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EUROPEAN, AMERICAN, AND AUSTRALIAN APPROACHES
TO THE STUDY OF PLANT COMPETITION

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ABSTRACT

A comparison is made of certain methods of investigating competition among plant species. An application to plant species dynamics in North American grasslands was made based on the Lotka-Volterra equations by developing a matrix of equations to represent multiple species interactions. The European approach describes a change in species abundance in terms of relative reproductive rates, which can be applied to weight or biomass, as well as numbers. An Australian approach has been developed which is based upon the filters or transfer functions between the different stages of plant development. These are related to express the relative change in two plant species over time. Each approach has merits and limitations.

INTRODUCTION

The subject of competition among organisms in biological systems has been exposed to considerable controversy throughout the last five decades. The reason for this is undoubtedly the lack of clarity in concepts and definitions. In an effort to alleviate some of this confusion, Harper (1961) suggested the term "competition" be replaced by the term "interference."

Comparing different approaches to studies of plant competition, one finds apparent dissimilarities. However, when these different approaches are considered in view of recent developments of mathematical expressions for competitive phenomena, the apparent dissimilarities disappear. The purpose of this paper is to demonstrate some basic theories and their application in a new approach to the study of plant competition in seasonal systems.

THE PROBLEM

The basic problem in competition is that of long-term equilibrium and stability. Consider an initial, nonequilibrium competition for the same space between three organisms (Fig. 1, I). There are two possible long-term end points: (i) exclusion, with only one species remaining in the available space and (ii) coexistence, where the competition has reached some equilibrium so that species partly share the same space.

Gauze (1934) stated that exclusion (i) is the general rule and that a niche would never be shared by two or more species in equilibrium. However, experimental observations and, as will be shown later, theoretical conclusions suggest that coexistence (ii) may occur in the same space.

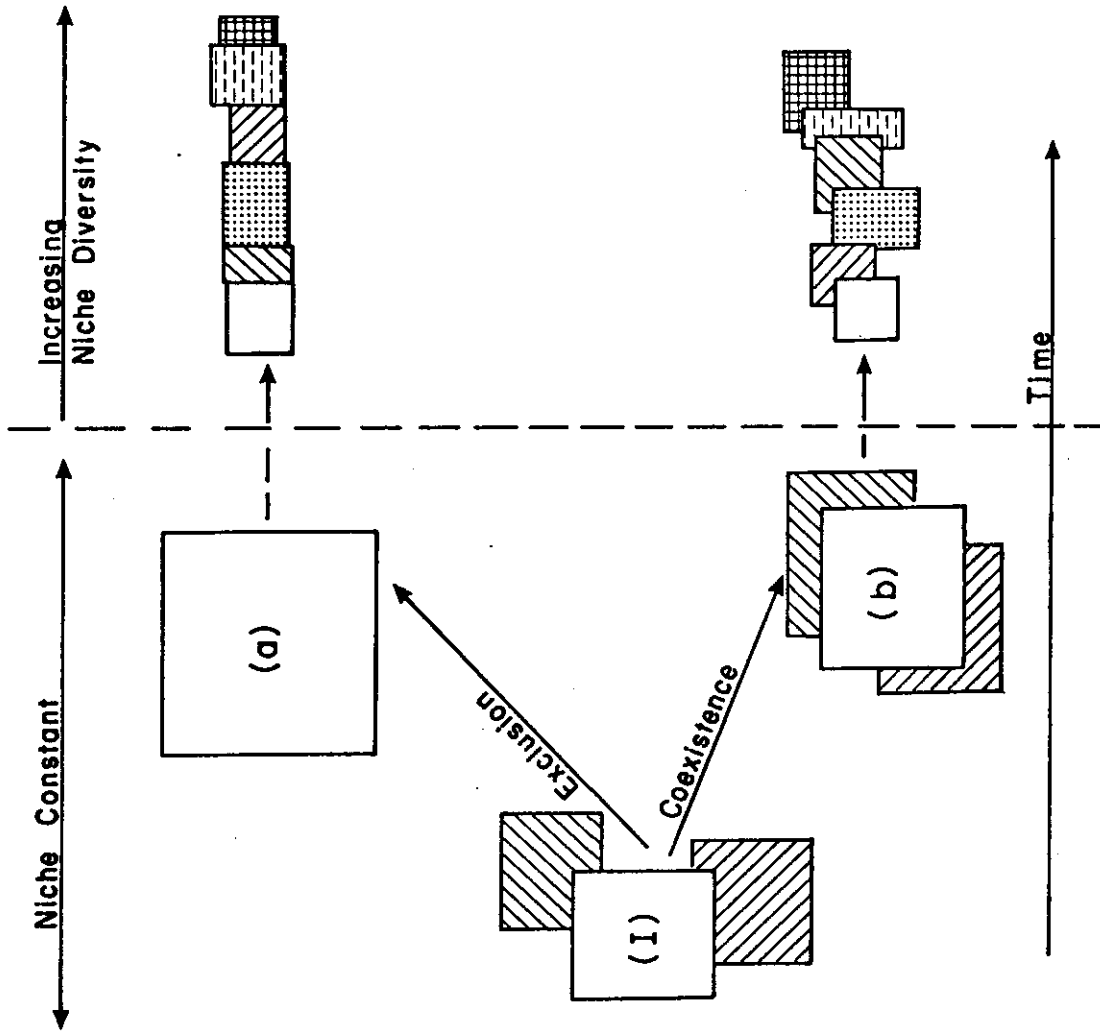


Fig. 1. Three species competing for the same space, initially in non-equilibrium (I), resulting in either exclusion (a) or coexistence in equilibrium in the same space (b).

Gauze's hypothesis has created a major controversy in ecology. The reason for this is primarily the interpretation of the concept of niche as space. Fig. 2 illustrates two species growing together in competitive equilibrium (only one plant of each species is drawn). If their common niche or space is defined as the area ABCD, the observed equilibrium does not agree with Gauze's hypothesis. However, if the niche is defined as the volume ABCDEFGH and postulate that one species (N_1) can obtain nitrogen only from the water in the soil and the other species (N_2) can obtain nitrogen from both the air and the water in the soil, the two species are occupying different niches. The observed coexistence would then agree with Gauze's hypothesis. De Wit (1960, 1961, 1971) and Van den Bergh (1968) would conclude that in both cases the two species were drawing on different resources in the same space.

