

Cyclic dynamics in simulated plant populations

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Despite the general interest in nonlinear dynamics in animal populations, plant populations are supposed to show a stable equilibrium that is attributed to fundamental differences compared with animals. Some studies find more complex dynamics, but empirical studies usually are too short and most modelling studies ignore important spatial aspects of local competition and establishment. Therefore, we used a spatially explicit individual-based model of a hypothetical, non-clonal perennial to explore which mechanisms might generate complex dynamics, i.e. cycles. The model is based on the field-of-neighbourhood approach that describes local competition and establishment in a phenomenological manner. We found cyclic population dynamics for a wide spectrum of model variants, provided that mortality is determined by local competition and recruitment is virtually completely suppressed within the zone of influence of established plants. This destabilizing effect of local processes within plant populations might have wide-ranging implications for the understanding of plant community dynamics and coexistence.

Keywords: field-of-neighbourhood model; nonlinear dynamics; oscillations; spatial effects; recruitment

1. INTRODUCTION

The study of nonlinear population dynamics has blossomed in recent decades. Especially in the animal ecology literature does one find widespread evidence for nonlinear dynamics of population sizes that arises from overcompensating density dependence, time-lags or high-fecundity values (Krebs 1996; Berryman 1999; Hansen *et al.* 1999; Bjornstad 2000; Johnson 2000; Sherratt *et al.* 2000; Dennis *et al.* 2001; Turchin & Batzli 2001).

For plant populations, however, it has been supposed that cyclic or chaotic behaviour is unlikely to be found and that the existence of a stable equilibrium has been the dominant notion in plant ecology (Crawley 1990). Very few publications discuss the role of nonlinear behaviour in plant populations and this topic mostly seems to be of minor importance to most plant ecologists (Cousens 1995; Stone & Ezrati 1996). Changes in population size have often been attributed to other mechanisms such as disturbances, variability of environmental factors and pathogens (Wiegand *et al.* 1998; Eriksson & Eriksson 2000). It has been assumed that the stability of plant populations comes from several fundamental differences compared with animals. First, plants show extreme physiological plasticity and can reproduce at very small sizes. The effects of crowding can be ameliorated by long-distance dispersal and, additionally, recruitment from long-lived seed-banks could also stabilize population dynamics (Rees & Crawley 1989; Crawley 1990).

Evidence for the nonlinear behaviour of plant populations is also rare but this does not necessarily mean that plant populations are inherently stable. Empirical examples of nonlinear behaviour in plant populations can be found in Symonides *et al.* (1986), Thrall *et al.* (1989),

Silvertown (1991), Tilman & Wedin (1991) and Crone & Taylor (1996).

However, as argued by Crone & Taylor (1996), it is generally difficult to interpret the results of studies that found stable equilibrium dynamics, because extremely few authors have studied population dynamics over several generations—an argumentation also made by Dodd *et al.* (1995). In their study, Crone & Taylor (1996) monitored population dynamics in a replicated experimental population of a greenhouse weed, *Cardamine pensylvanica*. They tested for density dependence and fitted the data to both non-lagged and lagged time-discrete density-dependent functions. By contrast to the prevailing notion of equilibrium dynamics, a strong cyclical population dynamics was found that could not be accounted for by changing environmental conditions (Crone 1997b).

Furthermore, few modelling studies exist that have searched for the conditions of nonlinear behaviour in plant populations (e.g. Pacala & Silander 1990; Silander & Pacala 1990). Silander & Pacala (1990) attempted to determine the conditions for oscillatory and chaotic behaviour in annual plant populations. Such behaviour was found to be more probable when annuals had a low seed dormancy, high germination success, a minimum plant-size threshold for reproduction or high soil fertility. They demonstrated with their model a range of dynamic behaviour from a stable equilibrium to damped and stable oscillations and apparent chaos. The authors argued that seed dormancy leading to a time-lag actually stabilizes a plant population that would otherwise tend to oscillate.

