreasing K:Na ratio in the fertilizer, even to such an extent, that the Na content increases to 1635 me. per kg dry matter compared with the highest K content of 1015 me. per kg dry matter. This difference is also shown in the ratio diagram (fig. 40): the treatment does not cause the K:Na ratio in foxtail to change proportionally to that in ryegrass. The same holds for the 4th cut.

To explain the controversy in the effects of the K:Na ratio in the soil on the monocultures and on ϱ_{LAp}, it may be supposed that in the mixtures the excess of sodium in the soil is taken up by ryegrass to the advantage of foxtail. But this

Table 5. Nutrient salts in me. per pot applied after the 2nd cut.

	KNO_3	$NaNO_3$	$MgSO_4$	$Ca(H_2PO_4)$
series I	0	40	10	2
series II	14	26	10	2
series III	26	14	10	2
series IV	40	0	10	2

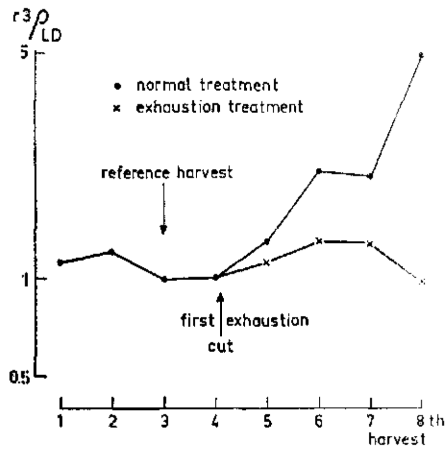

Fig. 26. Relative replacement rates for *Lolium* (L) with respect to *Dactylis* (D).

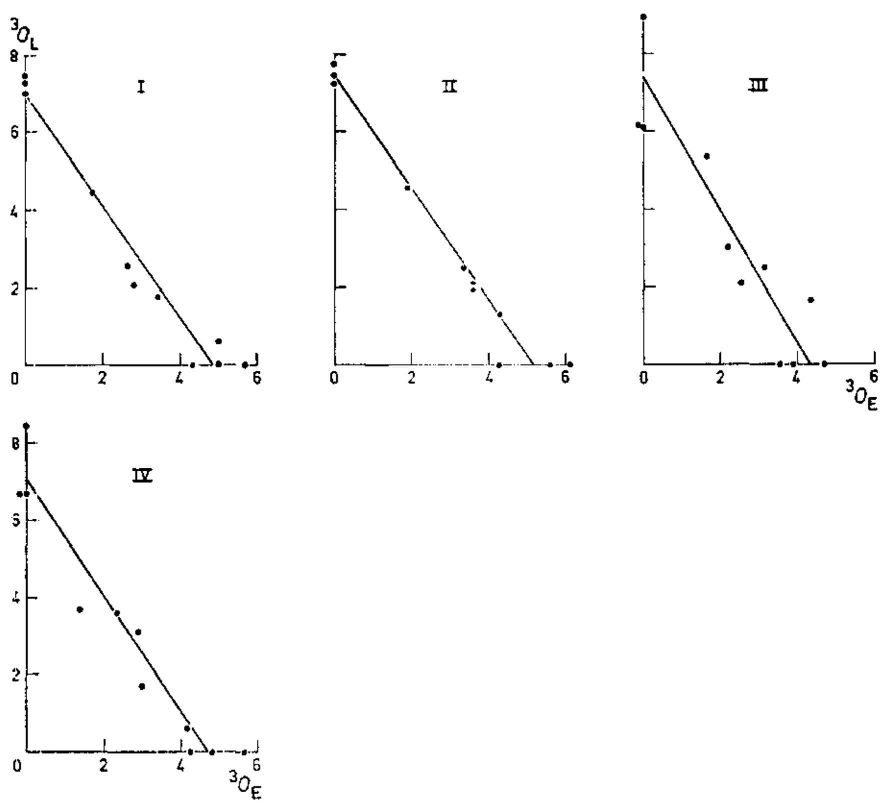

Fig. 27. Dry matter yields in grammes of the 3rd harvest of *Lolium* (^3O_L) and *Elytrigia repens* (^3O_E) plotted against each other. After this harvest the series were fertilized according to table 3.

supposition does not accord with the observation that Na contents in the species in monoculture and mixed culture are the same. In section 6.1.2 another attempt will be made to explain this phenomenon.

A similar experiment with ryegrass and vernal grass showed no effect of the treatment on competition, the ϱ values being the same. In this case both species accumulated sodium if potassium was absent (fig. 41). This resulted in a proportional change of the K:Na ratio in ryegrass and vernal grass (fig. 40) in the 3rd and the 4th cut.

5.5 pH of the soil

5.5.1 Common bent and cocksfoot in a growth room

To examine the influence of pH on competitive phenomena more closely, common bent *(Agrostis tenuis)* and cocksfoot *(Dactylis glomerata)* were sown in pots (table 6); common bent under Dutch conditions is an indicator of poor acid soils and cocksfoot of fertile, sligthly alkaline soils (Kruijne & de Vries, 1967).

The soil used was a very poor and acid sandy soil (pH = 4.2). By adding 28 or 100 g $CaCO_3$ per 7 kg soil, pH values were obtained of 6.2 and 6.7, respectively. The pH effect was studied at two NPK levels. At the high level 20 me. KNO_3, 5 me. $MgSO_4$ and 2.5 me. $NH_4H_2PO_4$ were supplied after each 4-weekly cut and at the low level a quarter of these amounts was added.

In contrast to the experiments discussed before, the treatment (in this case $CaCO_3$) had already been applied before the species were sown. To facilitate comparison of the course lines for the different treatments, the relative seed frequencies instead of the relative yields are used as a reference 'harvest'. The relative seed frequencies of common bent are plotted on the horizontal axis in fig. 42. The curves through the observations in the replacement diagrams compensate each other (RYT values about 1), so that the species exclude each other in all the treatments. The effect of applying $CaCO_3$ on the monocultures at low and high NPK is clearly illustrated in table 7. The considerable response of both

Table 6. Number of viable seeds of *Dactylis glomerata* (D) and *Agrostis tenuis* (At) per pot, relative seed frequency of *Agrostis* (${}^0r_{At}$) and number of replicates for each replacement series.

	mono. D	mixtures					mono. At
D seeds	90	75	60	45	30	15	0
At seeds	0	20	40	60	80	100	120
${}^0r_{At}$	0	0.17	0.33	0.50	0.67	0.83	1.0
replicates	3	1	1	2	1	1	3

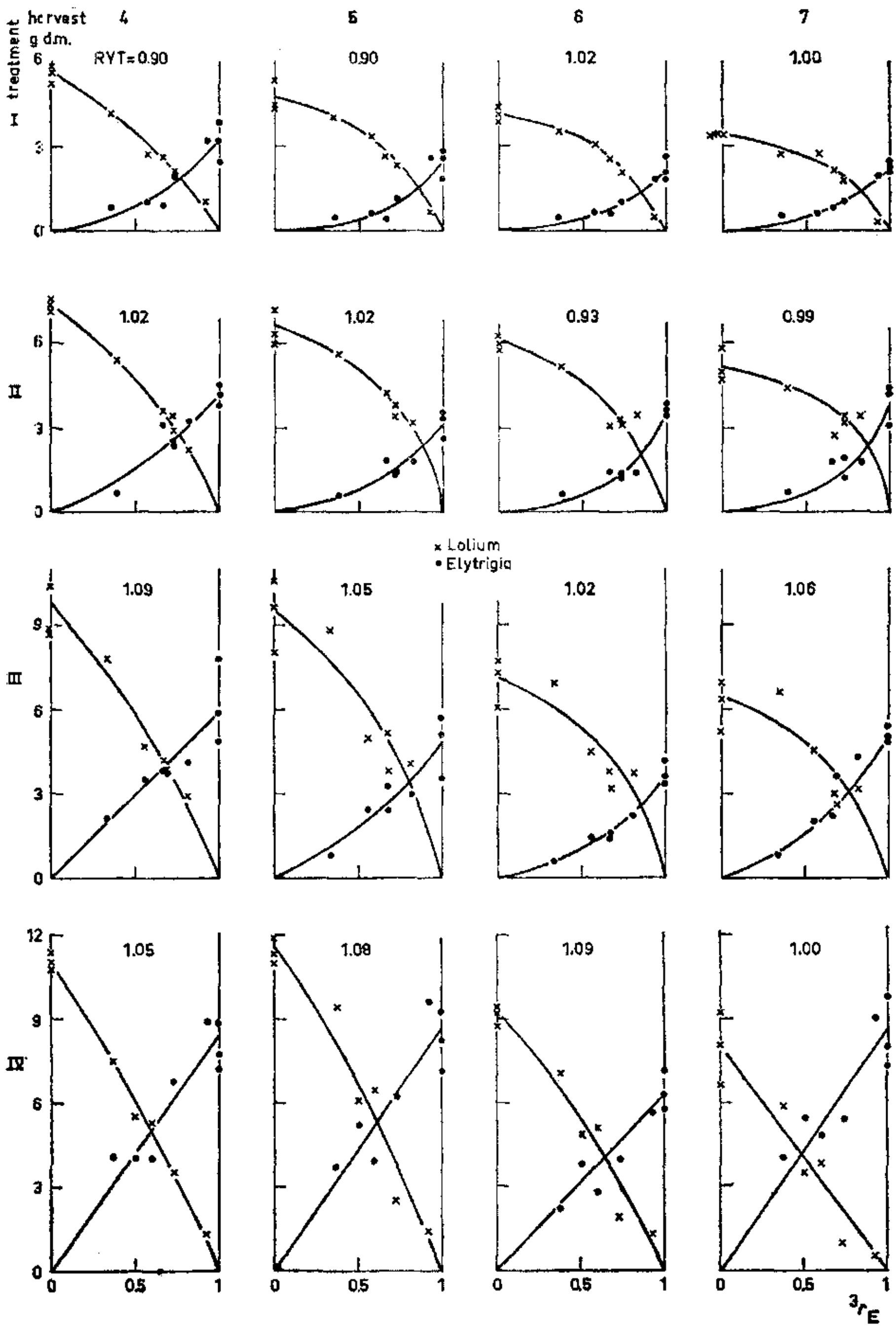

Fig. 28. Replacement diagrams of 4 successive harvests (4-7) of a competition experiment at 4 NPK levels (I-IV of table 3).

