Nutrient gradients and spatial structure in tropical forests: a model study

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ABSTRACT

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We studied the competitive relationships between two life history strategies of tropical trees in a mixed-age spatial model. The two life histories differ primarily with respect to longevity, biomass per unit nutrient and amount of nutrients shedded.

We show that stable coexistence in a homogeneous environment is not feasible, but that both types represent a climax vegetation on appropriate soils. In a smooth gradient of soil nutrient content a sharp transition occurs between the two tree types.

The most important factors determining the outcome of the competition are longevity and the presence or absence of disturbance, and not, as earlier assumed, the differences in nutrient hoarding.

INTRODUCTION

Van Schaik and Mirmanto (1985) examined a series of topographical units of varying age and soil fertility in a Sumatran rainforest. They found that with increasing soil age, and decreasing plant-available soil P content, there was a decrease in the production of leaf litter and fruit, and an increase in the proportion of what is called 'mature phase' forest and the abundance of VAM mycorrhizas (see also Van Noordwijk and Hairiah, 1986). They suggested that each of the forest types was the climax of its soil type (Tilman, 1982, 1985), and concluded that the growth strategies of trees vary according to soil fertility. In particular, they suggested that trees live

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longer on poor soils. It is well documented that in tropical forests tree longevity varies with altitude and geographic location (Leigh and Smythe, 1978; Proctor et al., 1983; Tanner, 1985; Guillaumet, 1987), as do forest structure and animal biomass. Given such a big variation in tree growth or allocation strategies, we naturally wonder whether a forest can contain a mixture of all possible types or whether one of the types will generally predominate. In other words, if there is a continuous gradient in the availability of a critical plant nutrient, and all other factors remain constant, will the transition from one type of forest to the other be sharp or gradual?

To investigate this question in a model we need to focus on different types of trees. In the literature two strategies of nutrient use are distinguished (e.g. Chapin, 1980; Vitousek, 1982). We will refer to these types as HOARDERS and SHEDDERS. HOARDERS are characterized by a lower content of limiting nutrients in the leaves and litter than SHEDDERS, a longer lifespan of the leaves (and hence lower litter production), and tend to have more scleromorphic leaves. HOARDERS also grow more slowly. Slow growth is often associated with low seed production and dispersal (Connel and Slatyer, 1977; Finegan, 1984; Huston and Smith, 1987). Moreover, it is suggested that HOARDERS are more efficient in retranslocating nutrients from senescent leaves, and may absorb nutrients in excess of their immediate requirements in order to tide them over periods of reduced supply. Finally, HOARDERS are found on poor soils. Indeed, tropical trees on poor soils shed fewer leaves (Vitousek, 1982, 1984; Proctor, 1984; Van Schaik and Mirmanto, 1985) than those on rich soils, and also conform to the other HOARDER traits (Golley et al., 1980; Edwards and Grubb, 1982; Golley, 1983b; Tanner, 1985; Vitousek and Sanford, 1986). HOARDERS and SHEDDERS do not differ with respect to the maximum height they can attain. We investigated the competitive relationships between these two tree types with respect to: (a) the conditions under which each of them can maintain itself indefinitely in a plot, (b) their coexistence, and (c) the shape of the transition (sharp or continuous) along a soil gradient. To this end we used a mixed-age, mixed-species, spatial model (Shugart and West, 1980; Shugart, 1984).

We like to stress that in this paper we investigated the competitive relationships between a *paradigmatic* HOARDER and a *paradigmatic* SHEDDER. Thus, we do not assume that any particular forest will resemble closely the 'forest' studied here. In order to elucidate the important factors influencing forest structure it is in our opinion more useful to study such a paradigmatic forest than a model of any particular forest. We define our paradigmatic forest on the basis of the measured parameters of particular trees, which conform to the HOARDER and SHEDDER syndromes (i.e. syndromes recognized in literature). We are able to use these measured parameters, because we initially formulate the model in terms of individual trees, and not in

terms of population numbers or biomass. If the empirical generalizations on which the model is based are empirically invalidated the conclusions as derived from the model are of course invalidated as well. Not withstanding the particular empirically derived parameters and relationships used in this model, we are careful to keep the model as simple as possible by excluding other properties of the trees than the nutrient related properties, in which we are interested. This simplicity facilitates interpretation of the results.

Thus, our model approach occupies a separate niche in between the parameter dependent application oriented models which try to mimic particular ecosystems, and the parameter independent mathematical models which barely take into account quantitative empirical findings and which try to achieve broad generalization. We think the time has come to invade this niche.

MODEL

Patch dynamics

We consider a field with an area of 3/4 ha, which is subdivided into 300 patches, each large enough to contain one mature tree. The patches are spatially coupled in a uniform way. All eight adjacent patches are treated as direct neighbours, i.e. the influence of all those eight is identical. This spatial structure is inspired by the cellular automata formalism (Dees, 1987; Toffoli and Margolus, 1987; Hogeweg, 1988). This representation means that a patch, rather than a tree is the basic unit of the model (Hogeweg and Hesper, 1985; Hogeweg et al., 1985). The equations for our model were derived from the JABOWA-like models which were originally developed for deciduous forests of north-east North America (Botkin et al., 1972), and later modified for a wide range of forests (Shugart and West, 1977, 1980; Shugart et al., 1980a, 1980b, 1981; Dale et al., 1986; Huston and Smith, 1987; Shugart, 1987). We used these equations because they have been tested in field observations, and have proved their worth in previous simulation experiments (see previous references). Furthermore, very few, easily obtainable, parameters are needed. Although the growth curves are derived for temperate forests, and tropical trees have somewhat different growth equations the model is fairly insensitive to changes in the equations (Shugart, 1984).