The example given illustrates a simple case that is easy to interpret conceptually. In nature, the definition of a niche may be a far more complex problem, and this accounts for the controversy surrounding Gauze's hypothesis.

MATHEMATICAL ANALYSES OF COMPETITION

The first to formulate competitive phenomena in mathematical terms were Lotka (1925) and Volterra (1926). Their simultaneous but independent work is based on the equation for logistic growth, from which they derived the following expressions for the competition between two species N_1 and N_2 :

$$\frac{dN_1}{dt} = r_2 \cdot N_1 \left(1 - \frac{N_1 + \alpha_o N_2}{K_1} \right) \quad (1a)$$

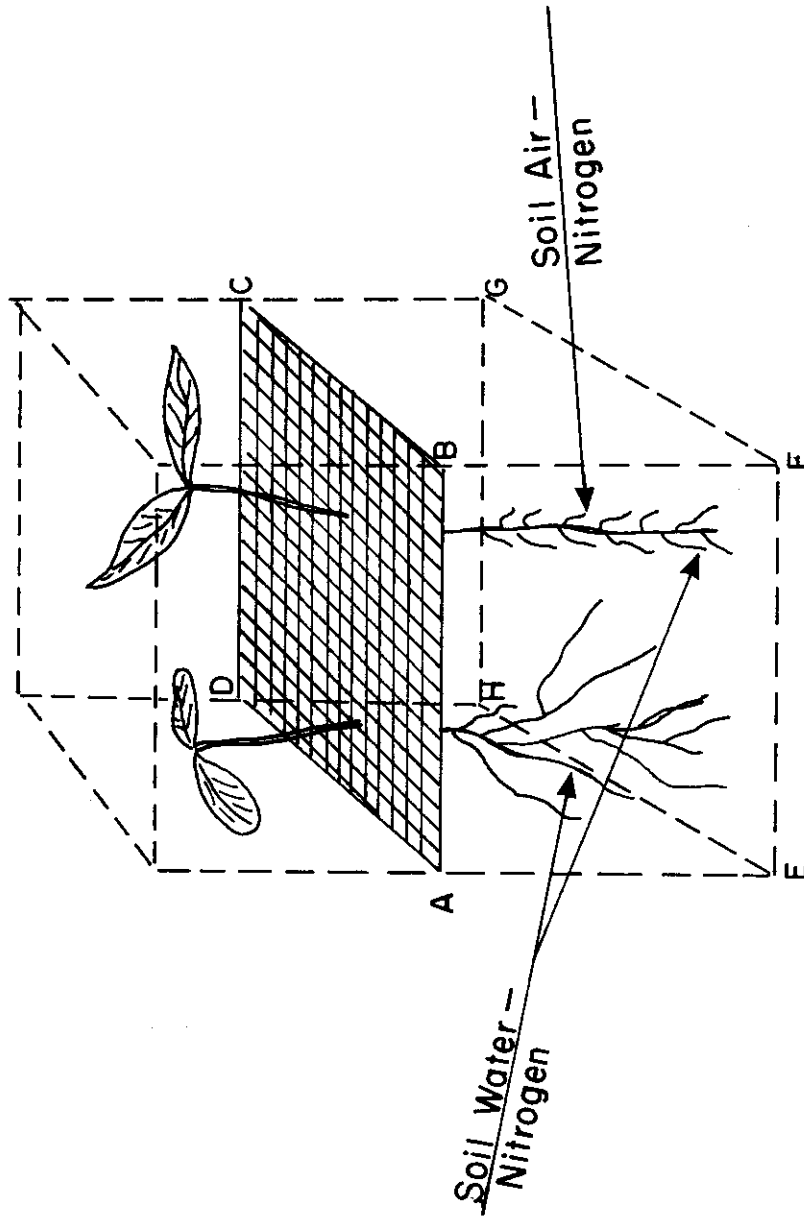


Fig. 2. Two species growing in competitive equilibrium in the same space, but drawing on different resources.

$$\frac{dN_2}{dt} = r_2 \cdot N_2 \left(1 - \frac{N_2 + \beta_0 N_1}{K_2} \right) \quad (1b)$$

where the subscripts 1 and 2 refer to species 1 and 2 and

N = abundance, yield, or space occupied by species N ,

K = the maximum abundance, yield, or space that a species can occupy,

r = relative growth rate,

α_0 = a conversion factor that expresses species N_2 in units of species N_1 , and

β_0 = a conversion factor that expresses N_1 in units of species N_2 .

These equations have primarily been applied to animal population dynamics. An application to the dynamics of plant species in natural grasslands was made by Ares (1973a,b) where he developed a matrix of equations for i species. The matrix arrangement allows expression of competition between any pair of species of those present. The competition coefficients for different species were examined under different conditions of resource availability to determine if habitat width increases resulted in a consistent change for a particular group of species. A simulation model was developed using equitability and competition coefficients to relate changes in biomass of species to concepts of fitness, dominance, and use of resources.

This dynamic approach to plant competition has been followed also by de Wit (1971) but in a modified form. The change in species abundance for one of the competing species is described by

$$\frac{dR_1}{dt} = \frac{dB_1/dt}{B_1} \cdot R_1 (1 - R_1) \quad (2)$$

where R_1 = relative abundance, yield, or space occupied by species 1 and defined as $R_1 = N_1/K_1$ and B_1 = the space (area) occupied by a single plant of species N_1 when grown alone ($m^2 \cdot \text{plant}^{-1}$).

In equation (2), $\frac{dB_1/dt}{B_1}$ corresponds to the growth rate term in equation (1) and expresses a time dependent space requirement. B_1 cannot be measured directly, but may be derived from spacing experiments (de Wit 1970) by fitting experimental data to

$$N_1 = \frac{B_1 \cdot S_n}{B_1 \cdot (S_n + 1)} \cdot K_1 \quad (3)$$

where S_n is the experimentally induced spacing of plants ($\text{plants} \cdot m^{-2}$). The time dependence of B is obtained through successive harvests, at times t_1, t_2, \dots, t_n , as indicated in Fig. 3.

In earlier work de Wit (1960) developed from the Lotka-Volterra equations an analysis of competition of a less dynamic nature than that now described. This approach appears quite different from the Lotka-Volterra approach. The theoretical compatibility between the two approaches is outlined by de Wit (1961).