Table 7. Calculated average values of the monocultures of *Dactylis* (D) and *Agrostis* (At) (see fig. 42) in grammes (and in percentages of the highest calculated yield of the same species at the same NPK level). Averages of 6 cuts.

	low NPK						high NPK					
g $CaCO_3$	0		28		100		0		28		100	
	g	%	g	%	g	%	g	%	g	%	g	%
D	15.2	(59)	23.2	(90)	25.8	(100)	75.5	(96)	79.0	(100)	72.5	(92)
At	15.2	(60)	21.0	(82)	25.5	(100)	42.0	(100)	42.0	(100)	39.0	(93)

species at low NPK disappeared at high NPK, indicating that pH affects growth within this range under marginal conditions only.

The result of competition is clearly illustrated in fig. 43. The slope of the course line from sowing to the first cut increases considerably with increasing pH. This means that during seedling establishment the composition of the mixture is very much influenced by pH: at the lowest pH the proportion of cocksfoot in the mixture is much smaller than at higher pH values. Close observation shows that tillering of cocksfoot seedlings is hampered appreciably by low pH values.

From the first cut onwards, however, the course lines of the series with the same NPK treatment and different pH values are closely parallel. This means that after the first cut the result of competition is independent of pH. Now the NPK supply determines whether the indicator of fertile soils, cocksfoot, replaces the indicator of poor soils, common bent (high NPK) or common bent replaces cocksfoot (low NPK). In the high NPK treatment common bent disappears rapidly after the 5th cut partly due to a mould infestation (notice also the declining yields of the monocultures of common bent at high NPK in fig. 42). In the long run cocksfoot will replace common bent also in the low NPK treatment, though very slowly (fig. 44).

It may be noticed that under these conditions at pH 4.2 cocksfoot replaces common bent slightly faster than at the higher pH values. Probably this is due to differences in fertility level, as will be shown. The total dry-matter production in 16 cuts is about 20 % lower than at the higher pH values. The removal of minerals must have been less at pH 4.2, resulting in a higher fertility, since all the pH treatments were supplied with equal amounts of nutrients. As is shown above, a higher fertility stimulates cocksfoot at the cost of common bent.

This also shows that with long-term experiments differences in yields between the treatments may finally fade away or even wipe out the effects observed at first. When different proportions of a species in a mixture cause differences in production between the treatments, it may look as though ϱ should be dependent on the compostion of the mixture. This only seems to be so, for reasons mentioned above.

In the next section it will be shown that this appreciable effect of pH during seedling establishment and the absence of an effect later on the result of competition, also holds under outdoor conditions in plots.

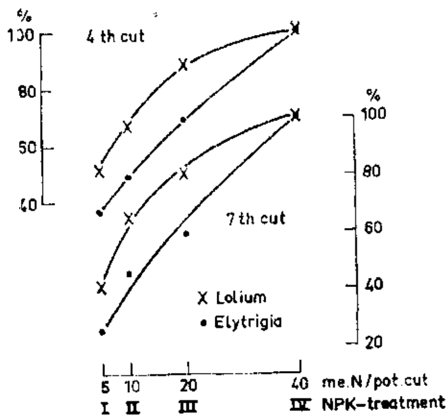

Fig. 29. Dry-matter productions (at the intersections of the curves and vertical axis in fig. 28) of *Lolium* and *Elytrigia* in percentages of their yields at NPK treatment IV.

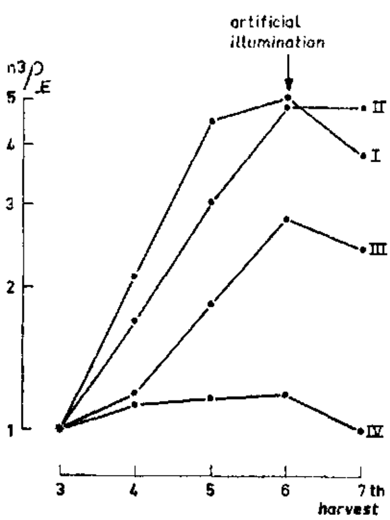

Fig. 30. Relative replacement rates for *Lolium* (L) with respect to *Elytrigia* (E) at 4 NPK levels (I-IV).

5.5.2 Ryegrass and several other perennial species on plots

De Vries (1940) published a preliminary report on competition on plots between grass species and white clover on acid sandy soil (natural pH 4.6) whose pH was altered by liming. Available file data made it possible to construct course lines, which enables comparison with the results of the previous experiment.

The composition of the mixtures sown is shown in table 8. The plots sown with these mixtures were 1.5 × 0.8 sq. metre and those with the monocultures 0.4 × 0.8 sq. metre. Three cuts were harvested each year in 1934, 1935 and 1936. Each species was weighed in the 1st and 3rd cut of the mixtures (except for the 1st cut in the 3rd year). The 3rd cut of the monocultures was not weighed in 1936.

The monocultures yielded much more per unit ground area than the mixtures, even where one species formed over 90 % of the harvested mixtures. Evidently, these large differences cannot be due to some poisonous excretion of one of the species but are caused by differences in the size of these small plots. Higher yields have often been observed from small plots (i.e. the monocultures) than from larger ones (i.e. the mixtures). As the position of the course line is determined by the double ratio

$$(O_a/M_a)\ (O_b/M_b)^{-1} = (O_a/O_b)\ (M_a/M_b)^{-1},$$

the absolute yield of the monocultures does not change the course line, assuming that the influence of the plot size is relatively the same for all species.

As mentioned, there is no data for the 3rd cut of the monocultures in 1936. To obtain a reasonable estimate of M_a/M_b, the mean value of this quotient is calculated for the 3rd cuts of the preceding years.

Table 8. Composition of the mixtures in kg seed per ha. The species below the space were present in too small quanities in many yields to make reliable comparisons with te other species.

mixture	I	II	III	IV	V
Agrostis tenuis	5	3 1/3	3 1/3	4	3 1/3
Lolium perenne	20	13 1/3	13 1/3	—	6 1/2
Poa pratensis	—	6	—	7	3
Anthoxanthum odoratum	—	—	12	14 1/2	6
Holcus lanatus	—	—	8	10 1/2	4
Festuca rubra	—	—	—	10	4
Poa trivialis	7 1/2	5	5	—	2 1/2
Phleum pratense	—	5	—	—	2 1/2
Festuca pratensis	—	—	—	—	6 2/3
Cynosurus cristatus	—	—	—	—	3 1/3
Trifolium repens	5	3 1/3	3 1/3	—	1 2/3

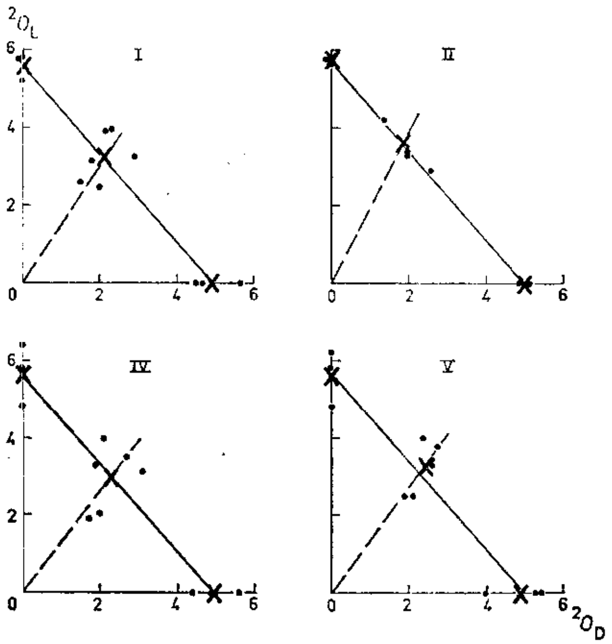

Fig. 31. Dry matter yields in grammes at the 2nd harvest of *Lolium* (^2O_L) and *Dactylis* (^2O_D) plotted against each other. After this harvest series I-V were fertilized according to table 4. X indicates the average value of the mixtures and monocultures.

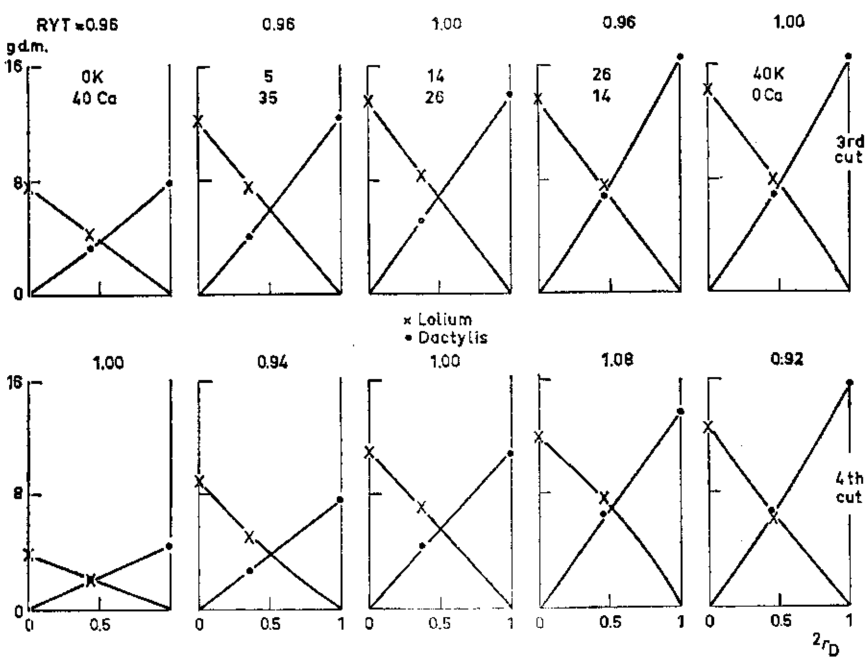

Fig. 32. Replacement diagrams of 2 successive harvests of a competition experiment with 5 K:Ca ratios (see table 4). The observations of the monocultures refer to averages of 3 pots and those of the mixtures of 6 pots.