In general, most models that investigate nonlinear behaviour in plant populations did not include space as an explicit feature (e.g. Solbrig *et al.* 1988, but see Durrett & Levin 1998). Space, however, is important because of the localness of competition, the monopolization of space by established plants and general issues of spatial distribution (Crone 1997a). A natural approach to modelling plant population dynamics would be a spatially

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explicit individual-based model (Huston *et al.* 1988; Grimm 1999). Realistic individual-based plant population models should contain the following key elements: each individual has an explicit spatial location, a basal extension where no other plant can exist and a zone of influence in which interactions with neighbouring plants occur (Stoll & Weiner 2000). Furthermore, the number, size and location of any neighbours should also be taken into account (Stoll & Weiner 2000). Although there exist such model approaches, for example the zone of influence (e.g. Wyszomirski *et al.* 1999; Weiner *et al.* 2001) and the ecological-field (Wu *et al.* 1985; Walker *et al.* 1989) approaches, questions concerning population dynamics have not been investigated under these approaches.

We investigated the dynamics of a hypothetical, isolated population of non-clonal perennials with an individual-based model based on the recently developed field-of-neighbourhood (FON) approach (Berger & Hildenbrandt 2000, 2001; Bauer *et al.* 2002; Berger *et al.* 2002). The FON approach fulfils the criteria of a realistic plant population model (Stoll & Weiner 2000). Individual plants are represented by circular areas around their stemming points. These circular areas determine the extension of a plant's zones of influence and, additionally, a field superimposed on the zone of influence defines the intensity of influence on a potential neighbour. In particular, we investigated the following points:

- (i) whether stable equilibrium, oscillatory or chaotic dynamics represent a model population of perennials based on the FON approach;
- (ii) the circumstances under which cyclic patterns occur in population dynamics; and
- (iii) whether reproduction, recruitment, seed dispersal or mortality mechanisms drive a population to cycle.

2. MODEL AND METHODS

(a) General model description

Our model is individual based and spatially explicit and based on the FON approach (Berger & Hildenbrandt 2000). At the beginning of each model run, an initial number of individuals is randomly distributed over a 50 m² study area. The results presented are largely independent of the initial number, age and spatial distribution of the plants. During each time-step individuals grow, reproduce or die according to the rules listed in § 2c–f. For the analysis of population dynamics, the model was run over 1000 time-steps.

(b) Individual characteristics

All individuals are characterized by their spatially explicit position, size and age. The size of an individual is represented by its basal extension, e.g. stem, tussock or tuft area. Furthermore, each individual has a zone of influence where it interacts with its neighbours. The extension of this zone is determined by a nonlinear function of the basal radius as follows:

$$R_{\text{FON}} = aR_{\text{basal}}^b$$

with $a = 10.0$ and $b = 0.9$. By contrast to the zone-of-influence models, the FON approach superimposes a field on the zone of influence to quantify the strength of competition (Berger & Hildenbrandt 2000). Herein, the influence of the focal individ-

ual on potential neighbours is described in a phenomenological manner and thereby avoids the definition of resource uptake dynamics. This approach also assumes that the influence of more neighbours and their position can be taken into account. For the quantification of the neighbours' influence on the k th individual, the field values in the overlap areas are calculated and summarized as:

$$F_A^k = \frac{1}{A} \sum_{n \neq k} \int_{A'} \text{FON}_n(x,y) da,$$

where A is the area of the FON of the k th individual and $\text{FON}_n(x, y)$ is the value of the FON of the neighbouring plant n in the overlap areas A' .

(c) Growth of individuals

Individuals grow according to their neighbourhood situation and their actual size. An isolated individual shows sigmoidal growth, i.e. its growth rate, GR, is quadratically dependent on its size, R_{basal}

$$\text{GR} = S \times \text{MGR},$$

where MGR is the maximum growth rate and the correction factor for size S is given by

$$S = c \frac{R_{\text{basal}}}{R_{\text{max}}} \left(1 - \frac{R_{\text{basal}}}{R_{\text{max}}} \right),$$

where R_{max} is the maximum basal radius, c is a constant proportionality factor and R_{basal} is the actual basal radius.