The JABOWA models consider a plot of about 500 m^2, a typical gap size (Vitousek and Denslow, 1986). In such a plot the location of a tree relative to other trees is not taken into account (Shugart and West, 1980). By contrast, our model has a spatial structure. This is a very important feature

of our model, because it can create within-plot variation. The spatial structure functions with respect to:

(1) *Shading*. In our model we used the eight direct neighbours to compute light reduction on a patch, whereas in the JABOWA models shading is computed by considering every tree in the plot which has a height greater than the tree under consideration.

(2) *Seed availability*. The seed availability on an empty patch is dependent on the trees which occupy the neighbouring patches. If there are many trees of the one species in the neighbourhood the total amount of seeds of that species is large, and therefore the probability that a tree of the same species will occupy that patch is also large.

(3) *Tree death*. When a tree dies it may fall, killing some of its neighbours. In the JABOWA models treefall is not incorporated, except in the KIAMBRAM model (Shugart et al., 1980b), where treefalls are simulated by giving each tree in the plot an increased probability of mortality in a year when treefalls occur.

(4) *Nutrient availability*. To simulate a gradient each patch has a different soil nutrient content and hence different growth conditions. The JABOWA models incorporate the nutrient availability as a global growth-reducing factor representing soil quality, except the succession model by Pastor and Post (1986), in which water stress and N cycling are incorporated.

The abiotic environment is defined by the availability of nutrients. We decided to use P as the limiting nutrient because it often limits plant production in tropical forests (Vitousek, 1984; Jordan, 1985), it is relatively stable in the soil, and lateral migration is very slight (Luse, 1970). Direct competition among individuals is restricted to competition for light. The dynamics of each patch is defined by the main subroutines: BIRTH, GROWTH, and DEATH (Fig. 1).

BIRTH. When a patch is empty, the total seed availability at this patch is computed for each species. This is done by using equation 1 (Table 1), which adds together the seed production per species for all neighbours, and then adds a global influx for each species representing the availability of seeds in the soil. A new occupant is chosen by making a random draw from the seed distribution.

GROWTH. To assess the growth of a tree, the maximum increment in the diameter of the tree under consideration is computed as a function of the size of the tree. This maximum growth is then multiplied by two factors that influence the growth, namely light- and nutrient availability. This gives the actual growth of the tree. The functions for computing maximum growth were derived from the JABOWA model (Botkin et al., 1972) (Table 1, eq. 2,
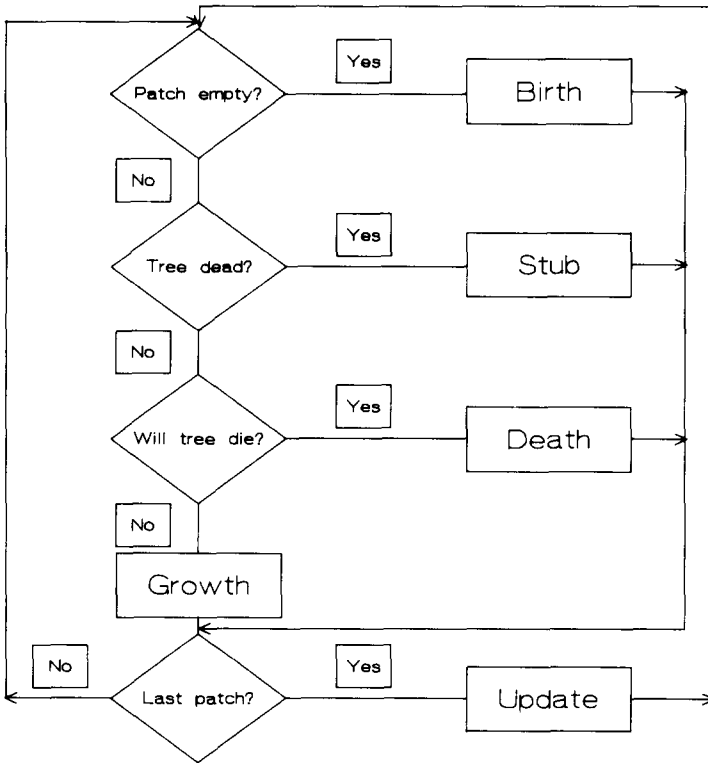
Fig. 1. Flow diagram of the spatial model.

3). The constant G (eq. 3) is chosen so that under optimum conditions a tree with half the maximum age of that species has a diameter two thirds of the maximum diameter. This constant G also sets the initial rate of growth of young individuals.

