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ON THE MODELLING OF COMPETITIVE PHENOMENA

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On the modelling of competitive phenomena

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Abstract

It is shown that the dynamics of interfering species is most conveniently characterized on the basis of their relative abundances, which is defined as the ratio of the abundance of a species (measured as yield, number, etc.) in a mixture and in a monoculture under the same conditions, except for the competitive situation. This procedure is justified by the observation that under many conditions, species exclude each other; i.e. that the relative abundance total of the interfering species is equal to one. Examples of such situations are presented and discussed.

Subsequently it is shown that in situations where species exclude each other, it may be possible to simulate the growth of the species in a mixture solely on the basis of observations of the growth of the species in a monoculture. A simulation model of this situation, written in one of the continuous system simulation languages is presented.

The relative reproductive rate

Animals as well as annual plants have a definite life cycle so that successive generations may be easily distinguished. When, moreover, the individuals are readily distinguishable it is customary to express the performance from one generation to the other in terms of the reproductive rate, which is often defined as the ratio between the number of animals in two successive generations. It is then often implicitly supposed that a ratio of two means that the species is twice as abundant. But this only holds when the individuals of the successive generations are of the same phenotype, which is often not the case. A good example of this is given by Dempster in these Proceedings. In some years his Cinnabar moths are small and in other years large; these changes are accompanied by a range in fecundity of about 70 to 300 eggs per female.

When two species are coexisting, it is customary to characterize their dynamics with respect to each other with a double ratio, sometimes called the 'relative fitness', but for which the more explicit term 'relative reproductive rate' will be used here.

This relative reproductive rate of two species a and b in two successive years is defined by:

$${}^2_1\alpha_{ab} = \frac{{}^2O_a/{}^1O_a}{{}^2O_b/{}^1O_b} \quad (1)$$

It is said that both species match each other when ${}^2_1\alpha_{ab} = 1$ and that species a gains on species b when its value > 1 ; it being again tacitly assumed that the individuals of each species are of the same phenotype in successive generations.

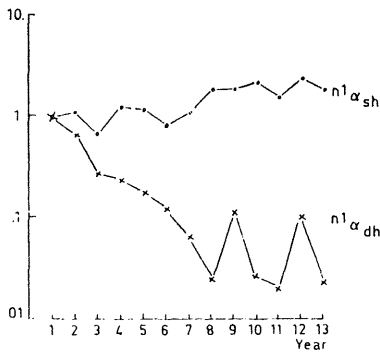


Fig. 1. 'Course lines' for the barley varieties White Smyrna (s) and Deficiens (d) with respect to Hannchen (h) calculated from the number of seeds in the yield of a mixture grown in Idaho (USA) (Harlan et al., 1938).

Without considerable experimental effort it is very difficult to prove or disprove the validity of the latter assumption. Hence, especially when the relative reproductive rate does not vary too much from one, it is always hard to conclude which species is actually gaining in a particular year.

An example is given in Fig. 1. This presents the results of a thirteen year experiment with some barley varieties done by Harlan and Martini. The species were sown in the first year in the same proportions and the harvested mixtures were resown in the following years. Even when the seeds of the species concerned are not the same in successive years, it is obvious that the cultivar Deficiens was much weaker than Hannchen in this situation. However, the cultivar Smyrna matched Hannchen fairly well over the 13 years.

An attempt can be made to correlate the relative decrease of Smyrna in, for instance, the 3rd, the 6th and 11th years with the particular circumstances in these years. But then it must be realised that the relatively bad performance of the cultivar Smyrna may be due either to a relative bad growth of the variety in those years or to the harvesting of relatively poor seeds of this variety in the preceding year. It is impossible to distinguish between the possibilities without further observations and analyses.

These difficulties are amplified in ecological studies where perennial plant species or long living animals are involved and one is interested in their year to year performance. This will be illustrated by considering grassland plants in pastures and meadows. With these vegetative species the generation concept loses its meaning, whereas it is also often impossible to distinguish individuals. Harvests, if any, are not resown, but stubbles and roots are left over for regrowth. Moreover, each harvest grows under different circumstances so that it is even impossible to assume that one gram of yield from one harvest is the same as one gram of yield from the other. Unless changes are very drastic, it is very difficult to say which species gains or loses on the other within a certain period. We may revert to counting, for instance, the number of sprouts of each species at intervals, but then it appears again that these may change systematically several-fold in size and vigour during the course of even a short experiment.