The influence of competition on growth is considered by a correction factor for competition, C , which takes into account the negative influence of the neighbouring plants, F_A :

$$C = \begin{cases} 1 - 2F_A & \text{for } F_A \leq 0.5 \\ 0 & \text{for } F_A > 0.5. \end{cases}$$

The increment of the basal radius, ΔR_{basal} , consequently is given by $\Delta R_{\text{basal}} = \text{GR} \times C$. Growth may thus be completely suppressed if local competition by neighbouring plants is too high. The competition under this approach is generally asymmetric (Bauer *et al.* 2002).

(d) Reproduction

Individuals in the model reproduce by dispersing seeds. Individuals started to reproduce at a particular size and seed production linearly increased with size such that a particular amount of seeds was reached at maximum size. Seeds are dispersed locally around the mother individual. For the calculation of the location of a seed, a two-dimensional exponential probability function was used,

$$p(r) = \exp\left(-\frac{r}{\lambda}\right),$$

where λ is the mean of the probability distribution and r is the particular dispersal distance.

(e) Establishment

Seeds can never establish themselves in the basal areas of established plants. On all other locations the seed's establishment depends on the competitive situation. Whenever the local field value $F(x, y)$, which is defined as the sum of all plants' fields at point (x, y)

$$F(x, y) = \sum_{i=1}^n F_i(x, y)$$

falls below a particular threshold, the seed is assumed to germinate and establish itself. If $F(x, y)$ exceeds this limit the seedling is assumed to die because the competitive pressure is too strong for germination and establishment.

(f) Mortality

We assumed that plants suffering from high competitive pressure have a higher mortality risk than isolated plants. Additionally, plants that have grown to their maximum size are senescent, and thus mortality increases. Competitive pressure and senescence are combined in an individual's vigour v at time t

$$v_t = \sqrt{C \times S},$$

where C and S are the correction factors for competition and size, respectively (see § 2c).

The vigour values of the last time-steps are averaged assuming that a plant remembers the experience of the competition past

$$\bar{v} = \frac{v_t + v_{t-1} + v_{t-2} + v_{t-3} + v_{t-4}}{5}$$

with v_t being the vigour at time t . If the average vigour falls below a particular threshold, the individual is assumed to die. The memory approach allows plants to be able to tolerate competitive pressure for some time, but then die. Alternatively, plants may recover from competition (i.e. forget former competition) if competitive pressure is released owing to the death of neighbouring plants.

(g) Model scenarios

The following parameterizations were used in all scenarios: maximum basal radius $R_{\max} = 0.3$, and local seed dispersal with a mean of the probability distribution $\lambda = 1.5R_{\text{basal}}$.

The base model includes growth, mortality and reproduction with the following attributes:

- (i) a growth rate of $\text{MGR} = 0.03$;
- (ii) seed production as a linear function of size, where with no size threshold and at maximum size, individuals disperse five seeds;
- (iii) establishment of seedlings when the local field value reaches $F(x, y) = 0.0$;
- (iv) memory mortality of $\bar{v} \leq 0.5$ with $\bar{v} = (v_t + v_{t-1} + v_{t-2} + v_{t-3} + v_{t-4})/5$. The model scenarios deviate from the base model as regards mortality, reproduction, establishment and growth.

Mortality varied according to the different memory functions and vigour thresholds. Hence, plants remembered the competition of preceding time-steps 1–5. Changing the vigour threshold led to plants being more robust ($\bar{v} = 0.3$) or susceptible ($\bar{v} = 0.7$) when faced with competition.

The scenarios for reproduction included an alteration of the minimum size for reproduction ($0.0 \leq R_{\text{basal}} \leq 0.2$) and different amounts of seeds at maximum plant size (between 5 and 25).

The establishment of the seedlings was changed so that they could bear different degrees of competition. The threshold local field value $F(x, y)$ for successful germination was varied between 0.0 (i.e. no other plant must overlap the germination point) and 1.0 (i.e. overlaps of fields of influence are allowed but no other plant must have its basal area at the germination point).