Thus, de Wit (1970) expresses the change in populations of animals or of annual plants in terms of the relative reproductive rate, α , as

$$\alpha = \frac{n_{N_1}/n_{N_2}}{m_{N_1}/m_{N_2}} \quad (4)$$

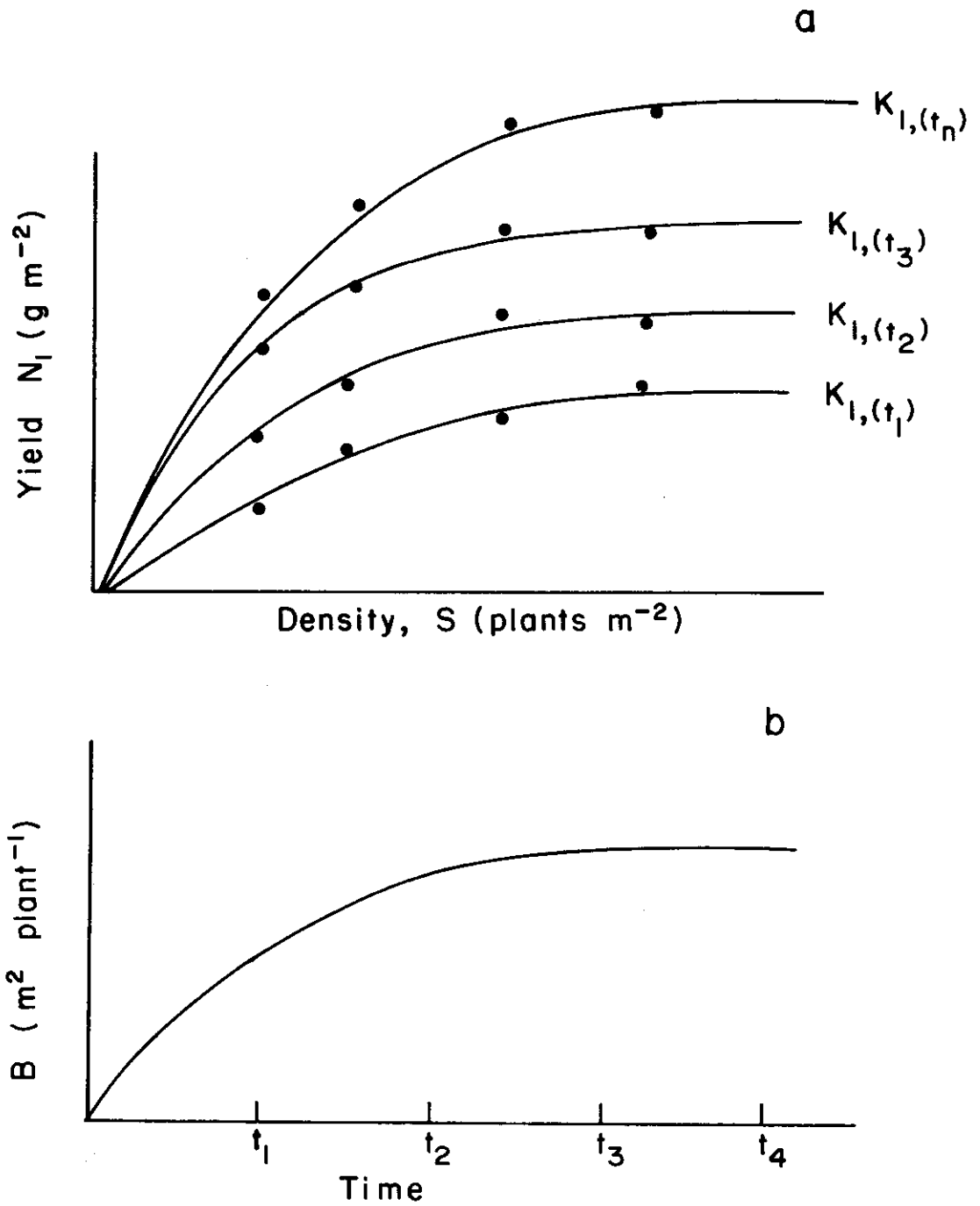


Fig. 3. (a) Determination of B by fitting equation (3) to yield-density experiments, harvested at times t_1, t_2, \dots, t_n . (b) B expressed as a function of time.

where superscripts m and n refer to successive times, the time increment normally being generation(s), life cycle(s), or year(s).

For the purpose of convenient graphic presentation of changes in species ratio, the terms in equation (4) are normalized to express the proportion of one species to the total ($N_1/(N_1 + N_2)$). Equation (4) can then be written

$$\alpha = \frac{\frac{n_{N_1}}{n_{N_1} + n_{N_2}}}{\frac{m_{N_1}}{m_{N_1} + m_{N_2}}} \bigg/ \frac{\frac{n_{N_2}}{n_{N_1} + n_{N_2}}}{\frac{m_{N_2}}{m_{N_1} + m_{N_2}}}$$

and substituting

$$\frac{m_{N_1}}{m_{N_1} + m_{N_2}} = x$$

$$\frac{m_{N_2}}{m_{N_1} + m_{N_2}} = 1 - x$$

$$\frac{n_{N_1}}{n_{N_1} + n_{N_2}} = y$$

$$\frac{n_{N_2}}{n_{N_1} + n_{N_2}} = 1 - y$$

we obtain

$$\alpha = \frac{y/(1 - y)}{x/(1 - x)}$$

and

$$y = \frac{\alpha x}{\alpha x + 1 - x} \quad (5)$$

Fig. 4 gives a graphical representation of equation (5), that is the relation between x and y for $\alpha > 1$, $\alpha = 1$, and $\alpha < 1$. Species N_1 wins if $\alpha > 1$ and loses if $\alpha < 1$. Neither species will lose or gain if $\alpha = 1$, and in that case any mixture will persist for generations.