The use of reproductive rates and relative reproductive rates in such situations may be very misleading, as is shown by the results of an experiment with *Lolium perenne* and *Anthoxanthum odoratum* grown in competition. In Fig. 2 the course lines for the mixtures, or the relative reproductive rates with respect to the fifth harvest on a logarithmic scale as a function of time are presented. Based on counts of the number of sprouts, it appears that the two species match each other to a large extent. But the experiment had to be termi-

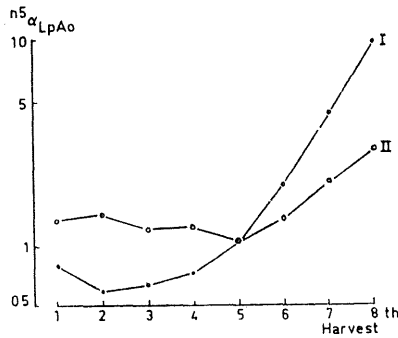


Fig. 2. The relative reproductive rate of *Lolium perenne* (Lp) with respect to *Anthoxanthum oderatum* (Ao), calculated on basis of dry matter yields (I) and number of sprouts (II) (de Wit et al., 1965).

nated at the ninth harvest, because *Anthoxanthum* had completely disappeared. The course line based on dry matter yields seems to reflect the situation much better, but this, of course, is a conclusion after the observation that the *Anthoxanthum* species has gone.

Thus, the conclusion of Harper (1961) may be reached that: 'if we neglect 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 ecological analyses'.

The relative replacement rate

But Harper's conclusion is unduly pessimistic. It can be shown that many of the difficulties may be overcome by studying these vegetative species both in mixtures and in monocultures under the same conditions, and by comparing their performances not on an absolute, but on a relative value of abundance. This relative abundance is defined as the ratio of the yield, or the number of sprouts or any other abundance measure, in the mixture (O) and its comparative value (M) in the monoculture, grown under the same conditions except for the competitive situation, i.e. as:

$$r = O/M \quad (2)$$

As long as the influence of weather, nutrient status and so on are relatively the same on the species in the mixture and the monoculture, this relative yield is a truly dimensionless value and should be independent of the type of yardstick used for measurement of the abundance of the species.

The main justification for this procedure lies in the observation that after some period of growth of the species, they often exclude each other in the mixture. This follows from the observation that the relative abundance total:

$$RAT = r_a + r_b = O_a/M_a + O_b/M_b \quad (3)$$

is equal to one. This phenomenon, which characterizes a competitive situation for the same niche, is illustrated in Fig. 3 for a mixture of *Lolium perenne* and *Anthoxanthum oderatum*.

This situation, where two species are mutual exclusive, is automatically achieved with pasture species, irrespective of original seed or planting rates in mixture and monoculture and of the yield limiting factors. With annual crops it is, of course, possible to synthesize

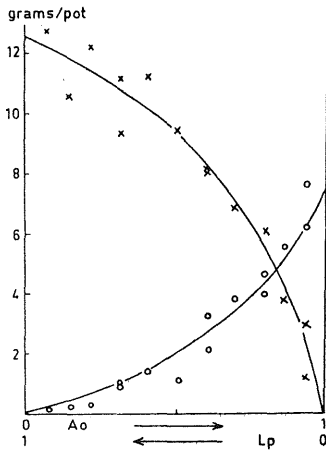


Fig. 3. A replacement diagram for the species *Lolium perenne* (Lp) and *Anthoxanthum oderatum* (Ao) with the relative planting frequency along the horizontal axis (de Wit et al., 1965).

the above situation in an experiment by planting a replacement series, i.e. by choosing the seed rates in the mixture in such a way that the sum of the relative seed rates is always one.

The relative abundance being defined, it is possible to define the relative replacement rate of species a with respect to species b for successive observation dates 1 and 2 by:

$${}^1_2\rho_{ab} = \frac{{}^2r_a/{}^1r_a}{{}^2r_b/{}^1r_b} \quad (4)$$

It is obvious that the species neither gain nor lose in the mixture as long as the relative replacement rate is 1. If this relative rate is greater than one, species a gains space on species b and when it is smaller than 1, species b gains space on species a. The course lines based on the relative abundances, calculated from dry matter yields and number of sprouts, are presented in Fig. 4 for the *Lolium* and *Anthoxanthum* mixture. Contrary to the course lines based on the relative reproductive rate in Fig. 2, it appears that here the course lines are practically the same and, whether based on dry matter yields or counts of the number of sprouts, both lead to the conclusion that *Anthoxanthum* disappears.

