Competition Between Plant Populations with Different Rooting Depths

I. Theoretical Considerations

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Summary. As an extension of De Wit's competition theory a theoretical description has been developed of competition between plant populations with different rooting depths. This model shows that in mixtures of plants with different rooting depths the value of the Relative Yield Total can be expected to exceed one. Moreover, it predicts the frequency-dependence of the relative crowding coefficient of the deep rooting population with respect to the shallow rooting population. The relationship between properties of plant species and the environment required to establish a stable equilibrium turns out to be surprisingly simple. The shallow rooting species has to have a larger competitive ability sufficient to compensate for the extra nutrients that are exploited by the deeper rooting plants. The dependence of equilibrium plant frequencies on the properties of plant species and the characteristics of the environment is discussed.

Introduction

It is not yet clear which mechanisms are responsible for the long-term coexistence of plant populations in grassland vegetation. Many investigators maintain that this phenomenon is due to the heterogeneity of the environment (Werner and Platt, 1976; Grubb, 1977). On the other hand, Van den Bergh and Braakhekke (1978) stress that the existence of equilibria between plant populations must be attributed at least in part to functional niche differentiation.

In most competition experiments carried out up till now plant species are found to compete for the same space (Van den Bergh, 1968; Trenbath, 1974). Mixtures of grasses and legumes however form an important exception (De Wit et al., 1966). The legume is able to draw on the nitrogen in the air in addition to the common pool of nitrogen in the soil.

Many grassland ecologists have pointed to the great diversity in rooting patterns between different plant species (Linkola and Tiirikka, 1936; Kutschera, 1960; Parrish and Bazzaz, 1976). Although Linkola and Tiirikka (1936) observed

many differences in the maximum rooting depth of species occurring in the same plot, they reported the absence of clear root layering. Therefore, they concluded that there is intense competition for soil factors such as nitrogen, minerals and water.

In this paper we shall investigate whether stable equilibria between plant populations may be caused simply by differences in rooting depths. On the basis of the theory of De Wit (1960) a description of competition between plant populations with different rooting depths will be developed.

Competition Between Plants with the Same Rooting Depth

In most experiments a linear relationship has been found between plant yield and the quantity of limiting nutrient absorbed (De Wit, 1953; Trenbath, 1976). If the growth of two plant species is limited by the same amount of nutrient (N) and the total plant density is sufficient for the uptake of the total amount available, then the yield of both species in monoculture is given by:

$$M_1 = X_1 N \quad \text{and} \quad M_2 = X_2 N \tag{1}$$

where X_1 and X_2 represent the conversionfactors for species 1 and species 2.

When both populations are grown in mixture, they have to share the same supply of nutrients. This process of mutual interference can be studied effectively by using replacement series. Because in these series the overall plant densities in mixed stands and monocultures are equal, the yield of both species in mixture can be compared with the yield in monoculture. The sharing of the limiting nutrient available can be described by the hyperbolic functions developed by De Wit (1960):

$$O_1 = \frac{k_{12} z_1}{k_{12} z_1 + z_2} N X_1 \quad \text{and} \quad O_2 = \frac{z_2}{k_{12} z_1 + z_2} N X_2 \tag{2}$$

in which O_1 and O_2 represent the yields of species 1 and 2 in the mixture, z_1 and z_2 the ratio of plant density of both species to total plant density and k_{12} the relative crowding coefficient that measures the effect of species 1 on species 2.

These equations are only valid at plant densities at which the total amount of available nutrient can be absorbed. Studying the dependence of yield on plant density, it is appropriate to consider the process that is taking place as competition between plants and empty space. Using this approach De Wit (1960) derived the next hyperbolic function, which has been found to agree with the results of most spacing experiments:

$$M = \frac{\beta Z}{\beta Z + 1} N X \tag{3}$$

where β represents the intraspecific crowding coefficient and Z the density of the planted species.