As previously stated, equation (4) applies for species dynamics in terms of time steps of one or more full generations (life cycles or years) where mN_1 and nN_1 refers to the same life form of the organism (seeds, seedlings, eggs, adults, etc.). This approach is not applicable to the study of (within) seasonal changes in perennial plant communities, because one unit weight of any species may change its biological significance during the season (Van den Bergh 1968). To overcome this problem the *relative yield* (abundance, space), R , is defined as in equation (2), i.e.,

$$R_1 = \frac{({}^{N_1})_{M1}}{({}^{N_1})_{M0}} \quad (6)$$

where subscript M1 refers to yield in mixture with the other species, and M0 refers to yield of one species when grown in monoculture under the same environmental conditions as in the mixture.

Obviously R is dimensionless, and if N_1 and N_2 are mutually exclusive, the *relative yield total* (RYT) is equal to unity or

$$RYT = R_1 + R_2 = 1 \quad (7)$$

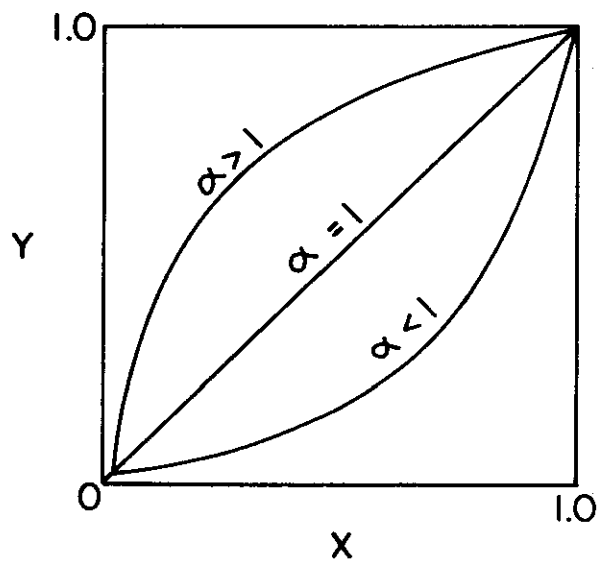


Fig. 4. Graphic representation of equation (5) for $\alpha > 1$, $\alpha = 1$, and $\alpha < 1$.

In analogy with equation (4) the *relative replacement rate* of N_1 with respect to N_2 is defined as

$$\rho = \frac{n_{R_1}/n_{R_2}}{m_{R_1}/m_{R_2}} \quad (8)$$

where superscripts m and n refer to different harvests (Van den Bergh 1968). From equation (7) and (8) we obtain

$$n_{R_1} = \frac{\rho m_{R_1}}{\rho m_{R_1} + m_{R_2}} \quad (9a)$$

and

$$n_{R_2} = \frac{m_{R_2}}{\rho m_{R_1} + m_{R_2}} \quad (9b)$$

which are analogous with equation (5). Fig. 5a gives a graphical representation of equations (9) in the case of $RYT = 1$. The species are then mutually exclusive and there is no mixture which would result in a stable competitive situation. In the more complex case of $RYT > 1$ (Fig. 5b), equation (9) would not apply and has given the relevant modifications (Van den Bergh 1968)^{1/}. In such a situation

$$\frac{1/}{n_{R_1}} = \frac{nm_{\rho_{12}} \cdot m_{R_1}}{nm_{\rho_{12}} \cdot m_{R_1} + m_{R_2}} \quad (9c)$$

and

$$n_{R_2} = \frac{nm_{\rho_{21}} \cdot m_{R_2}}{nm_{\rho_{12}} \cdot m_{R_2} + m_{R_1}} \quad (9d)$$

where $nm_{\rho_{12}} \neq nm_{\rho_{21}}^{-1}$

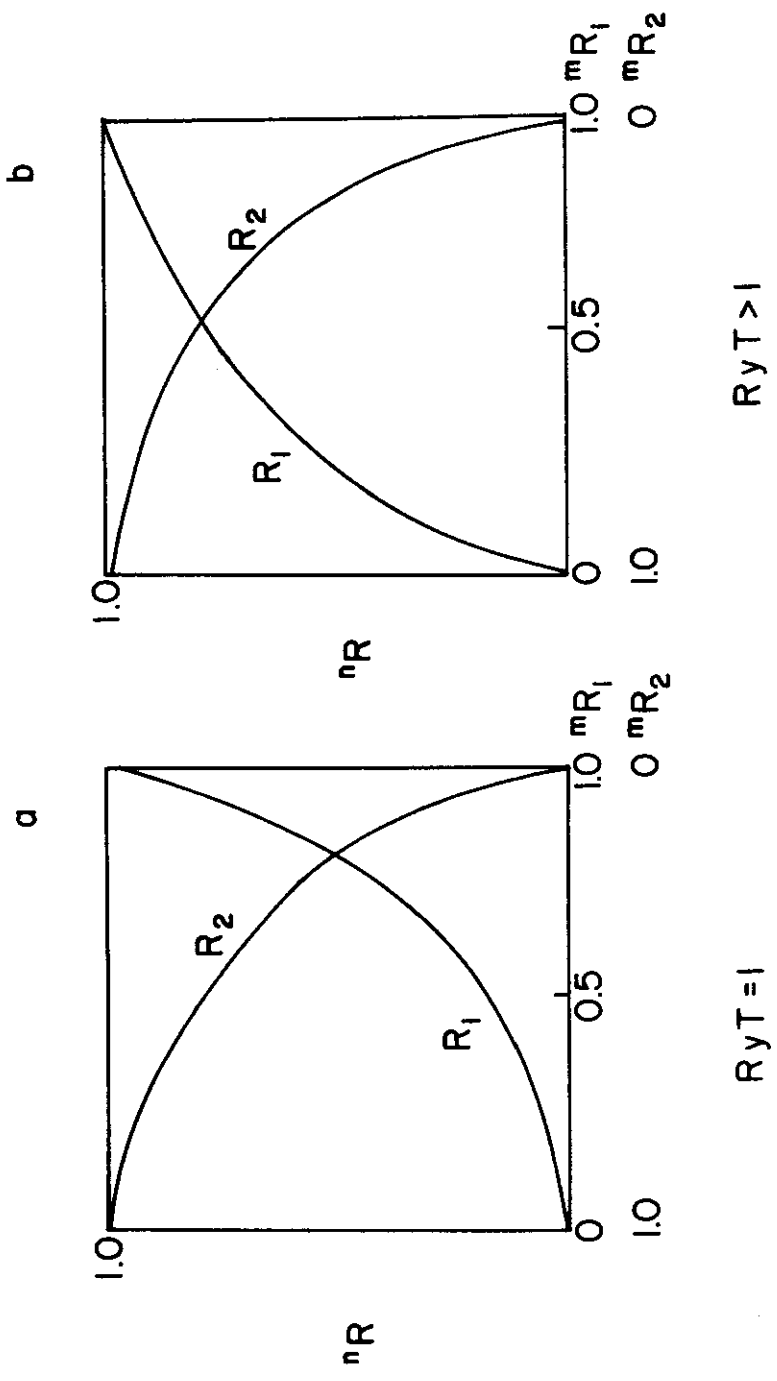


Fig. 5. Graphic representation of equation (9a,b) in the case of $RyT = 1$ and of equation (9c,d) in the case of $RyT > 1$.