The actual growth rate is obtained by multiplying the right hand side of eq. 3 by the two growth influencing factors. Nutrient availability is expressed as a saturation curve with maximum 1 (eq. 5). This means that when there are plenty of nutrients growth is not suppressed, and when nutrient availability equals K_m (saturation constant) the growth reduction caused by a nutrient insufficiency is 50%. To compute light availability it is necessary to know the SLA (shading leaf area) of the trees in a plot. The SLA of a tree is computed using the equations developed by Kira (1978) (Table 1, eq. 6, 7, 8). The shading to which a tree is subjected by each neighbour is proportional to the height difference between the trees and the SLA of the neighbour. It is 0 when the neighbour is smaller than the tree under consideration (eq. 9). The available light was computed by using the approximation given by Botkin et al. (1972). They approximated a light extinction curve by the

TABLE 1

Equations used in the spatial model

Seed availability

$$\text{SA} = \sum \left[\text{SEED}_n \left(H_n / H_{\max,n} \right)^2 \right] + \text{GLOB} \tag{1}$$

where

SA	total amount of seed for a species
SEED$_n$	maximum seed production
H_n, $H_{\max,n}$	height, max. height of neighbour
GLOB	global seed availability

Rate of volume increase

$$\mathrm{d}[D^2 H]/\mathrm{d}t = R \cdot \text{LA} \cdot \left[1 - DH / (D_{\max} H_{\max}) \right] \tag{2} \quad \text{B}$$

where

LA	leaf area
R	constant
$D_{\max}$	maximum diameter
$H_{\max}$	maximum height

Rate of diameter increment

$$\mathrm{d}D/\mathrm{d}t = \frac{GD\left[1 - DH / (D_{\max} H_{\max}) \right]}{\left(274 + 3b_2 D - 4b_3 D^2 \right)} \tag{3} \quad \text{B}$$

where

G	constant
b_2	$= 2(H_{\max} - 137)/D_{\max}$ $\qquad$ (4) $\quad$ B
b_3	$= (H_{\max} - 137)/D_{\max}^2$

Growth reduction by nutrient insufficiency

$$r(N) = N/(N + K_m) \tag{5}$$

where

$r(N)$	fraction of growth
N	nutrients in soil
K_m	saturation constant

Available light and shading

$$w_s = 0.313 (D^2 H)^{0.9733} \tag{6} \quad \text{K}$$

$$1/w_l = 1/\left(0.124 w_s^{0.794} \right) + 1/125 \tag{7} \quad \text{K}$$

$$\text{SLA} = 11.4 w_l^{0.9} \tag{8} \quad \text{K}$$

where

w_s	stemweight (kg)
w_l	leaf weight (kg)
$D^2 H$	volume (dm^3)
SLA	shading leaf area (m^2)

TABLE 1 (continued)

$$\text{SHADE} = \sum (H_n - H_0)\text{SLA}_n/H_n \tag{9}$$

where

H_n	height neighbour
H_0	own height
SLA_n	shading leaf area neighbour

$$\text{AL} = e^{-\text{KP} \cdot \text{SHADE}} \tag{10} \quad \text{K}$$

where

AL	available light
KP	constant (0.01)

Growth reduction by shading

$$r(\text{AL}) = 1.345[1.095 - e^{-1.136(\text{AL} - 0.08)}] \tag{11}$$

where

$r(\text{AL})$	fraction of maximum growth

Mortality

$$P_m = 1 - (1 - 4/\text{AGEMAX})^t \tag{12} \quad \text{K}$$

where

P_m	probability of death in year t
AGEMAX	age at which one would expect only 2% of the trees to be alive

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[B] Derived from Botkin et al. (1972).
[K] Derived from Kira (1978).

equation given by eq. 10. To compute the reduction of photosynthesis as a function of the available light we used only one curve (eq. 11), and made no distinction between shade-tolerant and shade-intolerant trees, although this distinction is made in most previous work. The reason for this is that we want to incorporate as few differences as possible between the tree species. The function is chosen so that when available light is maximal no growth reduction occurs.

DEATH. It is assumed that each tree has an intrinsic mortality rate such that under optimum conditions only 2% of the individuals live long enough to attain maximum height and diameter. This gives a probability that a tree will die in any one year (eq. 12), Very slow growing trees (due to shading or insufficient nutrients in the soil) have an additional probability of dying ($P = 0.368$) (Botkin et al., 1972).

A tree can die standing up or it can fall. When a tree dies standing, the patch is not cleared immediately. Each year the height of a stub decreases,

until it is so small that the patch is cleared and available for new seedlings. A falling tree has a major impact on its surroundings. When it falls it can kill up to five neighbouring trees, depending on the height of the falling tree and the height of the tree it falls on. Trees, killed by a treefall, die standing. The patch of the falling tree is cleared immediately.

STRUCTURING THE INITIAL CONDITIONS

Two tree species

We performed our simulation experiments with two tree species, one a HOARDER type and the other a SHEDDER type. Provided that these trees have the same maximum height the slower growth of a HOARDER implies a longer lifespan. Maximum age and height of a tree are relatively easily estimated, and can be used to select a paradigmatic HOARDER and a paradigmatic SHEDDER. We took *Cryptocarya foveolata* as an example of a HOARDER species: it has a maximum height of 3048 cm, a maximum diameter of 61 cm, and a maximum age of 300 years (Shugart et al., 1980b) and we inferred a P content of 77.5 μg/cm^3. As a paradigm for the SHEDDERS we have chosen *Polyscias elegans*, which has a height of 2743 cm, a diameter of 76 cm, and a maximum age of 80 years (Shugart et al., 1980b), and inferred a P content of 233 μg/cm^3. P content is expressed per unit tree volume because the model computes changes in volume rather than biomass. The nutrient contents were estimated from the amount of nutrients in the above ground standing crop. The differences between HOARDERS and SHEDDERS are summarized in Table 2. The plot was initialized by calling the subroutine BIRTH for every patch in the plot, resulting in an equal number of SHEDDERS and HOARDERS.