Ryegrass and common bent Fig. 45 shows the course lines of ryegrass (L) and common bent (At) growing with other species in various mixtures. The solid lines are for the pH values indicated; the logarithm of r_L/r_{At} is averaged for all mixtures. The broken lines refer to the mixtures indicated (as in table 8); the logarithm of r_L/r_{At} is averaged for all pH values. The 1st cut in 1934 is not presented in this figure because the monocultures and mixtures were not harvested at the same time. The point of the 3rd cut in 1936 has been calculated from table 9. As there is no interaction between average value for M_L/M_{At} and pH, the average of all treatments, 1.20, is used for all pH values.

The level of the course lines along the vertical axis does not show the rate at which one species replaces the other but indicates that from the beginning of the experiment the ratio of these two species in the mixtures depends closely on pH. From table 10 it may be derived that O_L/O_{At} may vary from 1.75 (pH 4.6, mixture I) to 300 (pH 6.8, mixture I). Obviously, the emergence and first development of ryegrass relative to common bent is much better at higher pH values than at the lower ones. The same is illustrated, though to a less extent, by the yields of the 1st cut of the monocultures in 1934; already at the 3rd cut of the same year ryegrass and common bent both grow better at high pH values (table 11).

Generally the solid course lines of fig. 45 are closely parallel, showing that the rate at which ryegrass is replaced by common bent (downward sloping curve) is not influenced by pH. The course line of pH 6.8 deviates at first but this pH effect disappears later. Apparently, the highest pH influences competition between ryegrass and common bent during the first year after sowing as well as during establishment.

The high degree of parallelism of the broken course lines in fig. 45 illustrates the negligible influence of the associated species (composition of the mixture, table 8) on the competition between ryegrass and common bent. This accords with sections 4.2 and 4.3.

Ryegrass and four other grass species Sweet vernal grass (Ao), Yorkshire fog (Hl), red fescue (Fr) and meadow grass (Pp) were compared with ryegrass (L), because the latter species is always present in the mixture in measurable quantities, except for mixture IV in which ryegrass was not included. It has already been shown that the composition of the mixture hardly changes the slope of the course lines of ryegrass and common bent. Consequently, the course line of ryegrass and any species X of mixture IV can be calculated as follows:

$$(r_L/r_{At})_{\text{log. mean all treatments}} \times (r_{At}/r_X)_{\text{mix. IV}}$$

In general the solid course lines in fig. 46b, 47a and b are parallel, showing that the influence of pH on the replacement rate of ryegrass and Yorkshire fog, red fescue and meadow grass is of minor importance. At first the slope of the course lines of ryegrass and Yorkshire fog increases sligthly with increasing pH (fig. 46b), whereas the reverse is observed with ryegrass and red fescue (fig. 47a). Between the 1st and 3rd cut in 1935 the replacement rate of ryegrass and red fescue or

Table 9. The quotient for dry-matter yields in monocultures of *Lolium* (M_L) and *Agrostis* (M_{At}) at the 3rd cut with different pH values in 1934 and 1935.

	pH	4.6	4.8	5.3	5.8	6.2	6.8
1934		1.27	1.37	1.06	1.20	1.02	1.45
1935		1.00	1.19	1.17	1.06	1.31	1.21
average		1.14	1.28	1.12	1.13	1.17	1.33
				1.20			

Table 10. Weight percentages of *Agrostis* (At) and *Lolium* (L) at the 1st cut in 4 mixtures at different pH values in 1934.

	mixture							
	I species		II species		III species		V species	
pH	At	L	At	L	At	L	At	L
4.6	30.0	52.4	23.5	34.0	13.4	49.6	16.6	38.2
4.8	18.4	74.8	14.7	47.1	7.9	64.5	10.2	46.5
5.3	9.2	73.2	7.5	47.1	4.2	71.0	5.1	57.4
5.8	3.6	81.8	5.9	47.2	2.4	71.5	4.0	51.1
6.2	5.1	74.2	4.2	53.2	2.6	74.1	2.0	53.0
6.8	0.3	91.0	1.2	61.1	1.1	82.5	3.5	51.5

Table 11. Grammes dry matter on 0.32 sq. metre for monocultures of *Agrostis* (At) and *Lolium* (L) at the 1st and 3rd cut with different pH values harvested in 1934.

	1st cut		3rd cut	
pH	At	L	At	L
4.6	112	100	60	76
4.8	80	108	60	84
5.3	88	116	72	76
5.8	80	128	72	88
6.2	80	136	108	112
6.8	48	136	88	128

meadow grass is much lower at the lowest pH than at the other values (fig. 47). The replacement rate of ryegrass and vernal grass is the only one influenced by pH; strangely enough in opposite directions at different times (fig. 46a). Until the 1st cut in 1935 this replacement rate increases at increasing pH; thereafter it decreases at increasing pH.

The broken course lines in fig. 46a and 47 are parallel so that the rate of replacement of one species by another is independent of the presence of other species in the mixtures. The only exception is Yorkshire fog: in mixture IV ryegrass replaces Yorkshire fog at a much higher rate than in the mixtures III and V, in which the species match (fig. 46b).

It should be realized, however, that the replacement rate will be influenced in the long term by the composition of the mixture, as there are differences in yields, which cause different fertility levels. This phenomenon is discussed in section 5.5.1.

Comparison of the course lines of the species In the preceding it has been shown that the shape of the course lines is generally independent of:

a. Soil pH
b. The associated species in the mixture
c. The ratio of the dry weights of the species in the mixture.

In view of this $(r_L/r_X)_{\text{log. mean all treatments}}$ may be plotted against time (fig. 48). The averages of the 3rd cut in 1934 are put on one level to allow comparison of the species.

Until the 1st cut in 1935, ryegrass gains on all other species. During this period red fescue and meadow grass are less vigorous competitors than common bent, vernal grass and Yorkshire fog, which ryegrass replaces at equal rate. After this period the picture changes entirely: ryegrass is replaced by all other species. Common bent is about the most vigorous and ryegrass and Yorkshire fog the least vigorous species.

5.6 Discussion

The rate at which ryegrass replaces cocksfoot decreases when the crop is harvested more frequently. It is supposed that this is due to specific differences in morphology of the stubble: just after cutting, the green stubble of cocksfoot seems to have much more assimilating tissue than the brown stubble of ryegrass. This supposition is supported by del Pozo Ibánez (1963), who found that the total soluble carbohydrate content in the stubble of ryegrass decreased after cutting to much lower percentages than that in the stubble of cocksfoot. Since regrowth depends on carbohydrate reserves (Alberda, 1966), the competitive ability of ryegrass with frequent cutting may be more affected than that of cocksfoot.

Earlier van den Bergh & Elberse (1962) showed that with a large supply of PK an indicator of high fertility (ryegrass) replaced an indicator of low fertility (vernal grass) at a higher rate than with a small supply of PK. The example of the two

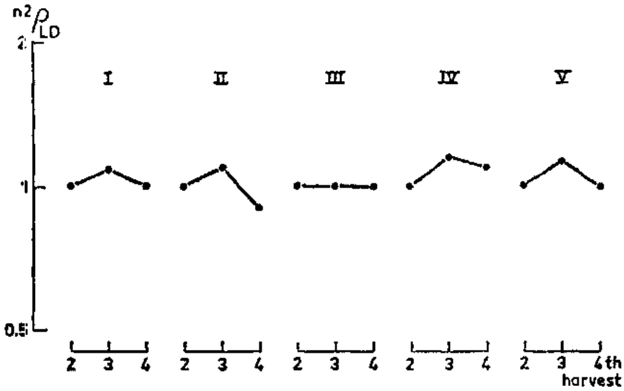

Fig. 33. Relative replacement rates of *Lolium* (L) with respect to *Dactylis* (D) at 5 K:Ca ratios of the added nutrients.

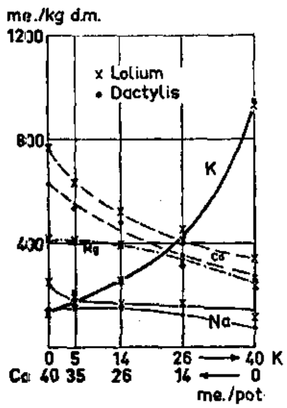

Fig. 34. Cation contents of *Lolium* and *Dactylis* in the 4th cut of the mixtures in a K-Ca replacement series.

clones of Yorkshire fog taken from a fertile and a poor site (section 4.4) and the influence of the NPK supply on competition between cocksfoot and common bent (section 5.5.1) also indicate that differences in ecological behaviour may be described in terms of competitive effects.

It has been shown that grass species have specific cation contents but that at increasing K:Ca ratio in the soil, the K:Ca ratio of ryegrass increases proportionally to that in cocksfoot. The same holds for the K:Na ratio of ryegrass and vernal grass with increasing K:Na ratio in the soil. With both experiments the relative replacement rate is not affected by the K:Ca or K:Na ratio in the soil. Obviously these ratios affect the competitive ability of these species to the same extent.

However, the K:Na ratio of ryegrass does not increase proportionally to that of foxtail with increasing K:Na ratios in the soil. In this case the effect of the treatment on the result of competition is the reverse of that on the monocultures: the competitive ability of foxtail is relatively greatest when K/Na is lowest in the medium, whereas its monoculture decreases to a much greater extent than the monoculture of its associate ryegrass. This phenomenon will be discussed in section 6.1.2.

Besides competitive ability, seedling establishment may be important in the distribution of species, in particular as influenced by soil pH. The most striking result of both pH experiments discussed in section 5.5 is the distinct effect of pH on the course lines during seedling establishment but not after the first cut. In other words pH affects propagation from seed but not competition between fully grown plants.

Accordingly, the great effect of the pH on mixed cultures of barley and oats (van Dobben, 1956; van Dobben & Wiersema, 1956) is mainly due to stunted root growth of barley seedlings at lower pH (van Dobben, pers. comm.). After some time, however, the stunted roots are replaced by normal growing ones, and in monoculture barley will still be able to produce a reasonable crop. In mixtures barley recovers to a much less extent, as oats is already established in the field. Here again, initial development of the seed is much more dependent on pH than growth later on.

To compare the effect of pH on the proportions of the various grass species, the value r_L/r_X on 18 September 1934 at the highest pH was divided by this value at the lowest pH (fig. 49). (Compare also the distance between the extreme course lines in fig. 45, 46, 47.) This effect of pH is greatest with the combination ryegrass with common bent and decreases successively if ryegrass is associated with vernal grass, Yorkshire fog, red fescue or meadow grass.