Anthoxanthum, as measured on the basis of dry matter yields rather than number of

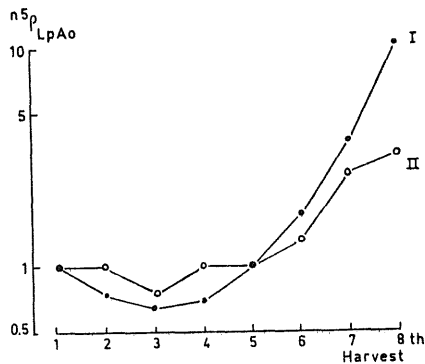


Fig. 4. The relative replacement rate of *Lolium perenne* (Lp) with respect to *Anthoxanthum oderatum* (Ao) calculated on basis of the relative abundance with respect to dry matter yield (I) and number of sprouts (II) (de Wit et al., 1965).

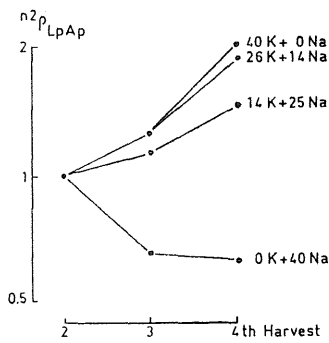


Fig. 5. The relative replacement rate of *Lolium perenne* (Lp) with respect to *Alopecurus pratensis* (Ap) at four K: Na fertilizer combinations in meq/pot (van den Bergh, 1968).

sprouts, still vanishes somewhat faster; but this is mainly due to clipping at 5 cm above the soil surface so that, especially at later stages, the small *Anthoxanthum* sprouts escape the treatment.

By using relative replacement rates it is now very easy to study quantitatively the effect of different conditions on the mutual interference of species. This is illustrated in Fig. 5, where the influence of the potassium-sodium ratio in the fertilizer on the relative replacement rate of *Lolium* with respect to *Alopecurus* is presented.

The relative abundance total

When the Relative Abundance Total (RAT) is one, it is good evidence of a situation where the species concerned compete for the same niche, to use an expression borrowed from animal ecology. In a replacement series, this phenomenon is reflected by the yield lines of the species concerned curving upward and downward to the same extent. As well as in Fig. 5, this is also illustrated in Fig. 6 for an experiment with oats and barley. It should be noted that in this experiment barley in monoculture yielded less kernels than oats, but also that in spite of this the yield line for barley is curved upward and that for

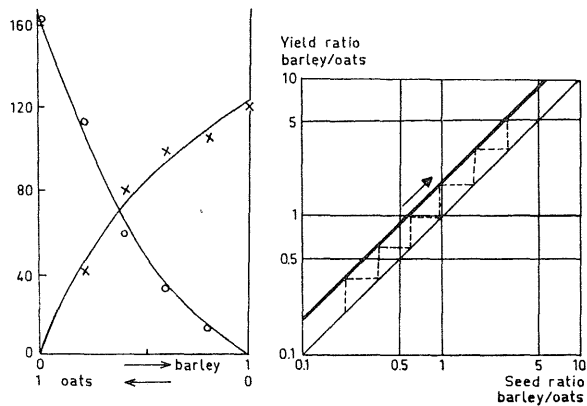


Fig. 6. The results of a replacement experiment with barley and oats and a frequency graph to illustrate that, in a case of repeated cultivation under the same conditions, the barley gains in spite of its lower yield in monoculture (de Wit, 1960).

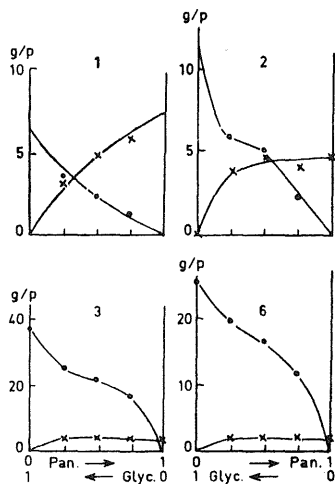


Fig. 7. Replacement diagrams for the dry matter yields in gram/pot of harvest 1, 2, 3 and 6 of *Panicum maximum* (P) and *Glycine japonica* (G), the latter being a leguminous grassland species (de Wit et al., 1966).

oats curved downward to such an extent that barley replaced oats in the mixture. This is illustrated in the frequency graph where the harvest ratio in the mixture is plotted against the seed ratio. The cause of this phenomenon is explained in the second part of this paper.