TABLE 2

Parameters used in the spatial model

Parameter	HOARDER	SHEDDER
Maximum age (years)	300	80
H_{max} (cm)	3048	2743
D_{max} (cm)	61	76
NUTCONC (kg P cm^{-3})	7.75×10^{-8}	2.33×10^{-7}
K_m (kg P per patch)	0.003	0.14
SEED (No. year^{-1} per tree)	30	30
GLOB (No. year^{-1} per patch)	0.5	0.5

When the saturation constants (K_m) were made equal they were put to 0.07 kg P per patch. NUTCONC refers to the concentration of phosphorus in the tree's tissue. The parameters in the top panel were derived from Shugart et al. (1980b).

Nutrient gradient

We studied the competition between the strategies in a nutrient gradient. This allowed us to consider all three questions posed in the introduction about the competitive relationships (survival, coexistence, and shape of the transition) in one set of experiments. The gradient in the model was initialized so that P availability at one end of the gradient was 0.06 kg per patch, whereas at the other end 0.25 kg per patch was available. This means that at the low end of the gradient 24 kg P per ha was available, and at the other end 100 kg per ha. These availabilities reflect the differences between poor and rich soils (Jordan, 1985).

Fixed versus Non-fixed nutrient gradient

The nutrient gradient was treated in two different ways. The first was to keep the nutrients in the soil at a fixed level. This means that trees do not influence the soil, and hence the influence of the soil nutrient level on the trees could be studied.

The second approach was to allow the nutrients in the soil to change. When this is done the trees can influence the amount of nutrients in the soil, so the initial nutrient gradient can fade away or become discontinuous. This approach allowed us to investigate the effect of the trees on the soil.

Saturation constants

In contrast to the other parameters of the model the saturation constants of nutrient uptake by HOARDERS and SHEDDERS are unknown. Chapin (1980) reports a higher saturation constant for SHEDDERS. This is indeed to be expected: the fast growth and the higher nutrient content of SHEDDERS should each imply the need for a higher nutrient supply if uptake behaviour is equal. Nevertheless we also studied the case of equal saturation constants for HOARDERS and SHEDDERS, thus minimizing the assumptions concerning the adaptation of HOARDERS to poor soils and SHEDDERS to rich soils. In the fixed nutrient experiments the only nutrient related difference between the two types is the saturation constant, but when nutrient concentration in the soil is influenced by the trees the difference in nutrient content of the trees indirectly yields a difference in growth conditions.

MODEL MINIMIZATION: THE RANDOM PHASE, RANDOM SPACE APPROXIMATION

The spatial model described above is fairly complex. The complexity of the patch dynamics is needed to derive the model parameters from tree

properties which are easily observable (height, diameter, and maximum age). To enhance our understanding of the crucial features of such a complex model it is important also to study a minimization of this model. The minimization conducted here is one which disregards the spatial structure and possibly inhomogeneous age distribution. This 'mini-model' is hence expressed in terms of total numbers of individuals of each species and the number of empty patches. Changes occur through birth and death. The form of the birth and death processes as well as the rate parameters are derived from the spatial model. The mini-model is formulated in differential equations and thus takes the general form of competition models of the Lotka–Volterra type (Table 3, eq. 13). The growth of the populations, the amount of reproduction, is dependent on the number of empty patches available. Each year each empty patch is recolonized by one of the trees, depending on the proportion of the amount of seeds from both tree species. The amount of seed per tree depends solely on the amount of nutrients in the soil. Tree death is incorporated as a fixed percentage of trees dying each year. This

TABLE 3

Differential equation model, developed from the spatial model, with parameters

$$S_h = a_h NH/(K_h + N)$$
$$S_s = a_s NS/(K_s + N)$$
$$T_d = (b_h + c_h)H + (b_s + c_s)S$$
$$PA = 300 - H - S$$
$$dH/dt = [S_h/(S_h + S_s)]PA - (b_h + c_h)H - (dT_d + e)(H/(H + S))$$
$$dS/dt = [S_s/(S_h + S_s)]PA - (b_s + c_s)S - (dT_d + e)(S/(H + S))$$

$$(13)$$

where
a_h, a_s maximum seed availability
b_h, b_s proportion of trees dying of age
c_h, c_s proportion of trees dying of growth insufficiency
d proportion of trees killed by falling trees
e number of trees killed by external disturbance
S_h, S_s total seed availability for tree species
T_d total number of trees dying of natural causes
PA   number of unocupied patches

parameter	HOARDER	SHEDDER
a	1	1
b	0.016	0.051
c	0.01	0.01
K	1.2	56

The K's differ from the K_m's in the spatial model, because these values are the values per ha, and not per patch.

percentage is divided into the 'natural' mortality (b), and the mortality caused by insufficient growth (c). As stated earlier the only way to obtain these parameters is to estimate them from our spatial model. Treefall is incorporated as the additional killing of a number of trees proportional to the number of trees that died already (d). The factor e gives the possibility of incorporating other causes of tree death.