Table 12 records relative average frequencies (raF) for some grasses in permanent grassland taken from Kruijne & de Vries (1967). The species are arranged in sequence of increasing raF at low pH and then formed a sequence of decreasing raF at high pH. The complete agreement between this sequence and that of fig. 49 suggests that also in the field the interaction between pH and botanical composition arises mainly from the effect on propagation from seed.

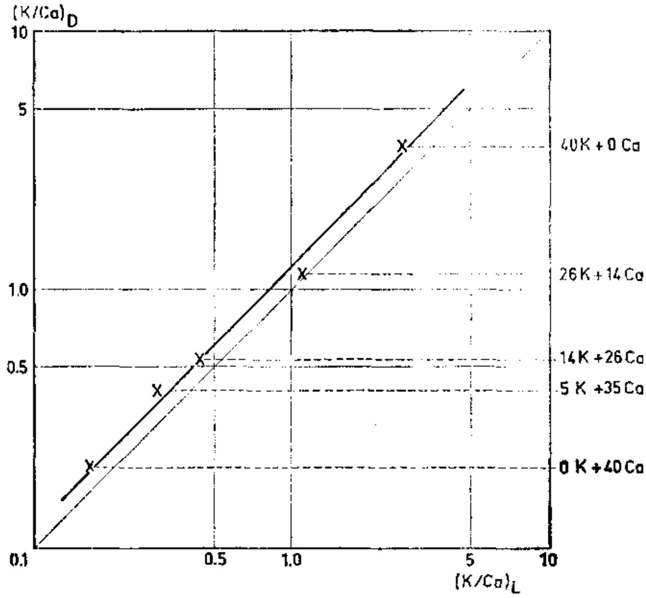

Fig. 35. K:Ca ratio of *Dactylis* $(K{:}Ca)_D$ plotted against K:Ca ratio of *Lolium* $(K{:}Ca)_L$ (on a logarithmic scale) in a K-Ca replacement series.

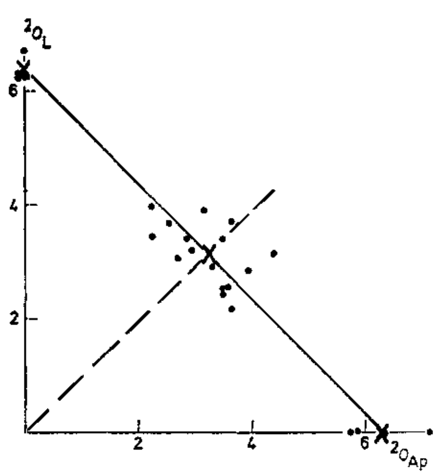

Fig. 36. Dry-matter yields in grammes at the 2nd harvest of *Lolium* $({}^2O_L)$ and *Alopecurus* $({}^2O_{Ap})$ plotted against each other. X indicates the average value of the mixtures and monocultures.

Table 12. Relative average frequencies (raF) of some species at different pH values of the top 5 cm soil (according to Kruijne & de Vries, 1967).

pH (water)	< 5.0	5.0 - 5.5	5.5 - 6.0	6.0 - 7.0
perennial ryegrass *(Lolium perenne)*	30	97	128	150
meadow grass *(Poa pratensis)*	57	105	126	124
red fescue *(Festuca rubra)*	68	96	107	110
Yorkshire fog *(Holcus lanatus)*	110	133	135	93
sweet vernal grass *(Anthoxanthum odoratum)*	103	145	145	83
common bent *(Agrostis tenuis)*	149	145	132	62

An experience which is in agreement with this conclusion is that in general liming has little effect on the botanical composition of permanent grassland (Klapp, 1954), whereas liming before sowing a ley may improve the botanical composition considerably (Heddle & Ogg, 1937).

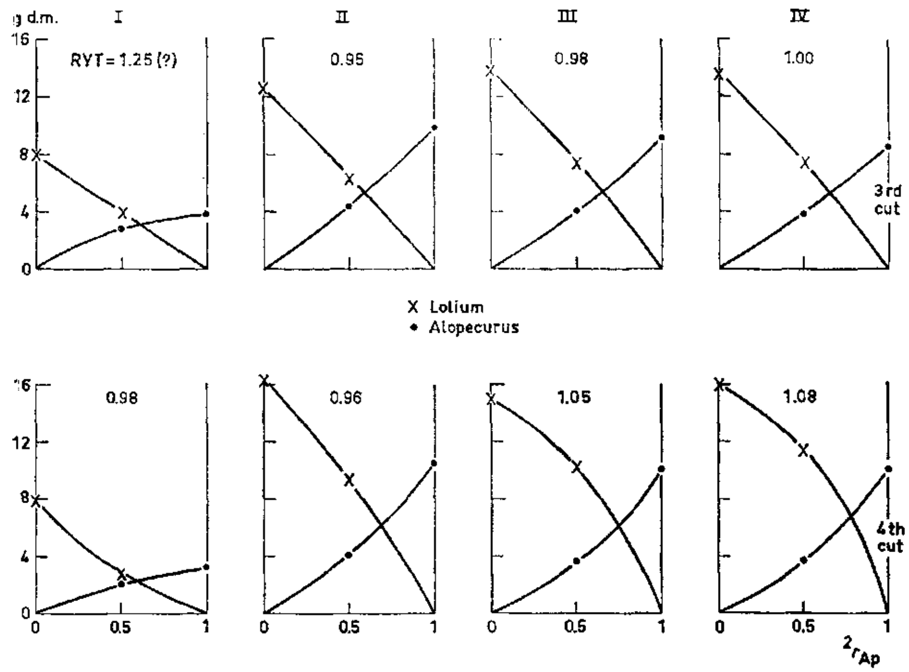

Fig. 37. Replacement diagrams of 2 successive harvests of a competition experiment with 4 K:Na ratios (see table 5). The observations of the mixtures refer to averages of 4 pots.

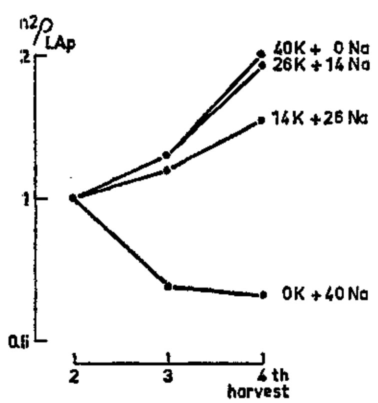

Fig. 38. Relative replacements rates of *Lolium* (L) with respect to *Alopecurus* (Ap) at 4 K:Na ratios of the added nutrients.

6 General discussion

The yield of a species in monoculture will first be examined for any relation with competitive ability. The influence of growth-limiting conditions on the botanical composition of a mixed culture will then be discussed. Finally the arguments frequently advanced in favour of mixed cultures will be considered.

6.1 Botanical composition

6.1.1 Yield and competitive ability

The species with the higher yield in monoculture frequently gains but not always as illustrated in figs 10 (first 3 cuts), 13, 37 (treatment I) and in section 5.5.2, in which the low yielding common bent (table 13) develops a considerable competitive ability (fig. 48). This is called the Montgomery effect (Montgomery, 1912; Gustafsson, 1951; de Wit, 1960) and rules out any predictions from the production of monocultures about competition in mixed culture. The consequences of this are discussed in section 6.2.1.

Table 13. Grammes of dry matter on 0.32 sq. metre for monocultures of 6 grasses with two extreme pH values (see also section 5.5.2).

	pH	sum of 3 cuts 1934	sum of 3 cuts 1935	first cut 1936	total
Agrostis tenuis	6.8	156	316	84	556
	4.6	188	258	52	498
Anthoxanthum odoratum	6.8	300	424	124	848
	4.6	212	326	84	622
Poa pratensis	6.8	148	456	184	788
	4.6	112	300	116	528
Festuca rubra	6.8	166	362	184	712
	4.6	128	264	104	496
Holcus lanatus	6.8	268	188	44	500
	4.6	208	244	52	504
Lolium perenne	6.8	356	418	156	920
	4.6	236	262	96	594

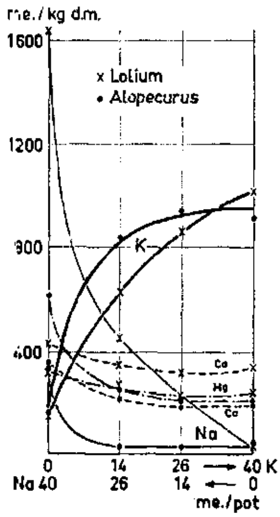

Fig. 39. Cation contents of *Lolium* and *Alopecurus* in the 3rd cut of the mixtures in a K-Na replacement series.

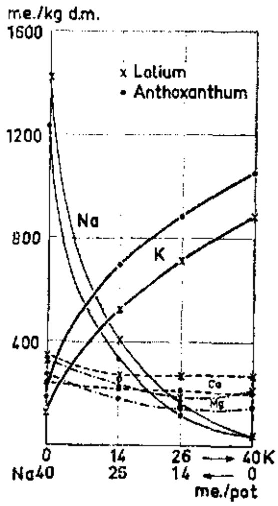

Fig. 41. Cation contents of *Lolium* and *Anthoxanthum* in the 3rd cut of the mixtures in a K-Na replacement series.

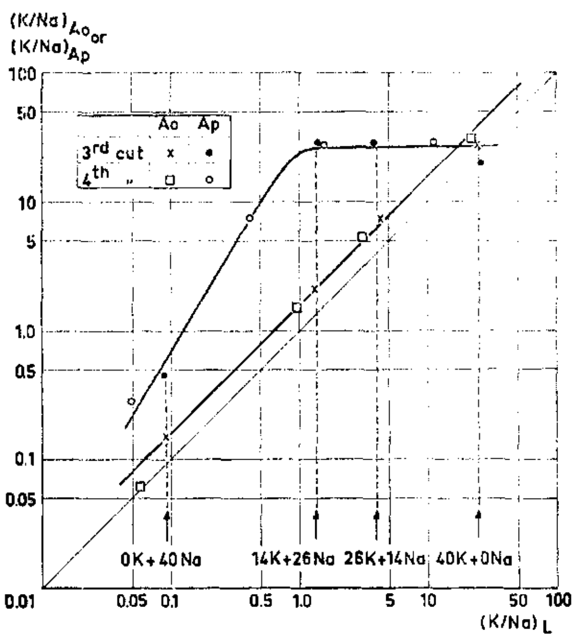

Fig.40. K:Na ratio of *Lolium* $(K:Na)_L$ plotted against the K:Na ratio of *Anthoxanthum* $(K:Na)_{Ao}$ or *Alopecurus* $(K:Na)_{Ap}$ (on a logarithmic scale) in a K-Na replacement series.