N_1 and N_2 would use different resources within the same space and there might be a certain mixture with competitive equilibrium. The mathematical conditions for such equilibrium are illustrated in Fig. 6, as the crossover point between the diagonal and the curve relating the species proportions at times n and m .

As pointed out earlier, the mathematical expressions of competitive phenomena derived by de Wit and coworkers are in theory compatible with the Lotka-Volterra equations. These equations will also predict stable situations for certain mixtures (Krebs 1972).

AN AUSTRALIAN APPROACH

An Australian approach to plant competition was developed for the study of an annual two-component pasture-ecosystem in a dry monsoonal tropical climate (Torssell 1973). This climate has a strong seasonal contrast between wet and dry season (wet season has 500 to 1500 mm rainfall from November to April; the remainder of the year practically no precipitation). The system involves an introduced legume, Townsville stylo, (*Stylosanthes humilis* H.B.K.) in competition with annual grass weeds (mainly *Digitaria ciliaris* and *Brachiaria ramosa*). These grass species are so similar that they can be lumped in a common group. The situation studied is on cleared land, phosphorus application and grazing being the main management measures.

The economical background to this work is the potential of 200 million acres of undeveloped tropical savannah in northern Australia (Begg 1973). This area supports an eucalypt woodland-bunchgrass community in its original state with a very low carrying capacity. Phosphorus application

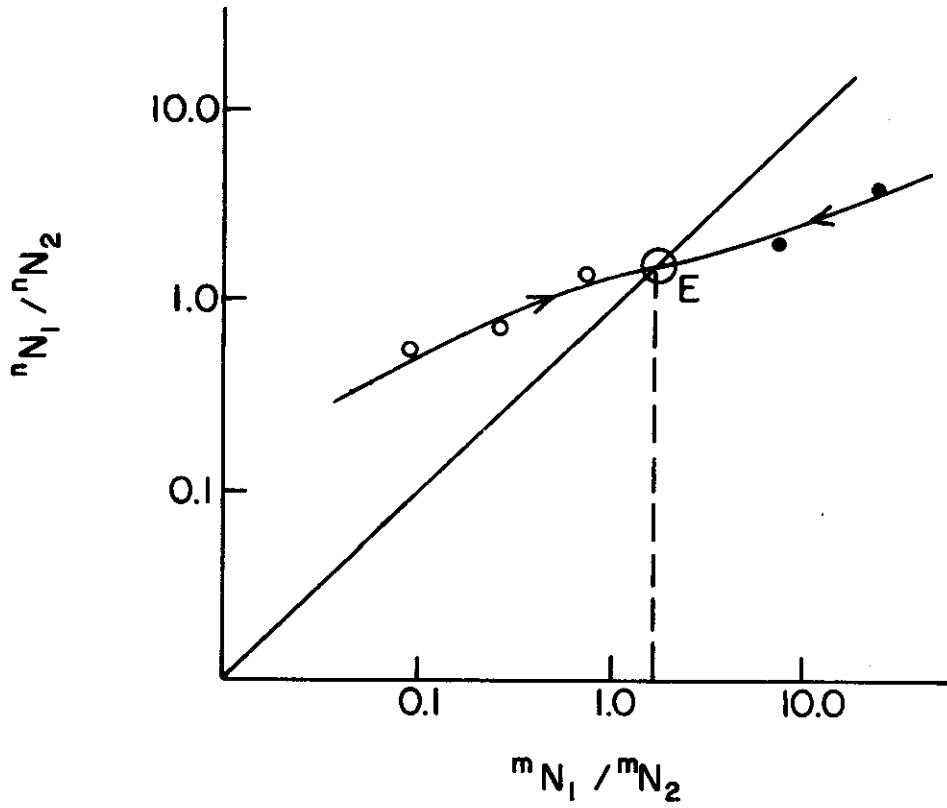


Fig. 6. Relation between species ratio at time n and m (initial) in the case of an equilibrium ratio at E .

and the introduction of *Stylosanthes* species increases the carrying capacity 10 to 20 times. Utilization may be with or without clearing the woodland; recent experience (Torsell 1973) indicates the cleared situation as being unstable because of erosion risks.

The study of this two-component annual system (the cleared situation) naturally called for a de Wit approach, such as equation (4). This course was taken; however, modifications were found necessary. Fig. 7 illustrates a model of the system in terms of state variables. Emphasis is made on the processes regulating the flow between the state variables. These regulators are called filters (Torsell 1973, Rose, Begg, and Torsell 1974) and integrate the change in species proportion between the state variables under consideration.

The effect of any filter is expressed by equation (5), i.e.,

$$y = \frac{ax}{ax + 1 - x} \quad (10)$$

where x = legume proportion at the beginning of a phenophase,
 y = legume proportion at the end of a phenophase, and
 a = the "filter constant"

Although α (equation (5)) and a (equation (10)) are mathematically identical, they are not so in strict biological terms. This is because α is dimensionless and refers to change in proportion of the same life-form between generations. The filter constant a , on the other hand, expresses change from one life form to another and biologically it has the dimension of, for example, seedling proportion/seed proportion.