The growth rate, MGR , was altered between 0.03 and 0.29

so that plants reached their maximum size in about 20 time-steps at $\text{MGR} = 0.03$ and in about 1 time-step at $\text{MGR} = 0.29$.

(h) Time-series and spatial pattern analysis

The model time-series were analysed regarding their auto-correlation function (ACF) with STATISTICA 5.0 so that cycles in the population dynamics could be identified in addition to their periodicity.

We characterized the spatial distribution of individuals in the model output via Ripley's L -function analysis (Ripley 1977; Cressie 1991; Bailey & Gatrell 1995) across a range of h scales. The scale h corresponds to a circular area of radius h around individual points of the pattern being analysed. All analyses are based on the general function of $L(h)$ used to characterize the degree of clustering or hyperdispersion in comparison with a randomly distributed set of points. We used the standard formulae for the calculation of $L(h)$ as given in Bailey & Gatrell (1995, pp. 120–121).

The values of $L(h)$ were interpreted as follows: a spatially random pattern at scale h has an expected value of $L(h) = 0$. Consequently, $L(h) < 0$ indicates clumping whereas $L(h) > 0$ results from overdispersion, i.e. more regular distributions. However, the absolute $L(h)$ value was of little use and any comparison between scenarios was not meaningful. We tested for the significant departure from spatial randomness by estimating the 95% confidence intervals using Monte Carlo simulations (Cressie 1991; Bailey & Gatrell 1995). The confidence intervals were constructed by randomizing 19 times the positions of the points in the pattern being analysed (Haase 1995; Jeltsch *et al.* 1999). Thereafter, the $L(h)$ values of these randomized patterns were calculated. We concluded that there was significant clustering when the $L(h)$ value of the model output was smaller than the smallest $L(h)$ value obtained from the randomized patterns. Accordingly, overdispersion, i.e. regularity, resulted in $L(h)$ values that were larger than the largest $L(h)$ obtained in the randomization procedure. $L(h)$ values that fell in between these boundaries were considered to be spatially random.

3. RESULTS

(a) The base model

In the base model the population size fluctuated between boundary population sizes of 550 and 900 individuals (figure 1a). Splitting the population into three size classes revealed that the smallest size class contributes most to the fluctuations (figure 1b). Additionally, the fluctuations of the medium- and large-size classes have lower amplitudes and follow the peaks of the lowest size class with a particular lag (figure 1b). The ACF of these time-series fluctuations showed cyclic changes that even at high lags did not fall below the significance level.

Age distribution in the population at a peak point ($t = 515$) was characterized by the dominance of young individuals. At a trough point ($t = 530$) the distribution was much flatter with a thicker tail indicating the larger occurrence of medium and high ages (figure 2).

The spatial distribution of the largest size class was regular at lower scales, i.e. to a distance of up to ca. 4–5 m (figure 3b). At larger scales the pattern was predominantly a random distribution. In the smallest size class, the spatial distribution showed mostly clumps (figure 3a).