6.1.2 Competition under suboptimum conditions

The production of monocultures under optimum conditions can be used to predict which species will take advantage of suboptimum conditions in mixed culture. In the experiments with a growth-limiting factor the more productive species, that is the one with high yields in monoculture under optimum conditions, declines proportionally more in competitive ability than the less productive one (figs 37 and 38, 42 and 43).

The following seems to be the explanation. Under optimum conditions a closed leaf canopy forms within 3 to 4 weeks (the period between two successive cuts). The shade at the lower layers of the leaf canopy in mixed culture will be more harmful to the lower yielding species than to the higher yielding one, because in general a larger proportion of the foliage of the higher yielding species reaches the upper layers of the leaf canopy (taller tillers). When growth is limited, the thinner canopy will give less shade at the lower layers and in competition this will be specially advantageous to the lower yielding species (van den Bergh, 1968). This phenomenon is also recognized by Antonovics, Lovett & Bradshaw (1967) in discussing response curves of the same pattern with differences in yield at the optimum. They stated that in exposed conditions selection for small plants may occur. Moreover, according to Curtis & Clark (1950), Brouwer (1966) and various other workers, the shoot/root ratio decreases with increasing light intensity, so that the competitive position of the lower yielding species is improved also underground.

In competition with ryegrass, meadow foxtail was more vigorous at an extremely low value for K/Na in the medium than at a higher one (fig. 38), although at this low value for K/Na foxtail in monoculture decreased much more than ryegrass (fig. 37; the yield of foxtail in monoculture decreased to about a third and that of ryegrass to about a half of that in the monocultures at higher values for K/Na). The arguments mentioned before make this result more acceptable, for under suboptimum conditions the less productive foxtail will compete better than the more productive ryegrass.

If the species in monoculture yielded about the same, a growth-limiting factor did not influence competition (fig. 32 and 33 and the results not presented of the competition experiment with ryegrass and vernal grass in a K-Na replacement series in section 5.4). This completely agrees with the arguments mentioned already: a yield decrease in one species does not necessarily imply that the other species will be in a more favourable competitive position.

In this light the result of the competition experiment with ryegrass and cocksfoot (section 5.1) may also be explained as follows. From the 4th cut onwards the monocultures of cocksfoot in the normal treatment clearly yield less than those of ryegrass (fig. 25b). Clipping two days after cutting (exhaustion treatment) decreased the yields of the monocultures appreciably (fig. 25c). Merely because of this, the less productive cocksfoot will be more vigorous in competition (fig. 26).

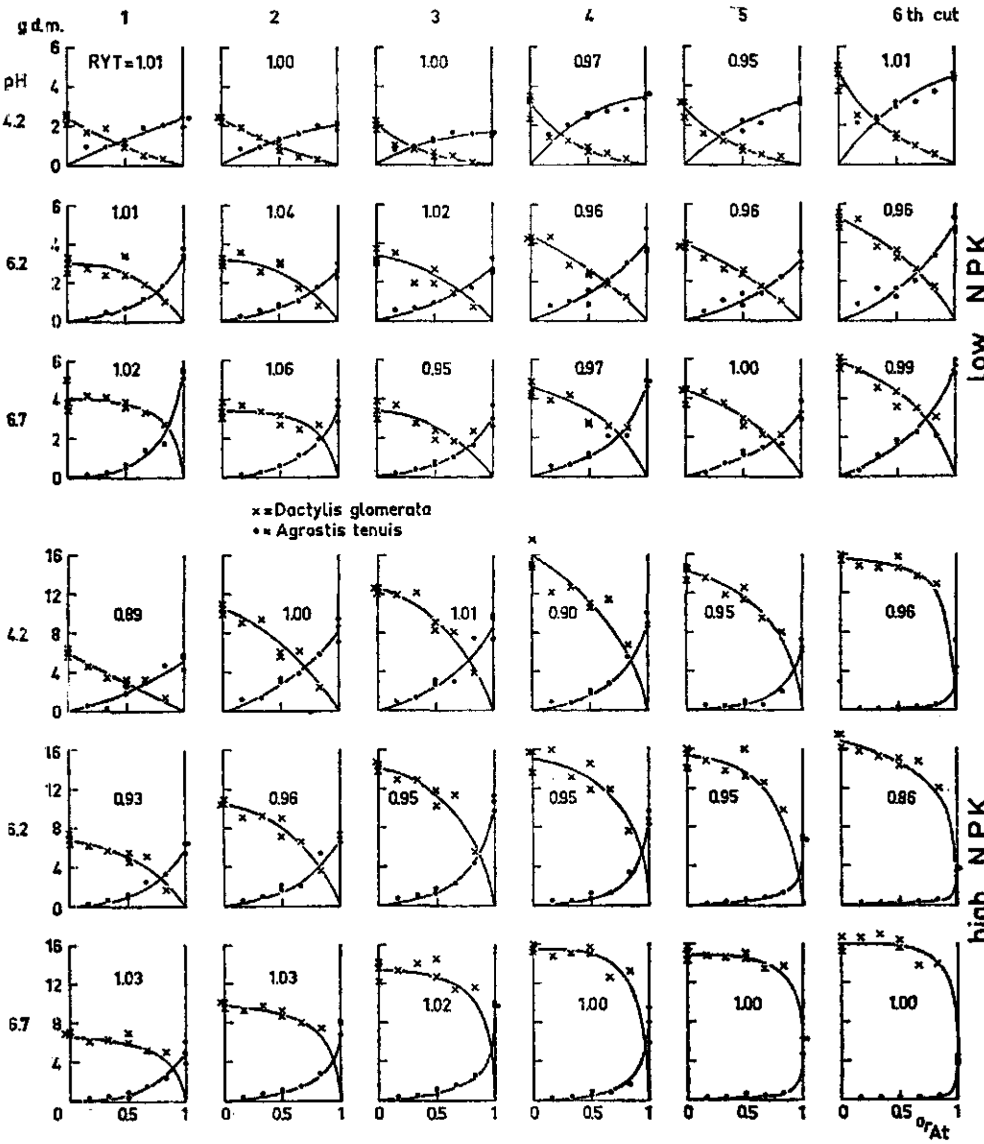

Fig. 42. Replacement diagrams of 6 successive harvests of a competition experiment with *Dactylis glomerata* and *Agrostis tenuis* at 3 pH values of the soil and 2 NPK supplies (see text). The relative seed frequency of *Agrostis* ($^{0}r_{At}$) is plotted on the horizontal axis.

This explanation is supported by the value of ϱ_{LD} midway between two cuts hardly differing from that of ϱ_{LD} at the preceding cut (fig. 50). (A few pots were harvested a week and a half after the regular three-weekly cut.) Ryegrass only gains towards the end of the period between two consecutive cuts. Probably, light deficiency at the bottom layer of the canopy only begins to occur in the second half of this period and in mixed culture this will be more harmful to the less productive species, cocksfoot. When this period is shortened by two days (exhaustion cut) this will be specially advantageous to cocksfoot in competition (fig. 26).

The lower production of a species is not always associated with shorter tillers. In the experiment with couchgrass and ryegrass under optimum conditions, the tillers of these species are about equal in length, despite the lower yielding monocultures of couchgrass (fig. 28, treatment IV). Suboptimum conditions will not therefore automatically favour competition by couchgrass.

6.2 Yields of monocultures and mixed cultures

In almost all experiments the monoculture of the more productive species yielded more than the mixed culture and this difference increased, as the proportion of less productive species increased in the mixture. This was true of each cut as well as of the total yield of all cuts. Yet under certain conditions a mixed culture of perennial grasses may well be more advantageous than a monoculture.

6.2.1 Choice of the species

Many people assume mixtures profitable when it is not known which species is more productive in a particular environment. But this assumption is based on the erroneous supposition that the species dominant in that environment will produce more than any other species in monoculture under the same conditions (negation of the Montgomery effect; see section 6.1.1).

If anyone sows a mixture, he will never learn which species would be more productive in that particular environment. Whereas, if instead of the mixture, monocultures of each grass species are sown next to each other, it will be found which species yields more on an average under these conditions. It will now be possible to retain the monoculture of the species and sow the rest of the field with it as well.

In addition there is the advantage that a productive species may also be higher yielding in monoculture under suboptimum conditions, even though this productive species is less competitive than under optimum conditions. Table 7 shows that the total yield of 6 cuts of cocksfoot monoculture is higher than or as high as that of common bent, even under conditions (low NPK) in which common bent gains (fig. 43). The same applies to the experiment with ryegrass and meadoy foxtail at various K:Na ratios in the soil (fig. 37 and 38): despite the greater competitive

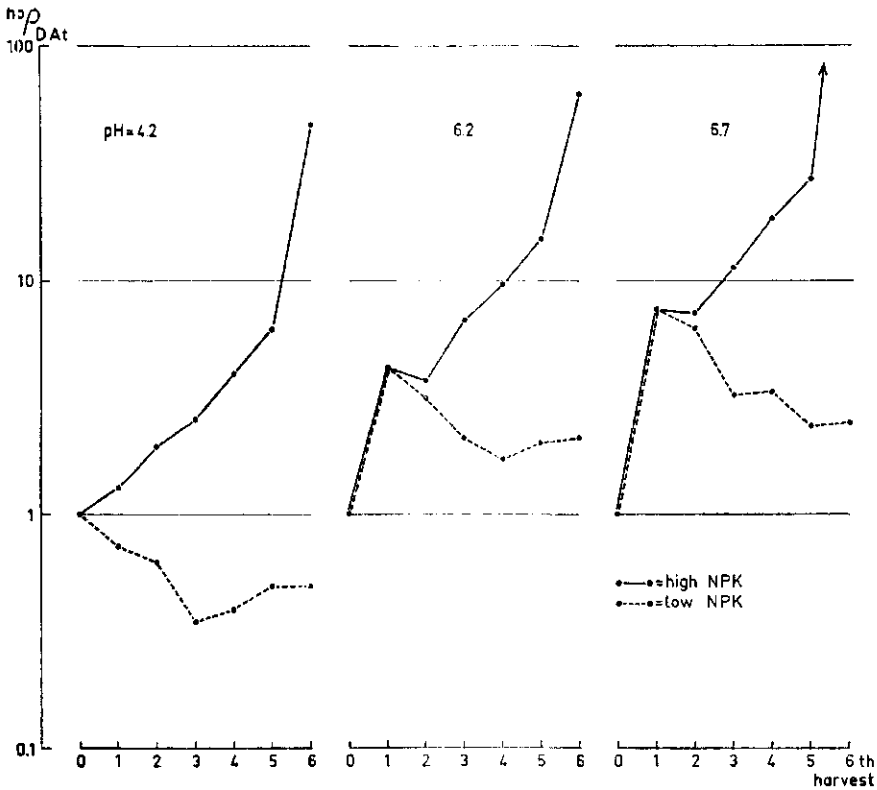

Fig. 43. Relative replacement rates of *Dactylis* (D) with respect to *Agrostis* (At) at 3 pH values and 2 NPK levels for 6 successive harvests. ϱ values are calculated in respect of the seed frequencies at the beginning of the experiment (harvest 0).

ability of foxtail at a very low value for K/Na, the monoculture of ryegrass produces more. Fig. 28 also illustrates that the monoculture of ryegrass produces on average more than that of couchgrass at all NPK levels, even though couchgrass is a more vigorous competitor than ryegrass at the higher NPK levels (fig. 30).