Equation (10) does not distinguish between those changes in species proportion which are caused (1) by differences between the species in

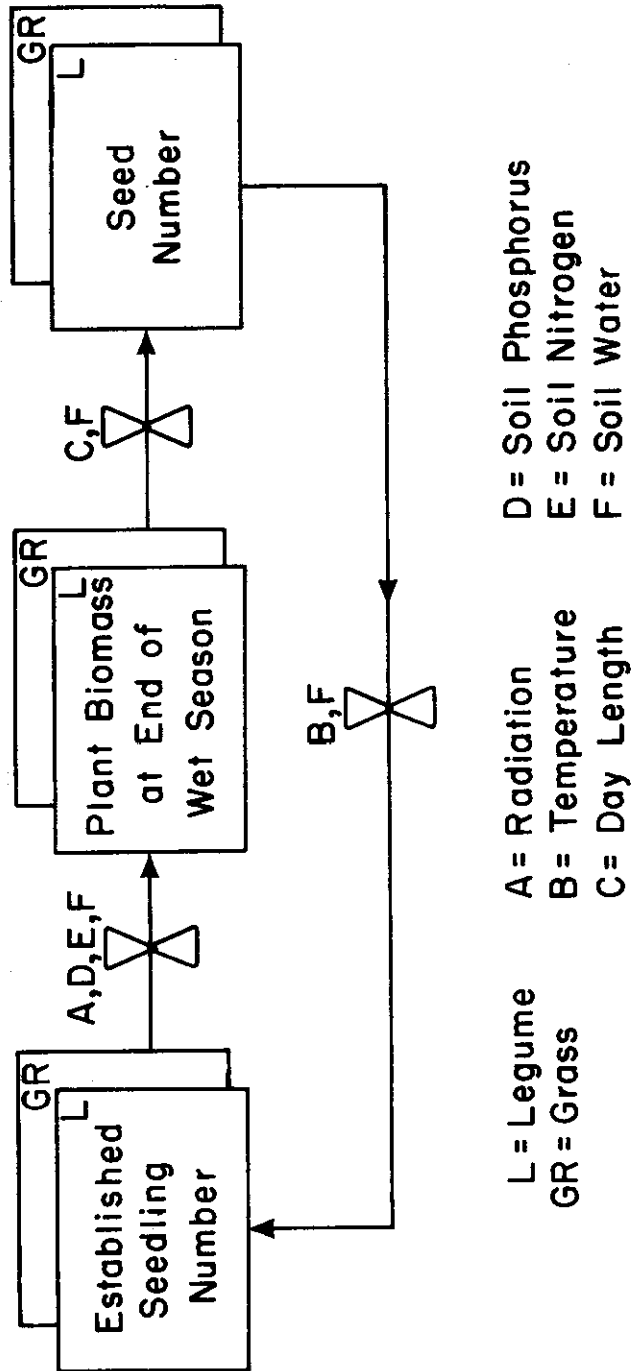


Fig. 7. State variables in the Townsville stylo-annual grass pasture ecosystems (Torsell 1973).

stress resistance and (2) by competition. Therefore this equation is only the first step in the analyses; applications of equation (8) and (9) would reveal true competition.

Note, that the filters express changes between two stages in one discrete timestep, the length of which varies with the filter under consideration. Not until the mechanism of a filter is modeled on a detailed process level can it be expressed as a time dependent function.

The behavior of the pasture system can now be expressed in terms of a series of filters, the output of one filter being the input to the next. This is shown in Fig. 8, where within a life cycle $y_m \rightarrow x_{m+1}$ and between life cycles $y_m \rightarrow x_1$. The filter constants a_1, a_2, \dots, a_m will determine the within-life cycle fluctuations in species proportions as well as the long-term trend of the system. It is possible to relate analytically the input of any filter to the output of any filter in any year (Torssell and Rose, in prep.). For instance, the output of filter m in year n is

$$y_{mn} = \frac{(a_1, a_2, \dots, a_i)^{n-1}}{(a_1, a_2, \dots, a_i)^{n-1} - 1 + (y_{m1})^{-1}} \quad (11)$$

Three years of observation of the variation in a -values in a Townsville stylo-annual grass pasture at Katherine (Northern Territory, Australia 14°S 132°E, elevation 108 m) are given in Fig. 9. It is obvious that the germination filter (a_1) operates as an important value to preserve the legume proportion each year. The biological background to this is the different germination characteristics of the legume and the grasses. Germination is often initiated by an intense convectional storm; however,

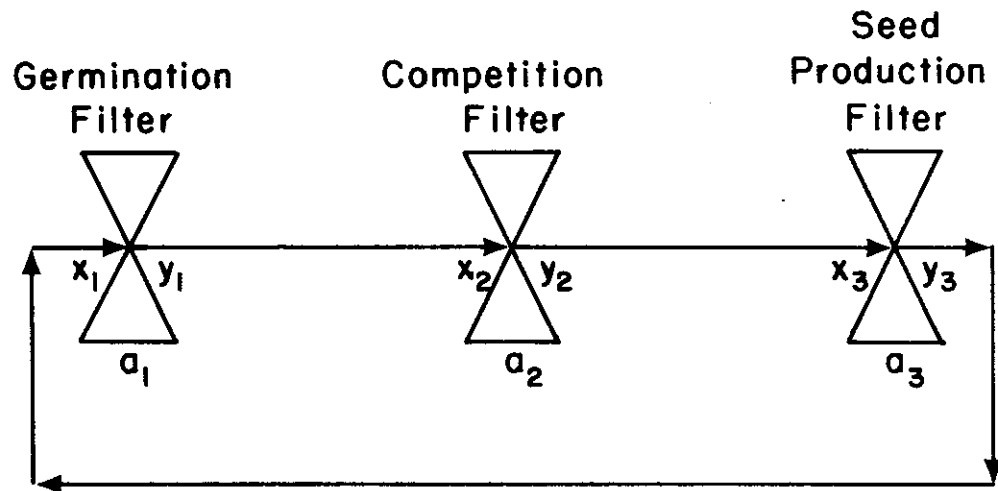


Fig. 8. Species filters in the Townsville stylo-annual grass pasture ecosystem (Torssell 1973).