De Wit and Van den Bergh (1965) introduced the concept of the Relative Yield Total for the purpose of measuring the degree of niche differentiation in
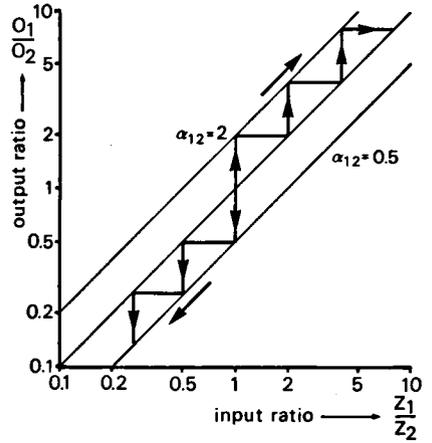
Fig. 1. The relation between the ratio of the yields of species 1 and species 2 and the ratio of the plant frequencies of these species. The arrows indicate the temporal behaviour of the mixture. If $\alpha_{12}=2$, species 2 will disappear out of the mixture; if $\alpha_{12}=0.5$, species 1 will be crowded out

replacement experiments. If two populations compete for the same space, the RYT can be calculated from Eqs. (1) and (2):

$$RYT = \frac{O_1}{M_1} + \frac{O_2}{M_2} = \frac{k_{12}z_1}{k_{12}z_1+z_2} + \frac{z_2}{k_{12}z_1+z_2} = 1. \tag{4}$$

When we study the changes in the composition of the mixture through time, it is essential to use the relative reproductive rate α_{12}, i.e. the quotient of the ratio between the yields of both plant species and the ratio between their planting frequencies:

$$\alpha_{12} = \frac{O_1/O_2}{z_1/z_2} \quad \text{or} \quad \log(O_1/O_2) = \log \alpha_{12} + \log(z_1/z_2). \tag{5}$$

The dynamics of the mixture can now be shown by plotting the proportion of yields versus the proportion of plant frequencies in a logarithmic ratio diagram. When both populations compete for the same amount of nutrients, i.e. Eqs. (2) are valid, the relative reproductive rate $(\alpha_{12}=k_{12}(X_1/X_2))$ is independent of the plant frequencies. In this case either species 1 $(\alpha_{12}<1)$ or species 2 $(\alpha_{12}>1)$ will be crowded out of the mixture (Fig. 1).

Competition Between Plants with Different Rooting Depths

In mixtures of plant populations with different rooting depths the deep rooting population can draw on an extra supply of nutrients present in the deeper soil compartment (N_2) in addition to the common pool of nutrients in the upper layer (N_1). The partitioning of N_1 is allowed to be described by the competition Eqs. (2). The part of N_2 that can be taken up will be dependent on the density of the deep rooting population. Assuming that this dependence can be formulated by the spacing hyperbola (3), the yields of both populations in mixture are given by:
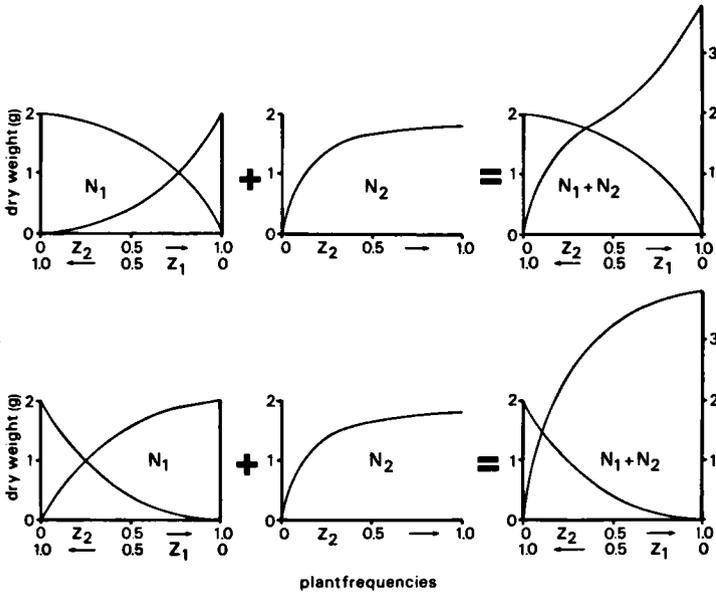
Fig. 2. The plant yield – produced by uptake from N_1, N_2 and $N_1 + N_2$ – plotted versus the plant frequencies of the shallow (z_1) and the deep rooting population (z_2). Above: diagrams for $k_{12} = 4$, $\beta Z_t = 10$ and $X_1 = X_2$. Below: diagrams for $k_{12} = 0.25$, $\beta Z_t = 10$ and $X_1 = X_2$