In all these cases the more productive species in monoculture also yields more under suboptimum conditions. A mixed culture does not cover the risk associated with lack of knowledge of species and may even be a disadvantage because the less productive species may dominate.

These facts and those mentioned in section 6.1.2 mean there is a greater risk of the less productive species becoming dominant under suboptimum conditions than under optimum conditions. Bradshaw *et al.* (1964) have emphasized that under conditions of low environmental potential, low yields may be a selective advantage. The consequences of this in relation to invading species is discussed in section 6.2.5.

6.2.2 Structure of the sod

In repeatedly harvested perennial crops are periods after cutting in which the leaf canopy of the crop is not closed. It should be possible to shorten these periods by using mixtures whose constituents have different growth forms. The competition experiment with ryegrass and cocksfoot in section 5.1 is an example. Fig. 25 shows, however, that the advantage is small and in this experiment occurs only when conditions are suboptimum. This might be the reason why Whittington & O'Brien (1968) obtained higher yields with mixtures than with monocultures, especially under simulated grazing (frequent clippings). In their experiments low supply of nitrogen and frequent clipping probably caused the canopy to be open for long periods so that light was not fully utilized and yields were low. Under these conditions differences in the structure of the sods of mixed and pure stands may result in mixtures outyielding monocultures.

In one other case (section 4.4) the mixture produces more than the monocultures even when conditions are optimum (fig. 20) but here too, the advantage is small since one of the species formed only a small proportion of the mixture (see also section 6.2.3).

6.2.3 Growth rhythm

During the growing season the productivity of a species may vary widely because of growth rhythm. A mixture of species with different growth rhythms may yield more (fig. 8a) than a monoculture. For instance in the experiment of England (1965) (section 4.2), the yield of the 2nd cut of the ryegrass monocultures was higher than that of cocksfoot, whereas the reverse was true in the next cut (fig. 12). Yet this did not result in the relative yield total for all cuts together being greater than 1. This is because cocksfoot could not suddenly take over in the mixture as

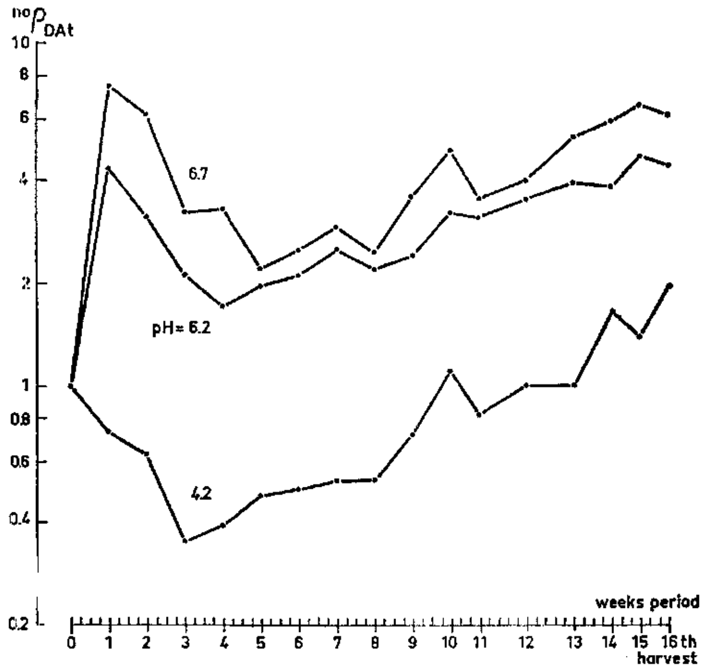

Fig. 44. Relative replacement rates of *Dactylis* (D) and *Agrostis* (At) at 3 pH values and low NPK supply for 16 successive harvests. See also fig. 43.

the determinant of yield at the 3rd cut (compare also the model in fig. 8a); the change in botanical composition is more gradual (according to the model in fig. 8b). In Englands' experiment ryegrass is replaced by cocksfoot during the season (fig. 14). The share of the less productive cocksfoot (fig. 13) is ever-increasing so that the yield of the mixture continually decreases relative to the yield of the monoculture of the more productive ryegrass (Montgomery effect). Any advantage of a more regular distribution of production over the season will therefore be at the expense of total production. To profit from the differences in growth rhythm, there is more sense in sowing the species next to each other in monoculture than in a mixed culture. In France and England the sowing of grass species with different growth rhythms in monoculture is indeed encouraged and an ingenious rotation has been devised to make most efficient use of differences in seasonal growth of the species. Farmers have not made much use of this system, probably because of its intricacy and because differences in seasonal growth of the species are only small compared with what may be achieved by applying nitrogen fertilizers at different times of the year.

6.2.4 Calamities

Mixed cultures are sometimes used to allow for special conditions, such as frost, drought and diseases, where the other species could rapidly fill the vacant space left by the much reduced main species. However, the second species included in the mixture to bridge the periods when yield of the main species is not maximum are generally less productive under optimum grassland management. The presence of this species may either delay recovery of the main species or, if the second is more competitive, may even prevent it. The advantage of a higher yield during the rather short periods after calamities will not offset the drawback of long periods in which the yields are lower than that of the monoculture of the main species.

In arable farming, one reason maintained for mixed cropping is the relation to diseases and pests (Zadoks, 1967). Because of differences between species in sensitivity, the spread in mixed culture is supposed to be less than in monoculture. But this is of less importance in grassland for leaf diseases, perhaps because this crop, contrary to arable crops, is repeatedly harvested during the season. As a result young vegetative material predominates and there is no time for the disease to spread.

Little is known about soil-borne diseases or pests in grassland. In case of nematodes monocultures will only stand more risk than will mixtures, if these organisms prefer certain grass species.

There even may be a danger in mixed cultures from pests and diseases. Van den Bergh & Elberse (1962) showed that vernal grass may carry a virus not harmful to itself but indeed so to ryegrass. In the mixture ryegrass was so badly affected by this virus that the relative yield total was much less than 1 and this highly appreciated species disappeared entirely.

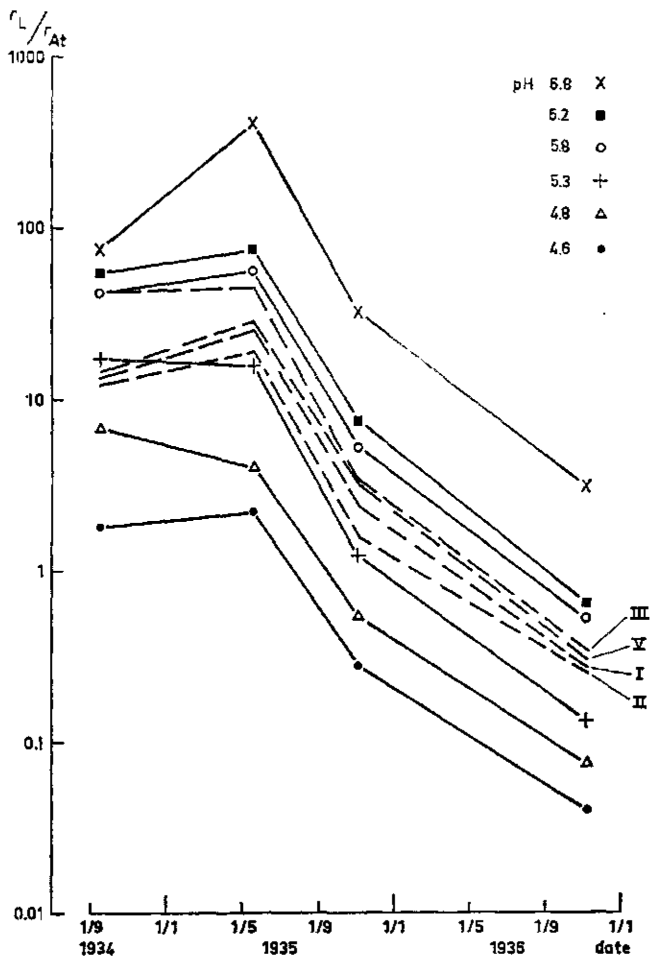

Fig. 45. The logarithmic mean of the quotients for relative yields of ***Lolium*** (r_L) and *Agrostis tenuis* (r_{At}) at successive harvests plotted against time in 4 mixtures with 6 values for soil pH.
——— same pH (averaged over the mixtures)
- - - - - - - same mixture (averaged over the pH values)

6.2.5 Resistance to invading species

The last three sections have shown that the risk of developing temporary open spaces may be greater in monoculture than in mixed culture. The open spaces can be occupied by invading undesirable species. In a ley system with a short grassland period and in semipermanent grassland this is of no importance. Sowing a mixture for permanent grassland may be sensible if the recovery from calamities of the main species is too small to resist invasion of less productive species, being more likely to occur under suboptimum growing conditions (section 6.2.1). The mixture will be superior only if the associated species will meet the following requirements: its productivity and competitive ability must be about the same as those of the main species and it must be resistant to conditions for which the main species is sensitive. It remains to be seen whether such a combination of species can be realized.