In plant mixtures it is often observed that a species gains in spite of its low yield. I do not know whether this is also the case with animals, but assumptions, as made for instance in Fisher's theory of natural selection or derivatives from this theory, which implicitly state that the high yielding species always wins are certainly wrong.

Situations where two species are not excluding each other are easily recognized in replacement experiments, since then the yield lines are not curved up- and downward to the same extent so that the relative abundance total is larger than one. This is illustrated in Fig. 7, which concerns a replacement series of a leguminous and a non-leguminous grassland species, the former taking its nitrogen from the air and the latter from the soil. Course lines for various mixtures (Fig. 8), calculated as the ratios of the relative yields of both species, approach each other, revealing that these two species, which grow as far as their nitrogen is concerned in different niches, arrived at an equilibrium situation.

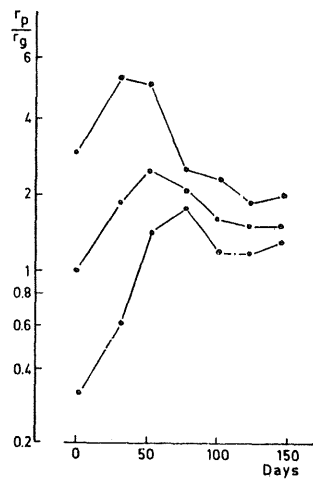


Fig. 8. Course lines for various mixtures of *Panicum maximum* and *Glycine japonica* (de Wit et al., 1966).

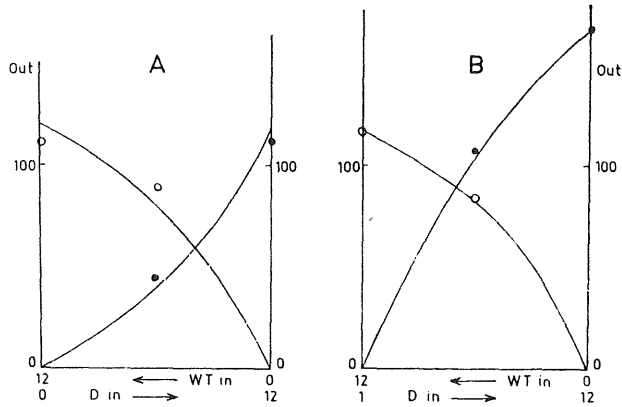


Fig. 9. Replacement diagrams for the *Drosophila* mutant 'Dumpy' (D) and 'Wild Type, (WT), taken from stock (A) and after selection for some generations in a competitive environment (B) (Seaton et al., 1967).

The sensitivity of this type of analysis is very well shown by the results of an experiment by Seaton and Antonovics (1967) with *Drosophila* 'Wild Type' and 'Dumpy', presented in Fig. 9. A replacement experiment with these two strains, after growing them in monocultures for several generations, showed that they practically exclude each other. However, if a similar experiment is done with the two strains after growing them for only two generations in a mixture, it appears that both yield lines are curved upward. Hence, within two generations the varieties were able to find separate niches. That this is possible in half-pint milk bottles with a maize/treacle medium seeded with dried yeast and kept at 23 degrees in the dark, seems very surprising to me. But the experimental technique is sensitive enough to reveal the phenomenon.

These examples must serve to show us that in experimental population dynamics it is worthwhile to consider not only the behaviour of the species when they are growing in situations of mutual interference, but to study at the same time their behaviour in monocultures. In the laboratory, this may be done as well with plants as with animals. Since animals often have the unfortunate habit of moving about, it may be difficult for animal ecologists to realise experimental situations of this kind under field conditions. Plant ecologists are here at a definite advantage.