The differential equation model is analysed with GRIND (De Boer, 1983). GRIND enables the user to analyse the static properties of models by the computation of 0-isoclines, as well as the dynamic behaviour by numerical integration. The model was analysed in the state space of HOARDERS, SHEDDERS, and nutrients. We decided to use a fixed nutrient gradient, and hence different saturation constants, because it is simpler and the differences between fixed and non-fixed gradients appeared to be small in the spatial model.

RESULTS

Spatial model

The results are summarized in Table 4.

1. *Minimum differences.* When the differences between the trees are restricted to the type properties mentioned earlier and all trees die standing, the plot develops into a HOARDER-dominated forest. The reason for this tendency to HOARDER dominated forests is the difference in longevity. The maximum age of HOARDERS is much higher than the maximum age of

TABLE 4

Summary of the results

	No Disturbance		Disturbance	
	fixed	non fixed	fixed	non fixed
Saturation constants equal	H	H	H	H
high seed production	HS	HS	HS	H/S
high dispersal	H	H	S	H/S [a]
Saturation constants differ	H	H	H	H
high seed production	H/S	H/S	H/S	H/S
high dispersal	H	H	H/S [a]	H/S [a]

H, HOARDER-dominated forest; S, SHEDDER dominated forest; H/S, Spatial separation of two forest types, with HOARDERS dominating on the low end of the gradient and SHEDDERS dominating on the high end; HS, unstable mixed forest.

[a] High dispersal alone is not enough to yield a spatial separation, and SHEDDER seed production is enlarged slightly.

SHEDDERS, resulting in a long occupance of a patch, whereas SHEDDERS must establish several times if it is to occupy a patch as long as one HOARDER individual. The higher longevity of HOARDERS also results in a higher total seed production for HOARDER individuals.

Since one of the reported differences between both tree types is a difference in reproductive potential, this competitive advantage for SHEDDERS is introduced.

2. *Higher seed production and / or higher seed dispersal for SHEDDERS.* We decided to keep the global seed availability equal and to change the local seed availability. This can be done in two ways:

(A) *Increase seed production for SHEDDERS.* When SHEDDERS produce more seeds, more SHEDDER saplings will be planted. When this surplus seed production is large enough a SHEDDER-dominated forest develops in all cases. However, when the seed production is not that large both tree types will remain present in the plot. The spatial distribution depends on whether the saturation constants are equal or not. When they are not equal a sharp transition from a HOARDER-dominated forest at soils with low nutrient levels to a SHEDDER-dominated forest at soils with high nutrient levels was observed. This is a stable phenomenon. When saturation constants are equal a mixed forest arises (Fig. 2a). However, this mixed forest does not represent a
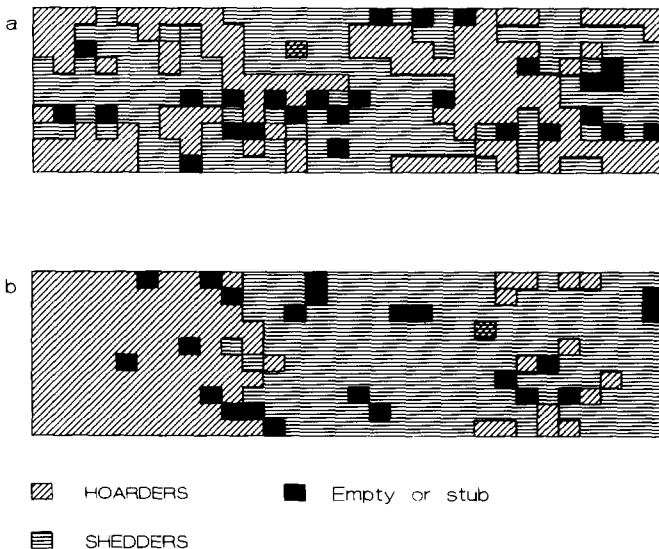

Fig. 2. Composition of the forest, as simulated by the spatial model. Nutrient content of the soil increases from left to right. (a) Mixed forest, an instable situation. (b) Spatial separation of HOARDER-dominated forest on the low nutrient level side, and SHEDDER-dominated forest on the high nutrient side.

stable situation, but a transition in a very slow development to an equilibrium. On the fixed nutrient gradient one of the trees will eventually outcompete the other, whereas on a non-fixed gradient a spatial separation of tree types will eventually occur.

(B) *Increase seed dispersal.* When a tree scatters its seeds further more empty patches can be colonized. Colonizing a patch which is further away also means that growth of the saplings on a patch is not suppressed by the shade of the parent. However, increasing SHEDDER seed dispersal has no effect on the outcome of the competition: HOARDERS still dominate the plot.

3. *Disturbance.* Levin and Paine (1974) stated that it is possible for subdominant competitors to establish themselves and remain in a plot when disturbance is sufficiently high. Disturbance was incorporated by the introduction of treefall. When treefall is introduced with equal seed availabilities this has no effect: HOARDERS win as always, so the disturbance is not large enough for SHEDDERS to become established and remain, and hence it is necessary to increase seed availability.