6.2.6 Conclusion

It should be stated that in general the monoculture of a persistent grass species, with the average highest yield under usual management, is to be preferred to a mixed culture with other grass species.

In sown permanent grassland, especially under suboptimum growing conditions, less productive or otherwise undesirable species may eventually invade. The question arises whether this invasion can be better prevented by a mixed culture than by a monoculture, without reducing the production too much by the presence of the associated species. With species not differing in yield this problem would not arise and a mixture may be more profitable than a monoculture.

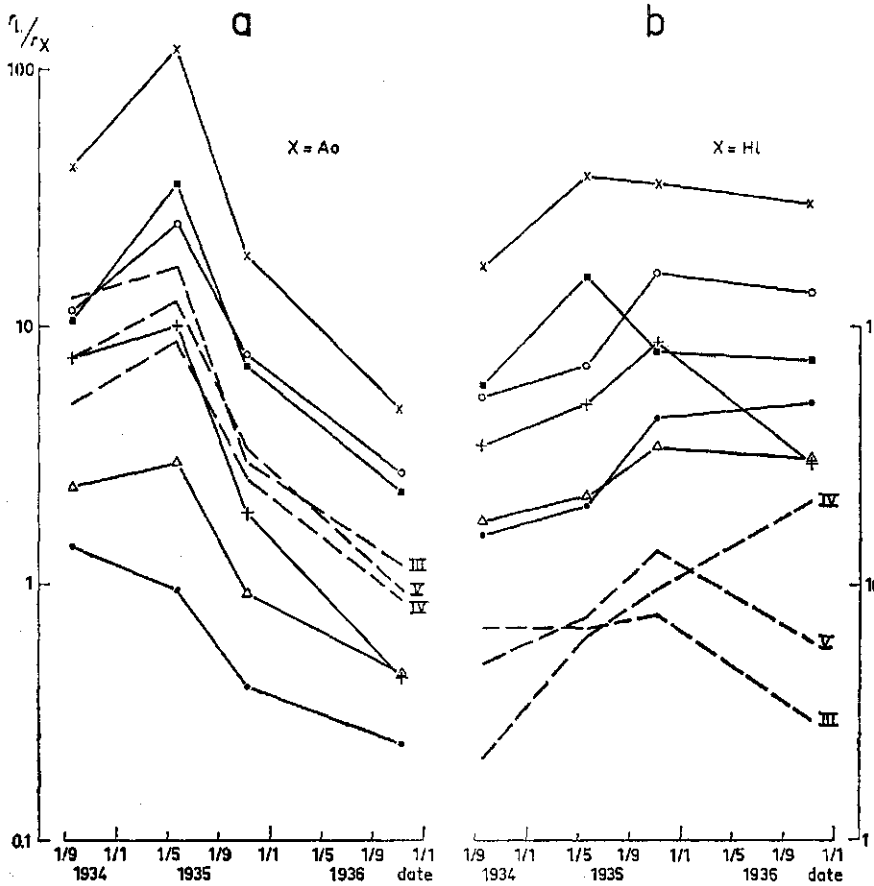

Fig. 46. The logarithmic mean of the quotients for relative yields of *Lolium* (r_L) and species X (r_X) at successive harvests plotted against time in different mixtures with 6 values for soil pH. For symbols see fig. 45.
Scale on the left refers to solid lines
Scale on the right refers to broken lines
Ao = *Anthoxanthum odoratum;* Hl = *Holcus lanatus*

7 Conclusions and summary

To describe competition species must be compared with a standard. By conventional standards, such as grammes dry matter, tiller number and sq. cm leaf area, two species and even one species cannot be compared in the course of the season. Therefore a standard without dimensions was needed. Dividing yield of a species (expressed in any unit) in mixed culture by that in monoculture gave a figure without dimensions, called relative yield.

Conclusions were based on my own pot experiments under controlled conditions and on field experiments of others.

1. The rate at which one species replaces another is independent of the proportion of a species in the mixture.
2. Competitive vigour of a grass species is independent of the other species or varieties associated with it in the mixture. This implies that if there are two experiments in which species A is competing with each of two morphologically identical varieties of species B, the result of competition between the varieties of B can be calculated. Competition in mixtures of two species will predict the competitive trend in more complex mixtures. In all these experiments the monocultures may never be omitted.
3. When a treatment limits growth, in general competition changes at the expense of the more productive species. This is because there will be less competition for light as yield decreases, so benefiting the lower yielding species. Under these conditions the shoot/root ratio of the lower yielding species seems to decrease, another reason why the lower yielding species benefits in competition by sub-optimum soil conditions. The above-ground production of a species with a large proportion of roots will respond less sharply to a shortage of minerals or water than a species with a higher shoot/root ratio. Hence, the change in competition in adverse conditions does not depend on the nature of the factor limiting growth.
4. Sowing experiments show that pH considerably affects the development of seedlings, even though pH values within the range 4.2 - 6.8 does not affect competition between fully grown plants. In general the period of establishment and the competition afterwards should be stricktly separated. If this is omitted, completely erroneous conclusions may be drawn about the competitive ability of the species.
5. Monocultures are preferred to mixed cultures for the following reasons.

a. Because the higher yielding species in a mixture is not always the dominant species (Montgomery effect); the apparent advantage is often even a drawback.

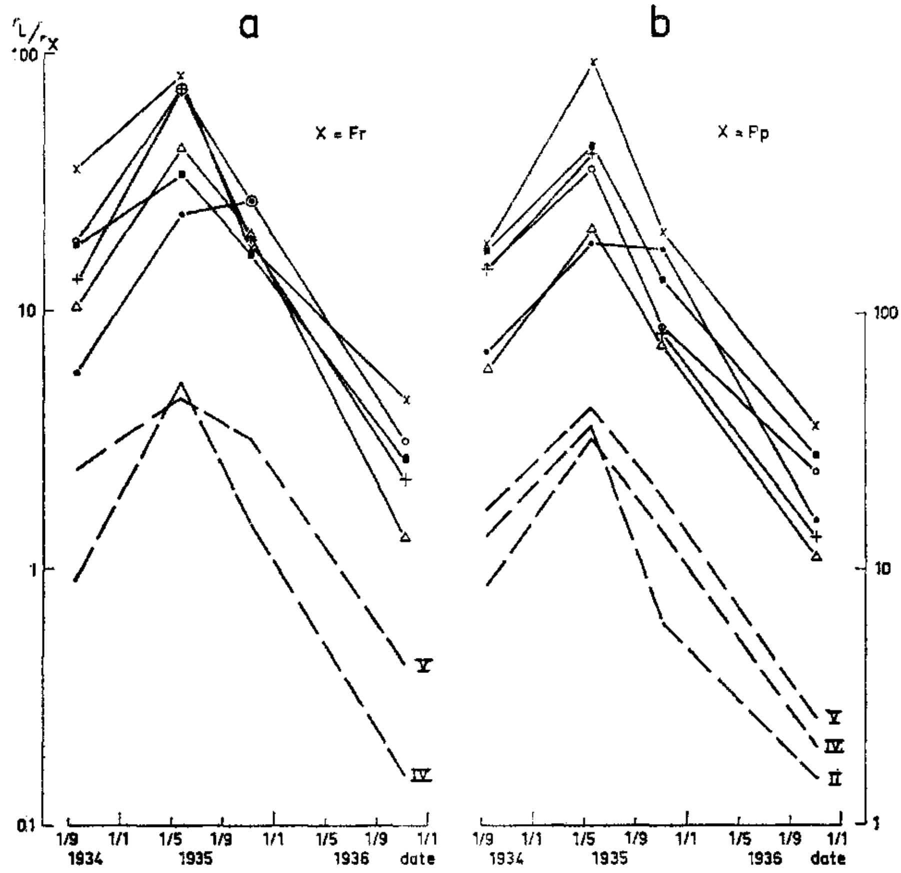

Fig. 47. As fig. 46 for *Festuca rubra* (Fr) and *Poa pratensis* (Pp).

The risk of the lower yielding species becoming dominant should not be underestimated.

b. The possibility that light is better utilized through the sod structure in a mixed culture can only be important during the period that the leaf canopy of the sod is not yet closed. In absolute terms this advantage is only small, especially if yields per cut are high; under grazing this possibility may be of more importance.

c. A mixture of species with different growth rhythms might yield more. If so the increased yield will only be worthwhile if the species alter their order of dominance within the growing season. But changes in botanical composition are more gradual, so that this advantage of a mixture is lost.

d. When the more productive species fails for some reason, the less productive species in the mixture could temporarily take over the production. But this temporary advantage may change into a persistent drawback, when recovery of the main species is hampered by the other species. On sown permanent grassland, especially under suboptimum conditions, less productive or otherwise undesirable species may in time invade the sward. It remains to be seen whether this is more efficiently prevented by a mixture or by a monoculture.

e. The problem in sowing grassland is the choice of the highest yielding species under the prevailing conditions, rather than the choice of the highest yielding mixture.

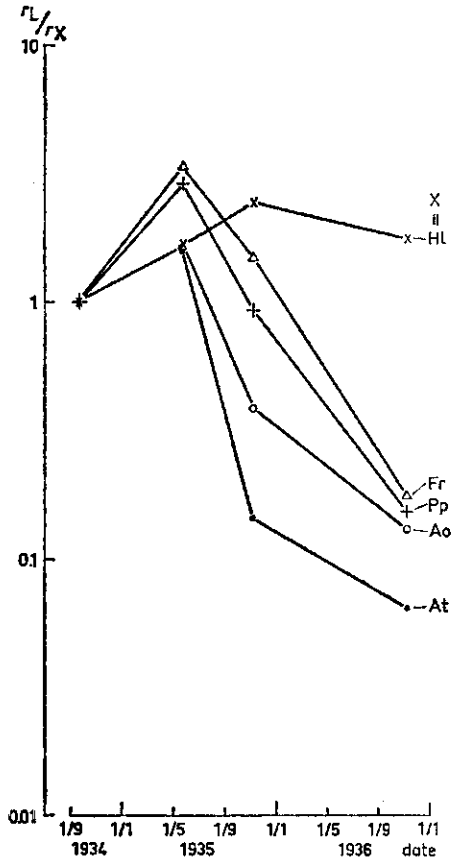

Fig. 48. The logarithmic mean of the quotients for relative yields of *Lolium* (r_L) and species X (r_X) of all treatments at successive harvests plotted against time. For abbrevations see fig. 45, 46 and 47.