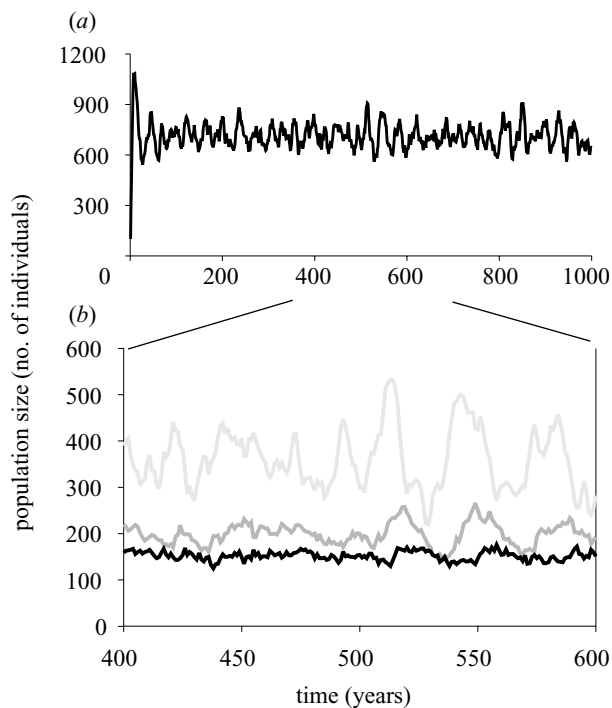


Figure 1. Population dynamics produced by the base model. (a) Time-series of total population size. (b) Same time-series as in (a) but distinguished by three size classes where size class 1 (light grey line) contains those individuals that have a size smaller than one-third of the maximum size, size class 2 (dark grey line) individuals have a size between one-third and two-thirds of the maximum size and size class 3 (black line) individuals are larger than two-thirds of the maximum size.

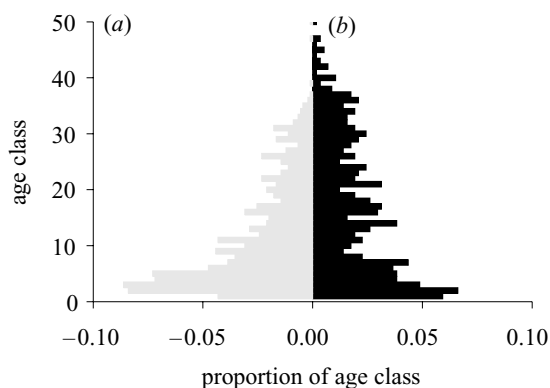


Figure 2. Age distribution in the population at the time-steps (a) $t = 515$ and (b) $t = 530$ of figure 1. The time-steps refer to a high population size at $t = 535$ and a low population size at $t = 550$. The age distribution shows that at high densities young individuals prevail, whereas at low population size the distribution is more flattened, indicating a higher proportion of larger individuals.

(b) Mortality scenarios

Cycles occurred in many mortality scenarios (figure 4a). In extreme cases, e.g. very high robustness against competition (vigour threshold = 0.3), the cycles disappeared or were not detectable. Both the memory function and the vigour threshold influenced the cycle period with a decreasing vigour threshold generally increasing the cycle period. High vigour thresholds indicate the strong influ-

ence of competition on mortality because plants that experience only slight competitive pressure already suffer higher mortality. By contrast, at low vigour thresholds plants can bear stronger competitive pressure before experiencing a higher risk of mortality.

The memory of a plant for the competition it experienced in the past has only a slight influence on the appearance of cycles and their period. The longer the plants remembered past competition the wider the range for cyclic behaviour was.

(c) Reproduction scenarios

Varying the seed amount or the minimum size for reproduction influenced neither the appearance of cycles nor their period (figure 4b). The cycles disappeared only in two extreme cases where the size from which the plants started to reproduce was very high so that the population crashed or when very few seeds were produced. In all other cases, the population fluctuated with a periodicity of between 30 and 40.

However, the average population size increased both with the amount of seeds a plant could release and with lower reproductive size thresholds. When no size threshold existed, the population size fluctuated between 320 and 900 individuals. Accordingly, with a size threshold of 0.2 the population fluctuated between 270 and 550 individuals.

(d) Growth scenarios

Increasing the MGR led to cycles in the population dynamics that showed decreasing periods (figure 4c). At low MGR values, the population fluctuated with a period of about 40. At an MGR value of 0.2 the lowest cycle period was reached (below 10) and then the cycles disappeared.

The population size in these scenarios decreased as the growth rate increased from an average population size of 1000 at MGR = 0.01 to 350 at MGR = 0.29.

(e) Establishment scenarios

Establishment criteria profoundly affected population cycling (figure 4d): low establishment thresholds still led to cycles although their periods decreased with a higher $F(x, y)$ threshold. Thresholds that were higher than $F(x, y) = 0.5$ led merely to damped oscillations or a complete disappearance of cycles.