(A) *High production.* The outcome of the competition is the same as without disturbance. The only difference is that disturbance decreases the amount of extra seed production required for the SHEDDERS to survive in the plot. The observation that without disturbance a mixed forest arises on a non-fixed gradient with equal saturation constants, and with disturbance a spatial separation just indicates that disturbance causes a more rapid development.

(B) *High dispersal.* High dispersal gives the same results as high production, but only if this is accompanied by a slight increase in seed production. When saturation constants are equal and the gradient is fixed the high dispersal alone is enough for the SHEDDERS to outcompete the HOARDERS (Fig. 2b).

Treefall is not the only cause of disturbance in a natural forest. Other biotic and abiotic agents can kill trees, for instance diseases, fires, or hurricanes. We introduced these external differences by killing at random a number of trees in the plot. If only a few trees are killed each year, the outcome of the experiments is the same as if treefall is present. Increasing the disturbance results in a shift of the transition to lower nutrient levels. A very large disturbance means that no tree reaches maturity, and SHEDDERS dominate the plot.

Fixed gradient versus Non-fixed gradient

The results show that the difference between the fixed and non-fixed gradients is not very large. The only qualitative difference arises when
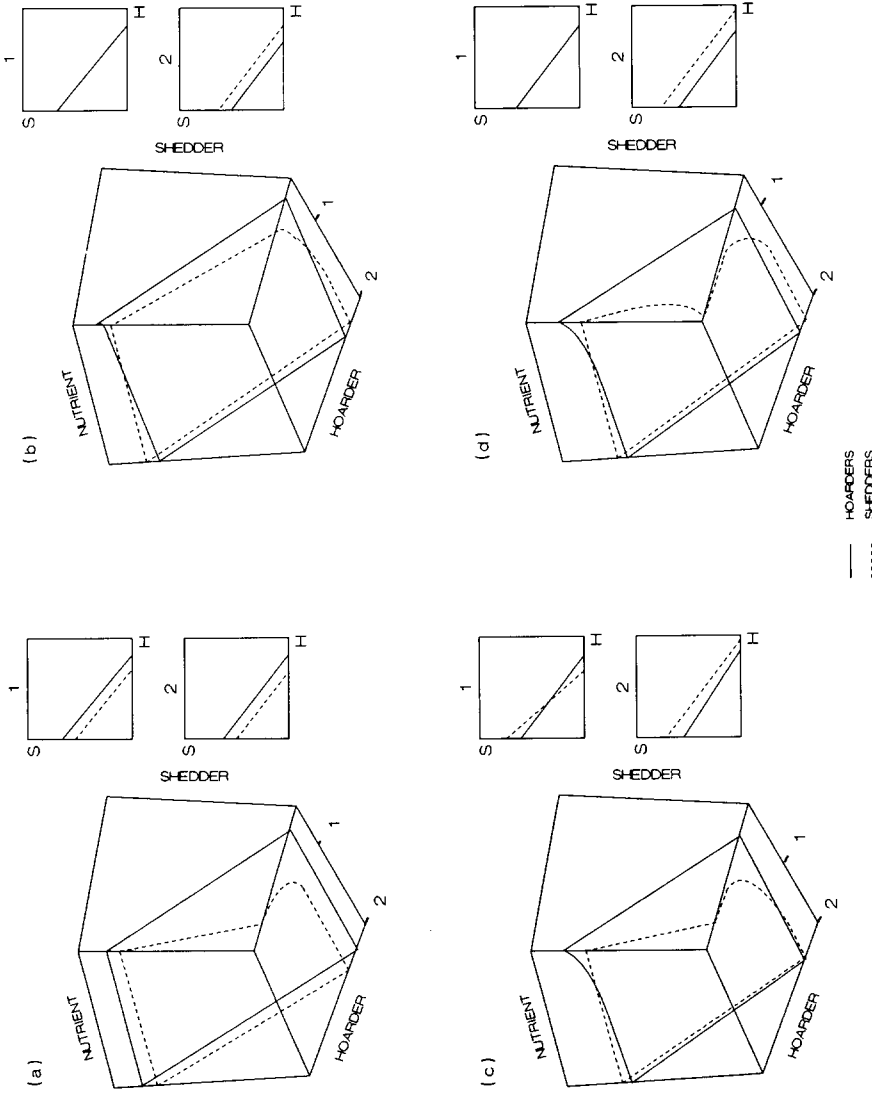
Fig. 3. State spaces of different parameter settings. (a) Minimal differences: no treefall or external disturbance. (b) Higher seed production for SHEDDERS. (c) Treefall incorporated. (d) External disturbance incorporated. The planes marked 1 and 2 are intersections of the state space at nutrient levels 1 and 2.

disturbance is present, SHEDDER seed availability is high and saturation constants are equal. On the non-fixed gradient a separation arises under these circumstances, whereas with fixed nutrients one of the trees dominates. This difference is caused by the influence trees can have on the soil in a non fixed situation. The effect of a tree on the soil is large. A mature tree has a large proportion of the nutrients in its tissue. In our experiments this means that the nutrient content of the patches differs considerably, and the soil gradient flattens out.