$$O_1 = \frac{k_{12} z_1}{k_{12} z_1 + z_2} N_1 X_1 \quad \text{and} \quad O_2 = \frac{z_2}{k_{12} z_1 + z_2} N_1 X_2 + \frac{\beta z_2 Z_t}{\beta z_2 Z_t + 1} N_2 X_2 \qquad (6)$$

in which O_1 and O_2 represent the yields of the shallow and the deep rooting population respectively and Z_t represents the total plant density. Using these equations RYT can be calculated:

$$RYT = \frac{k_{12} z_1}{k_{12} z_1 + z_2} + \left(\frac{z_2}{k_{12} z_1 + z_2} \frac{N_1}{N_2} + \frac{\beta z_2 Z_t}{\beta z_2 Z_t + 1} \right) \bigg/ \left(\frac{N_1}{N_2} + 1 \right). \qquad (7)$$

RYT exceeds one if $\dfrac{\beta z_2 Z_t}{\beta z_2 Z_t + 1} > \dfrac{z_2}{k_{12} z_1 + z_2}$, i.e. if the part of N_2 absorbed by the deep rooting population is greater than the part of N_1 that it absorbs. This is roughly true, if at higher frequencies of the deep rooting species there is intraspecific competition for the nutrients in the deeper soil layer. RYT increases with decreasing N_1/N_2 and increasing k_{12} and β.

The relative crowding coefficient of the deep rooting population with respect to the shallow rooting population (k_{21}) appears to be dependent on plant frequencies. If $k_{12} > 1$, one obtains an inverse sigmoid curve when yield is plotted versus plant frequency (Fig. 2).

To investigate whether these phenomena can cause inter-population stability, the relative reproductive rate has to be calculated by combining (5) and (6):

$$\alpha_{12} = k_{12} \frac{X_1}{X_2} \left(\frac{N_1/N_2}{k_{12}(z_1/z_2) + 1} \right) \bigg/ \left(\frac{N_1/N_2}{k_{12}(z_1/z_2) + 1} + \frac{\beta z_2 Z_t}{\beta z_2 Z_t + 1} \right). \qquad (8)$$
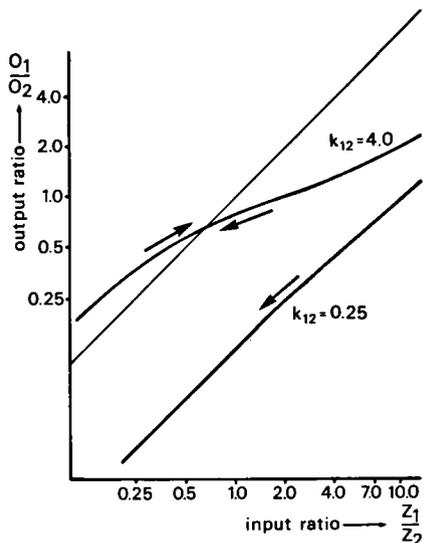
Fig. 3. The relation between the ratio of the yields of the shallow (O_1) and the deep rooting species (O_2) and the ratio of the plant frequencies of these species for $k_{12}=4$ and for $k_{12}=0.25$. The two curves are calculated supposing $\beta Z_t = 10$, $N_1 = N_2$ and $X_1 = X_2$

Unlike the relative reproductive rate for mixtures of populations competing for the same space, α_{12} in the above expression is a function of the plant frequencies z_1 and z_2.