Stochastic and deterministic models

Numerical characteristics like relative yield, reproductive rate or replacement rate are approximations of the endpoint of a continuous and deterministic process of growth and development of the organisms involved. The use of these characteristics implies that we abstract from the underlying continuous process and simplify our world view by separating the phenomena in time. If the dispersion of the population in space is considered simultaneously, it is also necessary to separate the phenomena in space. As a consequence, it is impossible to analyse in detail the influence of the diversity of circumstances on the behaviour of the species, so that this diversity has to be accounted for by the introduction of stochastic elements.

If, moreover, the number of individuals of the species is so small that there is also a definite chance of extinction, it is necessary to consider many sequences of random events to arrive at meaningful conclusions regarding the abundance and dispersion of species. This stochastic approach is advocated by Birch, Reddingius and den Boer in these Proceedings.

Just as discrete and stochastic models abstract from the underlying continuous and deterministic growth processes, it is possible to abstract from the discrete and stochastic aspects and pay special attention to the continuous and deterministic processes.

A simple example may be used to illustrate this. In the first part of this paper, attention was drawn to the phenomenon that barley gains on oats in spite of the fact that in monoculture oats is the higher yielding species. This phenomenon can only be understood by considering the continuous process of growth and development, and since this can be done by means of an analysis which is an extension of the Lotka-Volterra approach in animal ecology, it is worthwhile to elaborate on this.

Growth analyses in a competitive situation

The yield of a plant species sown in monoculture depends on plant density and the length of the growing period. At earlier stages or within low density ranges, the yield is almost proportional to plant density, but later on and at higher plant densities a maximum yield will be approached. These saturation type of yield curves may be represented within a wide range of densities by:

$$O = \frac{B \cdot S}{B \cdot S + 1} OM \quad (5)$$

where S is the density of sowing or planting, O the yield and OM the maximum yield which is obtained at very high planting densities (the condition where all space is occupied) and B is the space occupied by a single plant growing alone. Both B and OM are functions of time which may be determined by the periodic harvesting of a spacing experiment. The quotient:

$$SO = O/OM \quad (6)$$

is called the relative space (or yield) occupied at the seed density S. The relationship between B and time for barley and oats, obtained in a particular experiment, is presented in Fig. 10. In the case of barley, B at first increases rapidly, but remains constant during the second half of the growth period; whereas for oats B increases slowly at first but continues to increase at an age when the curve for barley has already flattened. Differentiating the equation:

$$SO = B \cdot S / (B \cdot S + 1) \quad (7)$$

and expressing S in the resulting equation in terms of SO and B, results in:

$$\frac{d(SO)}{dt} = \frac{dB/dt}{B} SO (1-SO) \quad (8)$$

which is the well known differential equation for the logistic curve, except that here the equivalence of the relative growth rate, i.e. $(dB/dt)/B$, is a variable function of time.

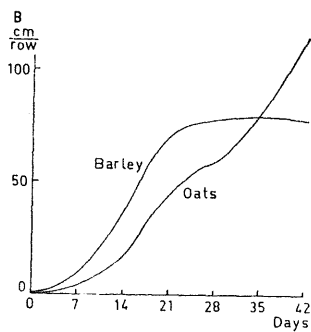


Fig. 10. The space (B) occupied by single row of barley and oats in relation to time, as calculated from periodically harvested spacing experiments (Baeumer et al., 1968).

If it is now assumed that barley and oats compete for the same niche in space, the Lotka-Volterra differential equations hold for the relative yield or space of each of the species:

$$\frac{d(SO)}{dt} = \frac{d B/dt}{B} SO (1 - \text{SUMSO}) \quad (9)$$

in which SUMSO is the relative space occupied by both species together. The actual yield of each species is then found according to Eq. 6 with:

$$O = SO \cdot OM \quad (10)$$

A simulation model

It is impossible to obtain an analytical solution of these differential equations. Instead a solution is obtained by means of a simulation language, called Continuous System Modeling Program (CSMP), which is very suitable for the simulation of biological systems (Brennan et al., 1970). As an illustration, the whole program, as presented to the computer, is set out below.

```

MACRO  O,SO = GROWTH (BTBL, OMTB, SOI, DBI, SUMSO, DAY)  (1)
        SO = INTGRL (SOI,RSO)  (2)
        RSO = RGR * SO * (1 - SUMSO)  (3)
        RGR = DB/B  (4)
        B = AFGEN (BTBL,DAY)  (5)
        DB = DERIV (DBI,B)  (6)
        O = SO * OM  (7)
        OM = AFGEN (OMTBL, DAY)  (8)
ENDMAC  (9)