DIFFERENTIAL EQUATION MODEL

1. *Minimum differences*. The dHOARDER/dt = 0 isocline is situated above the dSHEDDER/dt = o isocline (hereafter called HOARDER, and SHEDDER isocline respectively) under all nutrient conditions (Fig. 3a). This means that the forest on the plot will develop into a HOARDER-dominated forest irrespective of the amount of nutrients in the soil.

2. *Higher SHEDDER seed production*. When the seed availability of SHEDDERS is increased the isoclines shift and planes cross. The result of this shift is that at high nutrient levels the SHEDDER isocline is situated above the HOARDER isocline, and SHEDDERS can dominate the plot at high nutrient levels (Fig. 3b). A further increase in the SHEDDER seed availability results in a shift of the transition nutrient level to lower amounts of nutrients in the soil.

3. *Disturbance*. When treefall is incorporated ($d > 0$) the isoclines shift, and again the planes cross at intermediate nutrient levels (Fig. 3c), provided, as in the spatial model, that seed production of SHEDDERS is somewhat higher. The nutrient level at which the planes intersect depends on the magnitude of d. The planes intersect in such a way that an unstable equilibrium occurs at intermediate nutrient levels. This means that the outcome of the competition at that level is dependent on the initial conditions, and a sharp transition can occur. When external disturbance is introduced ($e > 0$) the situation is different. Because an increase in external disturbance affects each species equally, the introduction of an external disturbance results in a parallel movement of the isocline planes (Fig. 3d). When external disturbance is sufficiently high ($e > 8$) the planes shift at an intermediate nutrient level from one being completely above the other to the reverse situation. In a nutrient gradient this would result in a sharp transition only when migration is not taken into account. In all other cases it yields a gradual transition.

We see that the results of the differential equation model are in accordance with the results found in our spatial model, and that the behaviour can be explained in terms of the location of the 0-isoclines. SHEDDERS

outcompete HOARDERS at high but not at low nutrient levels if seed availability is sufficiently high or if treefall or external disturbance is incorporated. The effect on the isoclines of increasing the seed availability of SHEDDERS and introducing external disturbance are identical i.e. the isoclines shift in a parallel way. The minimodel predicts that in the spatial model the boundaries at the transition from HOARDER to SHEDDER forest are sharper when disturbance is caused by treefall, because this disturbance causes an unstable equilibrium, and hence a sharp boundary, whereas the external disturbance results in two coinciding isoclines at an intermediate nutrient level, and hence a less sharp boundary. The differential equation model shows that a stable equilibrium never occurs. This means that, whatever the causes of the shift in dominating species along the gradient, this shift will never be continuous.

DISCUSSION

Major outcomes of the model experiments:

1. *HOARDERS outcompete SHEDDERS.* When all traits of the trees are equal, except age and size (Table 2), HOARDERS outcompete SHEDDERS because of their longevity and hence their longer occupancy of a patch.

2. *SHEDDERS can counteract via high seed availability.* The competitive advantage of HOARDERS caused by their longevity can be compensated by introducing a high seed production or high dispersal for SHEDDERS. When a tree has a relatively low maximum age it must produce enough seeds to re-establish. Producing a large number of seeds usually means producing small seeds, because of the limited amount of energy which can be invested in reproduction. Smaller seeds will often be better dispersed than larger seeds. In general HOARDERS produce fewer, and larger, seeds.

3. *Disturbance favours SHEDDERS; SHEDDERS produce disturbances.* The effect of disturbance operates via longevity. In our model undisturbed HOARDERS can live for up to 300 years, whereas the maximum longevity for SHEDDERS is only 80 years. Thus disturbance affects HOARDERS more strongly, because they die much earlier than they would if not disturbed. When a tree dies and the patch is recolonized there is a risk that the sapling will be of a different species. Disturbance does not necessarily refer to external disturbances such as hurricanes (Doyle, 1981) or fires (Dale et al., 1986), but can be an intrinsic property of the forest. Treefall causes SHEDDERS to outcompete HOARDERS, unless nutrients are too scarce. So, it can be concluded that SHEDDERS are not only more tolerant to disturbances, because they regener-

ate faster (via high seed production, and faster growth), but they do in fact create the disturbances by falling, and hence favour their own growth conditions.

The effect of external disturbance is similar to that of treefall, although the differential equation model shows that it is not quite equal. In the spatial model this difference is obscured by the large influence neighbouring patches have on a patch. In our model the large effect of a neighbour can cause some problems, because the scale of our experiments is very small (only 30 by 10 patches). This means that the gradient we incorporated is not very smooth but is in fact a stepwise gradient: the difference in growth conditions of two adjacent patches may be too large. However, even with a smoother gradient (0.08–0.12 kg per patch) the results do not change although development to the 'climax' stage of the plot is a very slow process, and is counteracted by the large influence of neighbouring patches. Moreover the differential equation model gives similar results as the spatial model.

4. *Climax forests are composed of either* SHEDDERS *or* HOARDERS. HOARDERS as well as SHEDDERS can be the final successional stage under the appropriate conditions. A SHEDDER climax is found on relatively rich soils because of the fast growth rate and high nutrient content of SHEDDERS. These properties also imply a difference in their saturation constants (K_m), but this difference is not a necessary condition for the predominance of SHEDDERS on rich soils. In a soil gradient, the HOARDER/SHEDDER transition is sharp.