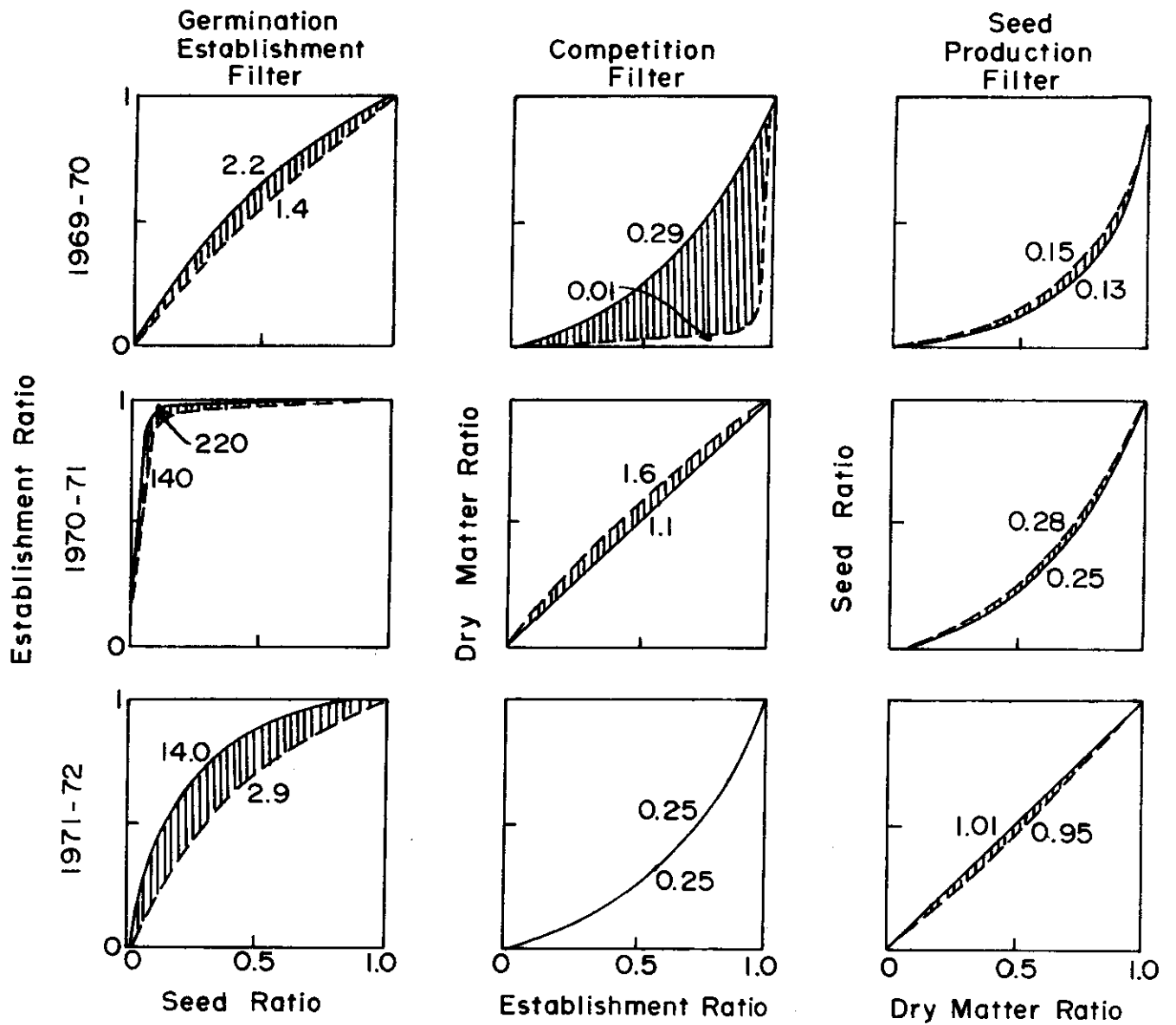


Fig. 9. Graphic representation of equation (10) using observed values of a in three filters in the Townsville stylo-annual grass pasture ecosystem at Katherine, N. T., Australia (1969-70 irrigation, no grazing; 1971-72 no irrigation, grazing) (from Rose et al. 1974).

the normally high radiation the following day limits germination conditions to 28 to 36 hours only. This pattern results in considerable grass mortality during germination and early root development (Torszell and McKeon, in prep.).

Simulation using equation (11) also reveals the dominating influence of the germination filter. The simulation is based on the assumption of stochastic variation in a , since a varies with the weather. Fig. 10 shows the simulated output of the second filter (legume proportion of total dry matter at the end of the wet season) after a 10-year period, plotted against the $a_2 \cdot a_3$ product for a range of a_1 values with stochastic variation around the a_1 means indicated.

FUTURE APPROACHES

The European, American, and Australian approaches to the study of plant competition all have their merits and limitations. The Lotka-Volterra based approaches applied in the U.S. Grassland Biome study is useful to describe population dynamics in perennial grassland communities. Its main limitation is the lack of biological insight into the autecology of the species involved. Combination with more process-oriented approaches, also developed in the Grassland Biome program such as that of Parton and Marshall (1973), may certainly contribute more autecological resolution.

The exemplified Australian approach has its main limitation in its restriction to a two-component system arrived at by lumping species into two groups. Its major advantage is the aim to define and describe those processes in which important changes in species proportion occur. This also gives the potential of separation between (1) those filters where species