```

The mathematical behaviour describing the dynamic behaviour of one species in a mixture is presented in a MACRO called GROWTH. In line (2) it is stated that the relative space occupied by the species is the integral of its rate of occupation and in line (3) that this rate of occupation is the product of the relative 'growth' rate, the relative space which is occupied by the species and the space not yet occupied by any species, according to Eq. 9. Line (4) defines the relative growth rate as the quotient of DB and B, in which B is the absolute space occupied by a single plant and DB its rate of increase. In line (5) it is stated that B is a function of the number of days after emergence, and that the

function itself will be provided in tabulated form (BTBL). DB is then defined in line (6) as the derivative of B with respect to time. Line (7) calculates the yield according to Eq. 10. Line (8) states that the value of OM is again obtained from the day after emergence by means of the tabulated OMTBL. Line (1) defines the input and the output of the MACRO and line (9) its end.

At the start of the simulation the initial values of the relative space which is occupied (SOI) and the rate of increase of B (DBI) have to be calculated out of the seed rate (S). This is done with a MACRO called BEGIN.

```
MACRO SOI,DBI = BEGIN (BTBL,S,START)
      SOI = B * S / (B * S + 1) (1)
      B = AFGEN (BTBL, START) (2)
      DBI = AFGEN (BTBL, START + 1) - B (3)
```

ENDMAC

Line (1) calculates the initial space that is occupied by the species by means of Eq. 7 from the seed rate (S). Line (2) calculates B, and line (3) states that the rate of increase of B is equal to the difference between the values of B at the start of the simulation and one day later. Eq. 7 can only be used in the early stage, when the species on a field do not as yet interfere with each other.

The actual simulation program for a mixture of two species is now as follows:

INITIAL

```
SOI1, DBI1 = BEGIN (BTBL1, S1, START)
```

```
SOI2, DBI2 = BEGIN (BTBL2, S2, START)
```

These two lines calculate the initial values for species 1 and 2.

DYNAMIC

```
O1, SO1 = GROWTH (BTBL1, OMTBL1, SOI1, DBI1, SUMSO, DAY)
```

```
O2, SO2 = GROWTH (BTBL2, OMTBL2, SOI2, DBI2, SUMSO, DAY)
```

These two lines define the growth of the two species. The remaining variables are:

```
SUMSO = SO1 + SO2
```

and

```
DAY = START + TIME
```

Now the values of B in cm/row are tabulated as a function of the time after emergence in days (the first value between each pair of brackets) with:

```
FUNCTION BTBL1 = (0,0), (30,3), (35,5), (40,9), (45,16), (50,26), (55,38),...
                (60,58), (65,88), (70,102).
```

```
FUNCTION BTBL2 = (0,0), (30,7), (35,13), (40,18), (45,28), (50,51),...
                (55,82), (60,130), (65,175), (70,194).
```

and the values of OM in kg dry matter/ha with:

```
FUNCTION OMTBL1 = (0,0), (70,5600)
```

```
FUNCTION OMTBL2 = (0,0), (70,5600)
```

These are values for the barley varieties Alasjmoen (1) and NHT (2), as obtained from periodic harvests of a spacing experiment with the rows 25 and 75 cm apart. (The data are from the M. Sc. thesis of J. G. Blijenburg, 1971). The values of the maximum yield at high seed densities (OM) are the same for both species and increase linearly with time because they reflect the growth rate of a closed crop surface (de Wit, 1968). Alasjmoen is a naked barley and in the beginning has a slower growth rate than NHT.

The simulation has to be started before the species interfere with each other in the mixture. This is achieved by starting the experiment with

PARAMETER START -- 10.

at the tenth day.

The seed rates are 1/50 row/cm if it is supposed that the species are sown alternatively in rows at a distance of 25 centimeter. These are introduced into the program with:

PARAMETER S1 = 0.02, S2 = 0.02

Now the simulation may proceed until the 70th day after emergence, because at that time the crops lodged seriously, whereas it is convenient to obtain calculated results every five days. This is achieved with:

TIMER FINTIM = 70 ,PRTDEL = 5

And the results to be printed are given by:

PRINT DAY, SO1, SO2, SUMSO, O1, O2

Then the program is finished in the customary way with

END

STOP

The CSMP programming system is able to write, on the basis of this system description, a numerical integration program in FORTRAN in which the integration is performed according to a standard numerical integration technique; in this case according to the fourth order Runge-Kutta method with variable time step.