Two instances of the dynamics of mixtures are presented in Fig. 3. When $k_{12} = 0.25$ the shallow rooting species is crowded out of the mixture in a short time. When $k_{12} = 4.0$ a stable equilibrium between the two populations can be established. The relationship of this equilibrium to the inverse sigmoid yield curve for the deep rooting population will be clear.

It is possible to determine the conditions which both populations have to fulfil to establish inter-population stability. The general conditions for the existence of an equilibrium point are:

$$\lim_{z_1/z_2 \to 0} \alpha_{12} > 1 \quad \text{and} \quad \lim_{z_1/z_2 \to \infty} \alpha_{12} < 1. \tag{9}$$

If at sufficient total plant densities z_1/z_2 approaches zero, the fraction of N_2 that can be absorbed approaches one. So we can calculate the equilibrium conditions for populations with different rooting depths:

$$\frac{N_1 + N_2}{N_1} < k_{12} \frac{X_1}{X_2} < \frac{N_1 + k_{12} \beta Z_t N_2}{N_1}. \tag{10}$$

For achieving stability the larger nutrient supply that can be exploited by the deep rooting population has to be balanced by the greater competitive ability of the shallow rooting population. If nutrients are distributed homogeneously in the soil, then it roughly may be said that the relative crowding coefficient has to exceed the value of the ratio between the rooting depths of the deep and the shallow rooting plants. When the relative crowding coefficient is greater than the maximum value given by (10), the deep rooting population will disappear out of the mixture unless its extra source of nutrients. If $\beta Z_t(X_2/X_1) > N_1/N_2$, the right hand of relationship (10) will be fulfilled by any value of $k_{12}(X_1/X_2) > 1$.
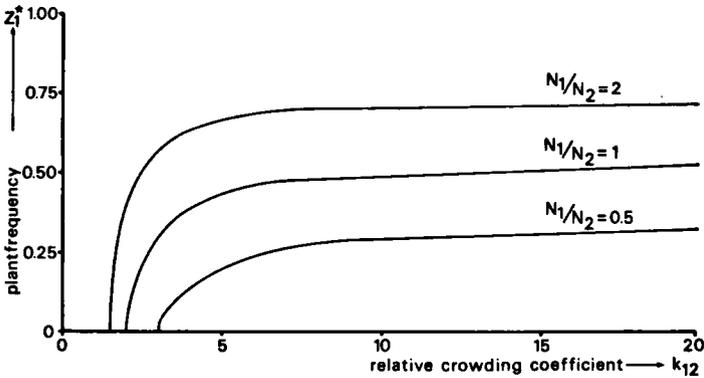
Fig. 4. The equilibrium plant frequency of the shallow rooting species (z_1^*) depending on the relative crowding coefficient k_{12} for three different values of the ratio of the amount of nutrients exploited by both species (N_1) and the amount of nutrients only exploited by the deep rooting species (N_2). The curves are calculated supposing $\beta Z_t = 10$ and $X_1 = X_2$

It has to be concluded from (10) that a necessary, but not sufficient, condition for the establishment of an equilibrium is that $k_{12}\,\beta Z_t$ exceeds unity. If $k_{12}\,\beta Z_t > 1$, any value of the ratio between plant frequencies that produce an equal ratio between yields of both populations must be considered as an equilibrium point (see Appendix). By setting $\alpha_{12} = 1$ we can calculate the equilibrium frequencies z_1^* and z_2^*:

$$z_1^* = \frac{1}{\beta Z_t}\,\frac{k_{12}(X_1/X_2)(\beta Z_t + 1) - \beta Z_t((N_2/N_1) + 1) - 1}{k_{12}((X_1/X_2) + (N_2/N_1)) - ((N_2/N_1) + 1)} \qquad (11a)$$

$$z_2^* = \frac{1}{\beta Z_t}\,\frac{k_{12}(\beta Z_t(N_2/N_1) - (X_1/X_2)) + 1}{k_{12}((X_1/X_2) + (N_2/N_1)) - ((N_2/N_1) + 1)}. \qquad (11b)$$