Larger $F(x, y)$ thresholds also led to higher population sizes. While at a threshold of $F(x, y) = 0.0$ the population size fluctuated between 600 and 900 individuals, with increasing threshold values for $F(x, y)$ population size increased accordingly: for $F(x, y) \leq 0.1$ the population size fluctuated between 1400 and 1700, for $F(x, y) \leq 0.5$ the population size fluctuated between 3800 and 4200 and for $F(x, y) < 1.0$ the population size was approximately 5000.

4. DISCUSSION

The occurrence of cycles in plant populations has been doubted with plant populations instead being supposed to show stable equilibria (Krebs 1996). Contrary to animal ecology literature, in theoretical plant ecology few investi-

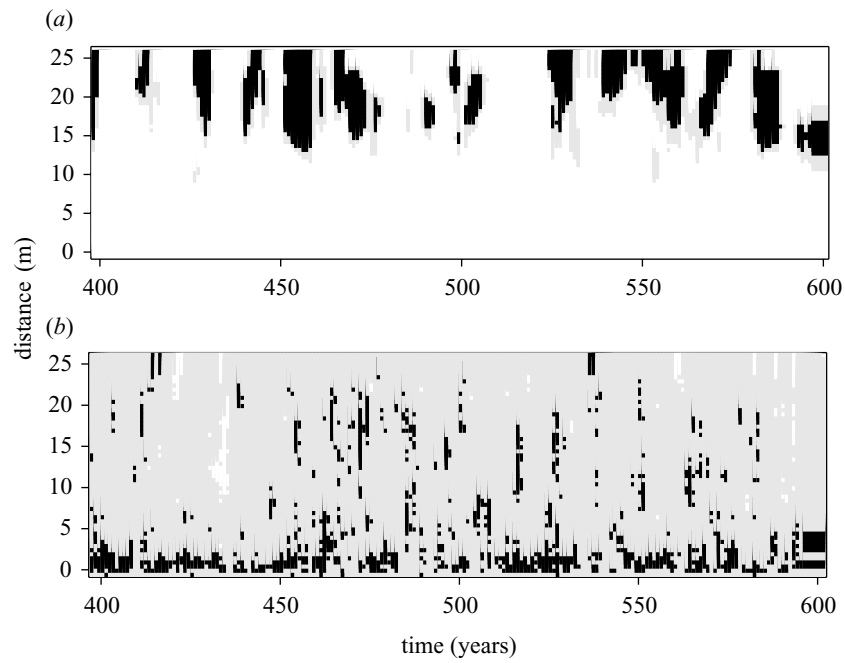


Figure 3. Spatial pattern of individuals from (a) size class 1 (small individuals) and (b) size class 3 (large individuals) is calculated for time-steps of 400–600 and distances up to 25 m using Ripley’s L -function. The black, grey and white areas indicate regular, random and clumped spatial distributions, respectively (see § 3a for details).