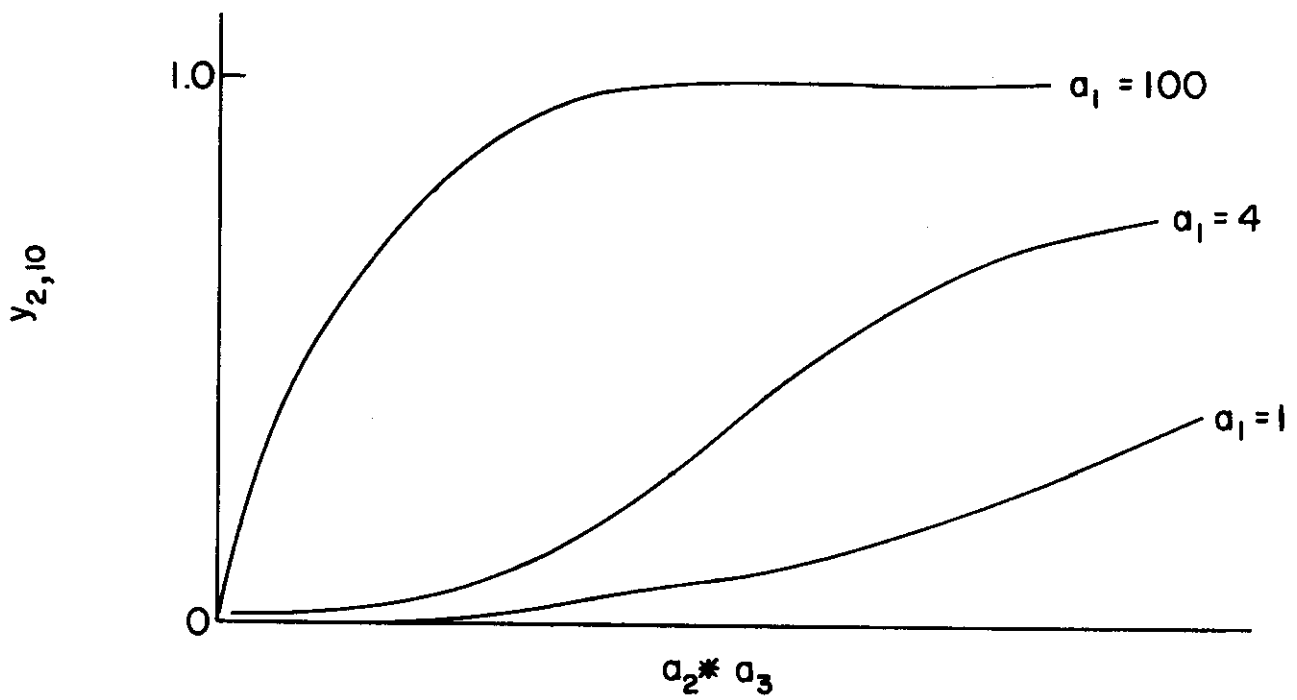


Fig. 10. Simulated output of the second filter (equation 11) plotted against the $a_2 * a_3$ product for stochastic variations of a_1 (10 years) around the mean values indicated ($y_{1,1} = 0.5$).

proportion change in response to different stress characteristics (e.g., the germination filter) or reproduction characteristics (e.g., the seed production filter and (2) those filters which are the result of true competition. For the extension of the analyses of the true competition filter into multi-component systems, the Lotka-Volterra equation matrix developed by Ares (1973*b*) could be applied. However, it is a challenge to replace equation (1) with equation (2) in this matrix including the determination of dB/dt in a context that is valid for natural grasslands.

An even more interesting development would be the application of these concepts in the resource-population growth model recently presented by Stewart and Levin (1973). Their resource equation can be modified to describe plant population and their population growth equation modified to describe dry matter production according to equation (2). This application is now being pursued.

LITERATURE CITED

- Ares, J. O. 1972. Equitability, competition and seasonal succession in a plant community. *J. Ecology* 60:325-331.
- Ares, J. O. 1973a. Structural characteristics of some grassland plant communities associated with the availability of resources. US/IBP Grassland Biome Preprint No. 80, Colorado State Univ., Fort Collins.
- Ares, J. O. 1973b. A model and experimental data on changes in plant community structure during a growing season. US/IBP Grassland Biome Preprint No. 81, Colorado State Univ., Fort Collins.
- Ares, J. O., and R. J. C. Leon. 1972. An ecological assessment of the influence of grazing on plant community structure. *J. Ecology* 60:333-392.
- Begg, J. E. 1972. Probable distribution of Townsville stylo as a naturalized legume in tropical Australia. *J. Aust. Inst. Agric. Sci.* 38:158-162.
- De Wit, C. T. 1960. On competition. Versl. Landbouwk. Onderz. (Agric. Res. Rep.) Wageningen No. 66.8. 82 p.
- De Wit, C. T. 1961. Space relations within populations of one or more species. *Symp. Soc. Exp. Biol.* 15:314-329.
- De Wit, C. T. 1970. On the modelling of competitive phenomena, p. 269-281. In P. J. DenBoer and G. R. Gradwell [ed.] Dynamics of populations. Proceedings of the Advanced Study Institute on "Dynamics of Numbers in Populations." PUDOC, Wageningen, The Netherlands.
- Gauze, G. F. 1934. The struggle for existence. Hafner Pub. Co., Inc., New York.
- Harper, J. L. 1961. Approaches to the study of plant competition. *Symp. Soc. Exp. Biol.* 15:1-39.
- Krebs, C. J. 1972. Ecology, the experimental analyses of distribution and abundance. Harper and Row, New York. 694 p.
- Lotka, A. J. 1925. Elements of physical biology. Reprint by Dover Publications, New York.
- Parton, W. P., and Marshall, J. K. 1973. MODENV: A grassland ecosystem model, p. 769-776. In Proceedings of the 1973 Summer Computer Simulation Conference. Vol. II. Simulation Councils, Inc., La Jolla, California.

- Rose, C. W., Begg, J. E., and Torssell, B. W. R. 1974. Townsville stylo (*Stylosanthes humilis* H.B.K.). In J. L. Montieth [ed.] Vegetation and the atmosphere. (In press)
- Stewart, J. M., and Levin, B. R. 1973. Partitioning of resources and the outcome of interspecific competition: A model and some general considerations. *Am. Natur.* 107(954):171-198.
- Torssell, B. W. R. 1973. Patterns and processes in the Townsville stylo-annual grass pasture ecosystem. *J. Appl. Ecol.* 10(2):463-478.
- Van den Bergh, J. P. 1968. An analyses of yields of grasses in mixed and pure stands. *Versl. Landbouwk. Onderz. (Agric. Res. Rep.)* Wageningen No. 714. 71 p.
- Volterra, V. 1926. Fluctuations in the abundance of a species considered mathematically. *Nature* 118:558-560.

LIST OF SYMBOLS

a	filter constant in equation (10)
α	relative reproductive rate, equation (4)
α_0, β_0	conversion factors for species N and N + 1, equation (1a)
B_n	space occupied by a single plant of species N when grown alone
K_n	maximum abundance, yield or space occupied by species N, when existing alone
MI	yield in mixture with other species
MO	yield of one species when grown in monoculture under the same environmental conditions as in the mixture
N_n	abundance, yield, or space occupied by species N
n,m	as superscripts: refer to time, where $n > m$
n,m	as subscripts: m = filter number, n = year number
ρ	relative replacement rate, equation (9)
R_n	relative abundance, yield, or space occupied by species N $(R_n = N_n/K_n)$
r_n	relative growth rate of species N
S_n	density of plants per unit area of species N
RYT	relative yield total
x	proportion of legume in a sward at the beginning of a phenophase
y	proportion of legume in a sward at the end of a phenophase