These expressions are hyperbolic functions with respect to k_{12} (Fig. 4). The decreasing effect of an increase in the relative crowding coefficient in terms of plant frequencies is striking. Obviously this phenomenon is important in understanding the process of natural selection for competitive ability within populations with different rooting depths. At high values of k_{12} a change in the competitive ability of one of the two species will cause only a slight in- or decrease of the part of N_1 that is absorbed. Consequently in this trajectory of k_{12} characteristics that lead to an increase of N_2 will be relatively important components of the fitness of the deep rooting population.

Concluding Remarks

Although the approach presented in this paper is a simple one, it permits one to draw the conclusion that stable equilibria may exist in homogeneous environments merely because of different rooting depths. Whether or not populations can coexist

is determined by the properties of the two plant species and the environment. It may be concluded that the relatively low nutrient content of deeper soil layers observed in many environments (e.g. Ernst, 1978) does not diminish the chance of the establishment of an equilibrium.

It is clear that our theory may be valid as well for other mixtures than those composed by plant populations with different rooting depths. Competition between populations of which one can draw on an extra source of some limiting factor frequently occurs. In competition experiments with grasses and legumes De Wit et al. (1966) obtained values of the RYT exceeding unity and an inverse sigmoid curve for the yield of the legume when plotted against plant frequency. This result was attributed to the transfer of nitrogen from the legume to the grass. If there is intraspecific competition for gaseous nitrogen within the legume population, our model offers an alternative explanation of the outcome of these experiments.

An important assumption underlying the model is the hyperbolic relationship between the density of the deep rooting population and the part of N_2 that can be absorbed. In many experiments carried out under agricultural conditions root weight has been found to decrease exponentially with depth (Russell, 1977). However, in natural grassland data on the vertical distribution of root density per plant species are lacking. Therefore, the assumption that there is intraspecific competition for nutrients in deeper soil layers should so far be regarded with caution. Experiments that seem to support the main conclusions from the model presented will be reported in two subsequent papers.

Appendix

To exclude the possibility of the existence of stable or unstable cycli, the slope of the $\log(O_1/O_2)$-curve in the logarithmic ratio-diagram has to be investigated. Differentiating $\log(O_1/O_2)$ with respect to $\log(z_1/z_2)$ we obtain:

$$\frac{d\log(O_1/O_2)}{d\log(z_1/z_2)} = \frac{\beta Z_t + \beta Z_t(N_1/N_2) + (N_1/N_2)}{\beta Z_t(N_1/N_2) + (N_1/N_2) + \beta Z_t + (z_1/z_2)(k_{12}\beta Z_t + (N_1/N_2))} + \frac{z_1/z_2}{\beta Z_t + 1 + (z_1/z_2)}.$$

It can be seen that $d\log(O_1/O_2)(d\log(z_1/z_2))^{-1}$ exceeds zero for any value of z_1/z_2. From this it may be concluded that population-dynamic cycli do not occur.

Supposing $\beta Z_t(\beta Z_t + 1)^{-1} \approx 1$ at sufficient total plant densities Z_t, we can calculate that

$$\frac{d\log(O_1/O_2)}{d\log(z_1/z_2)} < 1, \quad \text{if} \quad k_{12}\beta Z_t > 1 \quad \text{and} \quad \frac{d\log(O_1/O_2)}{d\log(z_1/z_2)} > 1, \quad \text{if} \quad k_{12}\beta Z_t < 1$$

for any value of z_1/z_2. Therefore, only one point for which $\alpha_{12} = 1$ can exist for a given set of parameters. The same conclusion may be drawn from Eqs. (11a) and (11b). Any ratio of plant frequencies that produce an equal ratio of yields has to be considered as an equilibrium point, if the necessary condition for satisfying relationship (10), i.e. $k_{12}\beta Z_t > 1$, is fulfilled.

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