Conclusions

The simulated results, in terms of dry matter yield for the barley-oat mixture (basic data in Fig. 10) and the mixture of the two barley varieties (basic data in the program), are given in Fig. 11 and 12, respectively, together with the actual results of an experiment. The agreement between the calculated and observed curves is excellent; especially since the calculation used no information that was obtained from the competition experiment itself. It is seen that in spite of the species being sown in a 1:1 ratio, the barley performs much better than the oats and the barley variety NHT much better than Alasjmoen. This is a consequence of their better growth in the period directly after emergence.

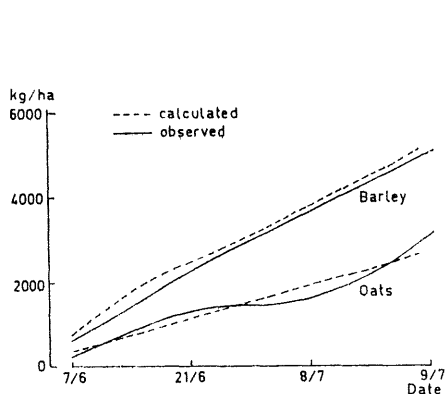


Fig. 11. The calculated and measured yield of barley and oats sown in a 1:1 ratio at normal densities (Baeumer et al., 1968).

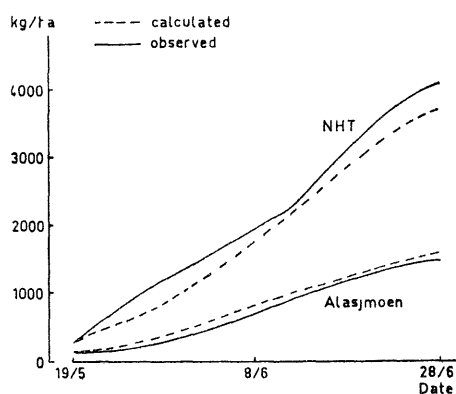


Fig. 12. The calculated and measured yield of the barley varieties Alasjmoen and NHT sown in a 1:1 ratio at normal densities (M.Sc. thesis J.G. Blijenburg, 1971).

More examples can be given to show that the classical Lotka-Volterra approach without the restrictions forced upon it by the lack of the technical equipment to obtain numerical solutions, is a very useful tool in plant ecology. The models are deterministic and it is impossible to introduce stochastic elements. Instead, consequences of variability in the basic experimental parameters are studied by means of a sensitivity analysis. In this analysis, runs are made not only with the average value of the experimental parameters, but also with the values of these parameters at their confidence limits. The sensitivity of a parameter is now judged by comparing the relative range of the output variables with the relative range of the input variables.

In more elaborate models, which cannot be discussed here, the analysis is not based on the observed behaviour of the species in a monoculture, but this behaviour is itself calculated from more basic physiological information obtained from experiments in the laboratory and under controlled conditions.

Statements to the effect that deterministic models are more oversimplified than stochastic models, or vice versa, do not have any foundation. There are modelling situations where it is more sensible to use stochastic models and other modelling situations where it is more sensible to use deterministic models; we should be versatile enough to use both or even combine them, when the necessity arises.

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Discussion

Participants: De Wit (Author), Bakker, (K.), van Biezen, Cavers, Jain, Kuenen, Platt, Reddingius, Rosenzweig, Walker and Watt.

Animals do compete for space but quite often it is known that ultimately competition is for food; moreover, contrary to plants, animals roam about. Therefore, a comparison between animals and plants will often be difficult or even impossible (KUENEN). Animals and

plants only behave analogously under certain circumstances. In order to be mutually exclusive, it is not necessary that the food is the same. It may very well be that species A is limited by resource X and species B by resource Y. As long as the species cannot invade each other's territory, and the food does not roam about, both species are mutually exclusive. This is the situation that occurs with many plants and some animals. Other animals may not have territorial behaviour but move about, or may have territorial behaviour but their food may move about (e.g. some insects). In that case, they may only be mutually exclusive when they are living on exactly the same food (AUTHOR).