5. *The nutrient gradient is barely visible in soils.* When the gradient is not fixed in our simulations, the slope of the soil gradient decreases. When this is extrapolated this means that it is very difficult to classify a forest when only soil nutrients are measured, because a rich (SHEDDER) forest does not necessarily mean that the soil has a high nutrient content (See Edwards and Grubb, 1982; Golley, 1983b). Moreover, it is very difficult to measure the amount of nutrients available for uptake by the trees, and the differences in nutrient content also reflect the difference in measuring methods (Whitmore, 1984).

6. *Differences in nutrient loss are not important.* The difference in the amount of nutrients in the litter is not an important factor in the HOARDER/SHEDDER issue, although it was the difference in litter production which inspired this study and led to the names HOARDERS and SHEDDERS. When the amount of nutrients dropped as litter is altered in our spatial model, both for HOARDERS and SHEDDERS, we find that this has little or no effect on the composition of

the forest. This is sustained by the fact that litter production is not included in the differential equation model, and this model gives the same results as the spatial model. The reason for the minor importance of differences in nutrient loss is that the time scale is totally different. It takes several centuries before a mature forest arises, whereas litter influences the environment only a few years.

ECOLOGICAL IMPLICATIONS

We like to emphasize two general ecological implications of our model studies:

(1) The role of disturbance in ecosystems has more and more come into the limelight in the last decennium. Our work shows, once again, that disturbance is not an external factor independent of the state of the system. In particular, we show that species which benefit from disturbance (i.e. SHEDDERS) are themselves a causal factor in producing disturbance (by falling).

(2) On the basis of our model we expect sharp boundaries to exist between tree types in forests. This should have large implications for the other organisms in the forest. For example we expect sharp boundaries between animal communities and epiphyte communities as well. If so, this is very important for nature conservancy.

IMPLICATIONS FOR LIFE HISTORY STRATEGIES OF TREES

Our results suggest that the HOARDER–SHEDDER contrast has arisen primarily through selection on the basis of longevity rather than on nutrient economy. This in contrast to the hypothesis which inspired our model experiments, according to which nutrient limitation is the cause of the HOARDER syndrome, i.e. high biomass production per unit of nutrient, the long life span of leaves and the low litter production, and consequently the slow growth of the tree. However this syndrome can also be regarded as a consequence of selection for long life span. Empirical evidence shows that longevity and growth rate are negatively correlated in trees (Botkin et al., 1972; Shugart, 1984). Long life span necessitates the protection of tissues against loss to herbivores or other inimical agents, and hence investment in chemical (e.g. McKey et al., 1978) and structural (e.g. Jordan and Herrera, 1981; Coley et al., 1985) defence. As a consequence, leaves should be retained longer. Structural protection of leaves also automatically causes lower nutrient contents. It is also expected that the need to attain a long life span necessitates the allocation of a relatively small proportion of the resources to reproduction. For regeneration in the small gaps created by the

death of a tree, large seeds are required. Thus, selection on longevity can also generate all traits of the HOARDER syndrome. It is doubtful whether one should seek primary causes in a complex feedback system like the evolution of life history properties. If one does, we prefer the alternative view presented here, because (1) the longevity difference is the crucial factor in the competition, (2) it solves elegantly the apparent paradox discussed by Chapin et al. (1986), namely that the nutrient limited species (HOARDERS) barely increase their growth rate in response to nutrient supply, and (3) there seem to be severe limitations in the hoarding capabilities of the HOARDERS, in particular in their ability to retranslocate nutrients from senescent leaves (ce. Chapin, 1980; Vitousek, 1982). Indeed the proportion of nutrients lost annually through litterfall is in fact equal for forests on rich and poor soils, even though the total amount of litterfall and the nutrient content of the litter are quite different (Proctor, 1984; Vitousek and Sanford, 1986). Thus trees on poor soils do not seem to be better at retaining nutrients. However, this is not to deny the existence of adaptations in order to capture of nutrients on very poor soils: root mats (Jordan, 1985), canopy roots (Nadkarni, 1981), mycorrhizal infections (Van Noordwijk and Hairiah, 1986), and direct transfer from leaf litter to roots (Herrera et al., 1978; Luizão and Schubart, 1987).

CONCLUSIONS

We conclude that the properties which define HOARDERS and SHEDDERS are tightly interrelated, and largely converge to the classical distinction between K and r selected species. They also largely coincide with the properties distinguishing late and early successional species as listed by Huston and Smith (1987). The syndromes can in principle be explained in terms of selection on either longevity or nutrient economy. In any case, the occurrence of a mixed HOARDER/SHEDDER forest in a homogeneous nutrient environment is not a stable situation, but can of course occur as a (long lasting) transition. When a nutrient gradient in the soil is present there is a sharp spatial separation between HOARDERS and SHEDDERS. HOARDERS dominate the low end of the gradient, whereas SHEDDERS occupy the soils with high nutrient levels. Both HOARDERS and SHEDDERS are climax stages on these soils and there is a sharp boundary between them.

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