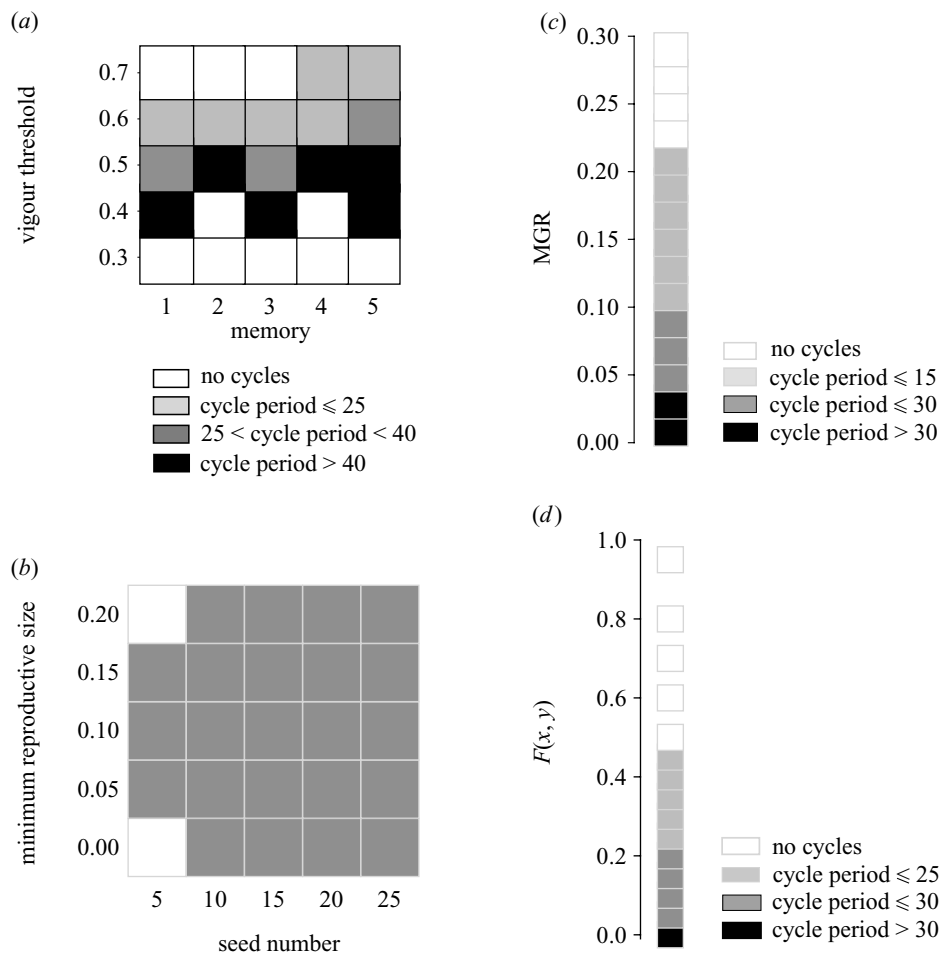


Figure 4. The analysis of scenarios of changed (a) mortality, (b) reproduction, (c) growth and (d) establishment. The parameters that are not specified were taken from the base scenario.

gations have focused on nonlinear dynamics (Cousens 1995; Stone & Ezrati 1996), with these investigations mostly not taking into account any spatial effects (but see Silander & Pacala 1990; Durrett & Levin 1998).

We developed an individual-based model using the FON approach (Berger & Hildenbrandt 2000) that assumed that individual plants have a zone of influence in which each plant interacts with its neighbours and that the strength of influence changes with the distance from the stemming point. These assumptions meet the conditions for realistic individual-based models as suggested by Stoll & Weiner (2000).

For the base model describing hypothetical perennials the population size was found to cycle between particular boundaries. These cycles were, in addition, characterized by the kind of individuals involved and the corresponding spatial pattern. We hypothesized that recruitment is restricted due to the limited availability of free sites for the establishment of seedlings. Consequently, we expected a reproductive and a senescent period during one cycle in the population. During the reproductive period, the population is growing and consists mostly of young and small individuals, whereas a senescent population contains mostly a few large individuals. In accordance with this hypothesis we found different age structures in the population at peak and trough points. Spatial pattern analysis indicated that large individuals are evenly distributed and small individuals show a random spatial pattern, and these patterns are relatively independent from cycle troughs and peaks (figure 3).

In agreement with theoretical and empirical expectations (e.g. Eccles *et al.* 1999; Mast & Veblen 1999), we found a clumping of seedlings and small plants. Limited seed-dispersal distances led to an augmented occurrence of small individuals around their mother plant. However, large plants were predominantly distributed in a regular pattern. Consequently, between the seedling and adult plant stages most individuals die. The cause of mortality is local competition: at the seedling stage, individuals are small and their FONs hardly overlap. Growth increases the basal and FON radii and accordingly augments overlap areas. This leads to the depression of growth and vigour that results in a higher mortality risk. Plants suffering from too much local competition over too long a time die. Such self-thinning is well documented from empirical observations (Kenkel *et al.* 1997; Guo & Rundel 1998; Mast & Veblen 1999; Puigdefabregas *et al.* 1999), but models of self-thinning mainly concentrate on even-aged stands.