Whether in mutually exclusive species the response to shortages is the same or not is immaterial, although the competitive ability – as measured for instance by the relative replacement rate – depends on it. Hence, the behaviour of two species in a mixture may be described by parallel course lines even when their efficiency to a limiting growth factor is not the same, provided that the two species are mutually exclusive (AUTHOR to PLATT).

Of course there are many cases where two species are not mutually exclusive. Perhaps this occurs often in mixtures of two (plant) species which do not grow at the same time. The most obvious example being the growth of two monocultures in two successive years. In a forthcoming paper this situation will be further analysed on basis of experiments with potato varieties with different lengths of growing period, and planted at different times of the year. The analysis is then done on the basis that the two species in a mixture are only mutually exclusive during a part of their growing period. This situation occurs much more frequently with natural vegetation than in the field crop situation, because in the latter the species are often selected on basis of the length of the growing period. It may be remarked in passing, that two species with a different period of growth may still be mutually exclusive when a limiting resource, like N-fertilizer, is only supplied before the first species starts to develop (AUTHOR to CAVERS).

The results of a competition experiment in one year can only be used to predict the behaviour of a mixture in successive years when the genetic variability is low (BAKKER). This is indeed the case. However, the only straightforward example known to me is the *Drosophila* experiment discussed in the paper and here the effect of selection is perhaps too remarkable to be true. In an experiment with grass species over several years any effect of selection was absent (van den Bergh and Elberse, 1970) (AUTHOR).

REDDINGIUS then opened a discussion on the merits of stochastic and deterministic models to which WATT, ROSENZWEIG, JAIN, WALKER and VAN BIEZEN contributed. It was concluded, that there are two 'world views', a stochastic and a deterministic one, that both are abstractions which have their field of application and that students and ecologists should be exposed to and be familiar with both of them (EDITORS).



P. J. den Boer and G. R. Gradwell (Ed.): Dynamics of Populations

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SCHEME OF CONTENTS

General information (Preface; List of participants; Presidential Address; Contents)

The dynamics of populations in general (M. E. Solomon, Bristol, England; J. L. Harper, Bangor, Wales and J. White, Dublin, Ireland; J. Reddingius, Haren, Netherlands)

The significance of heterogeneity, complexity and dispersal (P. J. den Boer, Wijster, Netherlands; H. Wolda, Haren, Netherlands; L. C. Birch, Sydney, Australia; Syun'iti Iwao, Kyoto, Japan, V. Ilmari Pajunen, Helsinki, Finland)

The significance of the physical environment (A. R. Main, Nedlands, W. A., Australia)

Interactions with the populations (H. Wilbert, Göttingen-Weende, West Germany; H. G. Andrewartha, Adelaide, S. A., Australia; P. Gruys, Arnhem, Netherlands; W. Baltensweiler, Zürich, Switzerland; P. M. Jónasson, Hillerød, Denmark; M. J. Way and M. E. Cammell, London, England; C. J. Krebs, Bloomington, Ind., USA; J. C. Coulson, Durham, England)

Interactions between populations in general (C. T. de Wit, Wageningen, Netherlands; T. B. Reynoldson and L. S. Bellamy, Bangor, Wales; J. H. Connell, Santa Barbara, Calif., USA; David Pimentel and A. Benedict Soans, Ithaca, N.Y., USA; C. B. Huffaker, Berkeley, Calif., USA)

Parasite-host and predator-prey relationships (T. Royama, Fredericton, New Brunswick, Canada; F. S. Andersen, Lyngby, Denmark; M. P. Hassell, Oxford, England; J. P. Dempster, Abbots Ripton, England; E. van der Meijden, Leiden, Netherlands; H. Zwölfer, Delémont, Switzerland)

Human intervention: the exploitation of marine populations (D. A. Hancock, Burnham-on-Crouch; England; P. Korringa, IJmuiden, Netherlands; J. A. Gulland, Rome, Italy)

Human intervention: introduction into Australia (A. J. Wapshere, Mont-Pellier, France; K. Myers, Canberra, Australia)

Special population analysis: bird populations (H. N. Kluyver, Arnhem, Netherlands; C. M. Perrins, Oxford, England; André A. Dhondt, Ghent, Belgium; Adam Watson, Banchory, Scotland)

Conclusions (K. Bakker, Leiden, Netherlands; K. E. F. Watt, Davis, USA; D. J. Kuenen, Arnhem, the Netherlands)

Indexes



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