Samenvatting

Voor een kwantitatieve beschrijving van de concurrentie is het noodzakelijk dat men beschikt over een maatstaf waarmee de soorten vergeleken kunnen worden. Aangezien aan de conventionele maatstaven, zoals grammen droge stof, spruitaantallen, cm^2 bladoppervlak, het bezwaar kleeft dat die van twee soorten en zelfs van één soort in de loop van het seizoen niet vergelijkbaar zijn, is gezocht naar een dimensieloze maatstaf. Door de hoeveelheid van een soort (in welke eenheid dan ook uitgedrukt) in mengcultuur te delen door die in monocultuur, verkrijgt men een dimensieloos getal dat de relatieve opbrengst is genoemd.

Aan de hand van eigen potproeven onder geconditionneerde omstandigheden en veldproeven van anderen is voor grassen het volgende aangetoond.

1. De snelheid waarmee een soort een andere soort vervangt is onafhankelijk van hun mengverhouding en onafhankelijk van de andere soorten in het mengsel.

2. Wanneer een factor groeibeperkend werkt wijzigen de concurrentieverhoudingen zich in het algemeen ten nadele van de produktiefste soort, dat is de soort die in monocultuur onder optimale omstandigheden bovengronds het meeste opbrengt.

3. De pH oefent een grote invloed uit op de ontwikkeling van kiemplanten, maar heeft binnen het traject 4,2 - 6,8 geen invloed op de concurrentiestrijd tussen volgroeide planten.

4. Om verschillende redenen verdienen monoculturen voorkeur boven mengsels.

a. De minder produktieve soorten in het mengsel kunnen gaan domineren.

b. Een eventuele betere benutting van het licht door het mengsel tengevolge van de structuur van de zode is bij hoge snedeopbrengsten van slechts geringe betekenis; onder beweidingsomstandigheden is dit voordeel misschien wat groter.

c. Mengsels van soorten met verschil in groeiritme zullen alleen meer opbrengen wanneer de soorten binnen het groeiseizoen van plaats verwisselen wat dominantie betreft. Gebleken is dat deze veranderingen veel geleidelijker plaats vinden.

d. Wanneer door één of andere reden de veel producerende hoofdsoort sterk gereduceerd wordt, kunnen de andere soorten van het mengsel de produktie tijdelijk overnemen. Dit tijdelijke voordeel kan echter in een langdurig nadeel veranderen wanneer deze soorten het herstel van de hoofdsoort vertragen of zelfs verhinderen. Voorts is het nog een open vraag of een mengsel de invasie van onproduktieve of anderszins ongewenste soorten beter kan tegengaan dan een monocultuur.

e. Het probleem bij de inzaai van grasland is niet zozeer de keuze van het meest producerende mengsel, maar de keuze van de meest opbrengende soort onder de gegeven omstandigheden.

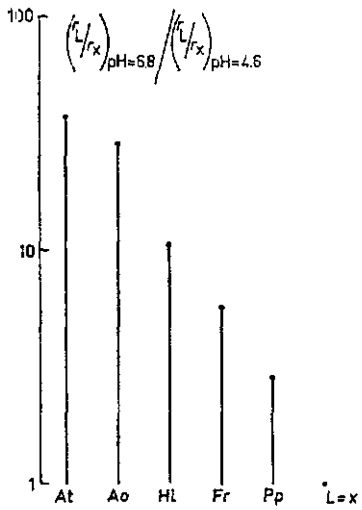

Fig. 49. Effect of pH on the quotient of the relative yield of perennial ryegrass (L) and several other grass species.

Pp = meadow grass
Fr = red fescue
Hl = Yorkshire fog
Ao = sweet vernal grass
At = common bent

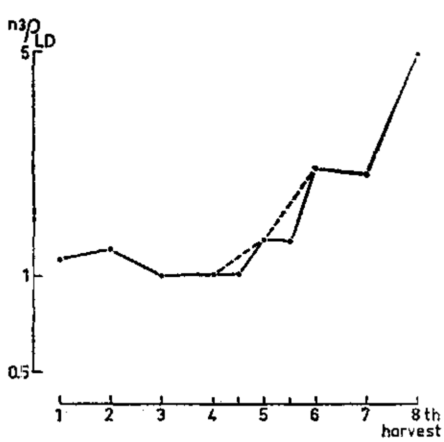

Fig. 50. Relative replacement rates for *Lolium* (L) with respect to *Dactylis* (D).

References

ALBERDA, TH. 1966 The infuence of reserve substances on dry-matter production after defoliation. *Proc. X intern. grassl. Congr. Finland:* 140-147.

ANTONOVICS, J., J. LOVETT and A. D. BRADSHAW 1967 The evolution of adaptation to nutritional factors in populations of herbage plants. Pp. 549-567 in: Isotopes in plant nutrition and physiology. *Proc. Symp. Intern. Atomic Agency, Vienna.*

BAEUMER, K. and C. T. DE WIT 1968 Competitive interference of plant species in monocultures and mixed stands. *Neth. J. agric. Sci. 16:* 103-122.

BAKHUIS, J. A. and H. J. KLETER 1965 Some effects of associated growth on grass and clover under field conditions. *Neth. J. agric. Sci. 13:* 280-310.

BERGH, J. P. VAN DEN 1968 Distribution of pasture plants in relation to chemical proporties of the soil. In: Ecological aspects of the mineral nutrition of plants. *Brit. Ecol. Soc. Easter Symp.* (in print).

BERGH, J. P. VAN DEN and W. TH. ELBERSE 1962 Competition between Lolium perenne L. and Anthoxanthum odoratum L. at two levels of phosphate and potash. *J. Ecol. 50:* 87-95.

BRADSHAW, A. D., M. J. CHADWICK, D. JOWETT and R. W. SNAYDON 1964 Experimental investigations into the mineral nutrition of several grass species. IV. Nitrogen level. *J. Ecol. 52:* 665-676.

BROUWER, R. 1966 Root growth of grasses and cereals. Pp. 153-166 in: The growth of cereals and grasses (eds F. L. Milthorpe and J. D. Ivins). *Proc. 12th Easter School Agric. Sci.,* Univ. Nottingham, 1965.

COWLING, D. W. and D. R. LOCKYER 1968 A comparison of the yield of three grass species at various levels of nitrogenous fertilizer sown alone or in a mixture. *J. agric. Sci., Camb. 71:* 127-136.

CURTIS, O. F. and D. G. CLARK 1950 An introduction to plant physiology. McGraw Hill Book Cy., New York.

DIJKSHOORN, W. 1956 De opneembaarheid der kationen uit oplossingen bij engels raaigras en kropaar. *Versl. centr. Inst. landbouwk. Onderz., 1955:* 187-195.

DOBBEN, W. H. VAN 1956 Concurrentie tussen haver en zomergerst op een pH-trappenproefveld. *Versl. centr. Inst. landbouwk. Onderz., 1955:* 128-131.

DOBBEN, W. H. VAN and A. C. WIERSEMA 1956 Potproeven met mengcultuur van haver en gerst bij verschillende zuurgraad. *Versl. centr. Inst. landbouwk. Onderz., 1955:* 131-133.

ENGLAND, F. J. W. 1965 Interaction in mixtures of herbage grasses. *Scottisch pl. breed. Sta. Rec. 1965:* 125-149.

GUSTAFSSON, A. 1951 Mutations, environment and evolution. *Gold Spr. Harbour Symp. on quant. Biol. XVI:* 263-280.

HARPER, J. L. 1961 Approaches to the study of plant competition. *Symp. Soc. exp. Biol. 15:* 1-39.

HEDDLE, R. G. and W. G. OGG 1937 Soil nutriens in relation to pasture maintenance and improvement. *Rep. 4th intern. grassl. Congr.*, Aberystwyth: 298-302.

KLAPP, E. 1954 Wiesen und Weiden. Paul Parey, Berlin. 519 pp.

KRUIJNE, A. A., D. M. DE VRIES and H. MOOI 1967 Bijdrage tot de oecologie van de Nederlandse graslandplanten. *Versl. landbouwk. Onderz. 696:* 1-65.

LAMPETER, W. 1960 Gegenseitige Beëinflussung höherer Pflanzen in bezug auf Sprosz- und Wurzelwachstum, Mineralstoffgehalt und Wasserverbrauch - untersucht an einigen wirtschaftlich wichtigen Futterpflanzen. *Wiss. Zeitschr. Karl-Marx-Univ., Leipzig. Mathem.-Naturwiss. Reihe 9 (4):* 611-722.

MONTGOMERY, E. G. 1912 Competition in cereals. *Bull. Nebr. agr. exp. Sta. XXIV, art. V:* 1-22.

POZO IBANEZ, M. DEL 1963 The effect of cutting treatments on the dry-matter production of *Lolium perrenne* L. and *Dactylis glomerata* L. *Versl. landbouwk. Onderz. 69 (17):* 1-74.

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.

SAID, I. M. 1959 Cation selectivity and cation-anion balance as factors governing the mineral composition of pasture herbage. *Versl. landbouwk. Onderz. 65 (16):* 1-64.

VRIES, D. M. DE 1940 Een oriënterende proef over den invloed van bekalking van zuren zandgrond op opbrengstvermogen en concurrentieverloop van eenige grassoorten en witte klaver. *Landbouwk. Tijdschr. 52:* 8-17.

VRIES, D. M. DE 1949 Survey of methods of botanical analysis of grassland. *Rep. 5th intern. Grassl. Congr. Neth.:* 133-142.

WHITTINGTON, W. J. and T. A. O'BRIEN 1968 A comparison of yields from plots sown with a single species or a mixture of grass species. *J. appl. Ecol. 5:* 209-213.

WIT, C. T. DE 1960 On competition. *Versl. landbouwk. Onderz. 66 (8):* 1-82.

WIT, C. T. DE 1961 Space relationships within populations of one or more species. *Symp. Soc. exp. Biol. 15:* 314-329.

WIT, C. T. DE and J. P. VAN DEN BERGH 1965 Competition between herbage plants. *Neth. J. agric. Sci. 13:* 212-221.

WIT, C. T. DE, P. G. TOW and G. C. ENNIK 1966 Competition between legumes and grasses. *Agric. Res. Rep. 687:* 1-30.

ZADOKS, J. C. 1967 Bespiegelingen over resistentie. *Zaadbelangen 21:* 162-168.