As known from theoretical ecology, the interplay of mortality and recruitment may alter population dynamics so that in overcompensating populations complex, i.e. cyclic or chaotic, dynamics can be expected (e.g. May 1976). In order to gain detailed insight into which process altered the cycles, all of these processes were varied as follows.

(i) Mortality is directly influenced by competitive pressure via the vigour threshold and indirectly by the growth rate as the latter rate determines how fast an individual reaches its maximum size, and consequently senescence and thereby an individual's vigour. The vigour threshold, which indicates how sensitive individuals are against competition, had a major influence on the appearance of cycles

and their period. At intermediate vigour thresholds, the cycle period decreased as the vigour threshold increased. Very high and very low competition sensitivity let the cycles disappear but for different reasons: high vigour thresholds cause a strong spatial coupling—even small overlaps in the FON lead to higher mortality—and probably cause the disappearance of cycles by converting population dynamics into chaotic dynamics. By contrast, low vigour thresholds macerate spatial effects and thus, decouple mortality and competition.

(ii) Population recruitment can be split into two processes: seed production and establishment. Although the population size changed with different minimum sizes for reproduction and maximum seed number, these parameters were of minor importance as regards the cycle appearance and period. Even discarding the size threshold for reproduction had no influence on the occurrence of cycles by contrast to former expectations (Rees & Crawley 1989; Thrall *et al.* 1989; Rees 1991). The existence of a seed bank was not assumed, but seeds were always abundant so that a shortage of seeds could not be held responsible for the cycles in the population. This assumption could be interpreted as low seed dormancy that would, according to Silander & Pacala (1990), lead to cycles. However, seeds in our model germinated only successfully when 'safe sites' were available. Safe sites are locations where the competitive pressure is low, i.e. no other plant extends its field of influence to the position of the seed.

However, changing the establishment rules resulted in profound changes in population dynamics. Seedlings became established at a given location whenever the local competitive pressure fell below a particular threshold. In the most restrictive (base) scenario, seedlings could only establish themselves when no other plant's FON overlapped the location. In further scenarios, this restriction was loosened so that seeds could establish themselves in border areas of a FON and finally, seeds could establish themselves everywhere except in the basal area of an already established plant.

The part that recruitment plays on cyclic population dynamics is thus not shortage in available seeds but shortage of suitable sites.

Interestingly, details of our modelling approach were of minor importance for the existence of cycles. We changed the extension of individual FONs by varying the relation between the basal and FON radii, which either resulted in compressed, rapidly decreasing fields or in extended, gradually decreasing fields. Although the population size was generally lower for extended fields, cycles appeared with approximately the same period and disappeared in the same scenarios as for compressed fields (results not shown).

We conclude from our results that populations of perennial plants may show complex, nonlinear dynamics, i.e. cycles, if established plants virtually prevent the establishment of seedlings within their zones of influence. Empirically, so far only one such case has been reported, by Tilman & Wedin (1991), where a population of perennials was found to cycle. These perennials accumulated litter and thereby prevented establishment of young plants. Such a litter layer caused a time-lag in the turnover. Theoretically, the same mechanism of cycles due to the monopolization of space by adults has been described

for models of sessile marine organisms, e.g. corals (Roughgarden *et al.* 1985; Roughgarden & Iwasa 1986).

Our theoretical findings suggest that monopolization of space by established plants may be a destabilizing mechanism of plant-population dynamics. This could also have implications for community dynamics, e.g. for the coexistence of similar species in diverse communities such as tropical forests. One reason for the high diversity of both coral reefs and tropical forests might be that in both ecological systems the monopolization of space is important. Further empirical studies and meta-analyses could possibly detect patterns in the relationships between the establishment and the temporal and spatial patterns of the plants populations and communities. Further understanding could be gained by a theoretical analysis of a model of annual plants based on the FON approach. Moreover, in the model presented here the strict threshold for establishment could be released by assuming seedling banks, i.e. cohorts of seedlings that are able to survive, without growing, for longer periods of time within the zone of influence of established plants.

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