

*Chapter 13*

## DIVERSITY BY TEMPORAL OSCILLATIONS IN PLANT COMMUNITIES WITH A DIFFERENTIAL TIMING OF REPRODUCTION

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### Abstract

**Background and Aims:** Species can coexist at non-equilibrium circumstances, for instance by oscillations in population densities or chaos, caused by non-linear responses of species to their environment. We analyzed whether plant genotypes that vary in their timing of reproduction can coexist under equilibrium or non-equilibrium circumstances when competing for light.

**Methods:** We used a game theoretical approach, based on a biologically mechanistic model of plant growth.

**Key Results:** In our model, the genotype switching to reproduction slightly later than its competitor attained a higher fitness. This caused a succession from early switching genotypes to those switching later to reproductive investment. However, there were cyclic opportunities for extinct genotypes that switch early to reproduction to re-establish and grow into the community. The cause was that genotypes that switched very late produced relatively very little seed because of an overinvestment in vegetative growth; especially when competing against individuals of the same genotype. Because the very early switch genotypes could establish, circumstances were such that other extinct switch genotypes could re-enter the vegetation as well. In this way the diversity of genotypes was maintained over time by temporal oscillations of genotype abundances.

**Conclusions:** We show that within a model, an externally undisturbed plant community can produce its own temporal cyclic or chaotic disturbances to promote diversity, rather than

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converge to a stable equilibrium when competing for light. Cyclic fluctuations in species composition can occur in a model community of plants sharing the same growing season and that are limited just by light as a single resource.

**Keywords:** Game Theory, Light interception, Cyclic, Annuals, Coexistence, Temporal, Mechanistic Model, Oscillations, Reproduction

## Introduction

In community ecology, many studies try to unravel the mechanisms by which species-rich communities overcome the competitive exclusion principle (Hardin, 1960). In most of these studies stable coexistence is considered, e.g. in communities or populations that are at equilibrium. As an alternative, however, the non-equilibrium view was proposed (Huisman and Weissing, 1999; Bauer et al., 2002; Nowak and Sigmund, 2004). It was predicted that it is possible that mechanisms that promote coexistence at non-equilibrium will prove to be most important for the maintenance of diversity (Hutchinson, 1961). Aside from regular disturbances that can create circumstances for species to coexist, species can coexist at non-equilibrium circumstances by non-linear responses that cause oscillations in population densities or chaos (Hutchinson, 1961; Huisman and Weissing, 1999; Bauer et al., 2002). So far, well-known examples can be found in the oscillating populations in trophic food-webs such as predator-prey systems (Peet et al., 2005), where predator, prey, and food source are dependent on the other for their survival. Aside from such dependence, non-hierarchical competitive relationships between species can cause species to coexist on a limited number of resources (Huisman and Weissing, 1999). Kerr et al. (2002), for instance, modeled and tested empirically the coexistence of a system of paper-rock-scissors (Maynard Smith, 1982). Species coexisted when interaction and dispersal was local and thus they emphasize, that spatially restricted patterns also may lead to coexistence of species. Similarly, species limited by one resource only may coexist indefinitely if they partition the growing season and each is active only in its “own” part of that season (Armstrong and McGehee, 1976). Huisman and Weissing (1999), on the other hand, found oscillating patterns in their model for well-mixed plankton species, on the basis of competition for three or more different resources. This was under the condition that species differed in their required resource ratio. Within oscillations, circumstances for growth differed and species with different requirements for growth found a window of opportunity. In their study, more species could coexist than there were limiting resources (Huisman and Weissing, 1999; Huisman et al., 2001).

We investigate whether or not in a system with one limiting resource coexistence of species is possible. We study this in virtual, competing, annual plants that differ in the timing of reproduction, just as species do in real communities. In this study we assume that in plants there is a trade-off between the production of vegetative parts and seed production. We also assume that the amounts of seed production and photosynthetic carbon gain are strongly correlated. Model studies have indicated that, to maximize seed mass yield, plants should show a sharp transition between the vegetative and reproductive phases of growth (e.g. Cohen, 1976; Iwasa, 2000). One would assume that the allocation scheme determining reproductive output is subject to strong selection because reproductive output is one of the main determinants of fitness (Stearns, 1992). Under strong selective pressure, all plants might

be expected to evolve towards a single or at most a few optimal reproductive allocation schemes (Cohen, 1976; Schmid and Weiner, 1993). However, this is only the case in a system where reproductive performance is not affected by the presence of competitor plants. Competitive optimization *sensu* Anten (2005) leads to a delayed switch from growth to reproduction. But whether or not this leads to a single switch time from growth to reproduction is still an open question. In natural vegetation stands, however, often large numbers of plants with widely different timings of the transition to reproduction coexist (Reekie et al., 2002).

Because a large investment in seed mass implies a low investment in vegetative mass and hence competitive strength, reproduction and competitiveness are closely related. As plants mostly do grow in close proximity to each other, competition will often play a role in affecting the fitness of plants with different growth strategies (Weiner, 1988). Part of the variability in reproductive allocation between genotypes may therefore stem from the influence of competition.

When, as is the case in the direct competition for light (Anten, 2005), the success of a genotype depends on the strategies of the other genotypes present, game theory is an appropriate tool to assess the possibilities for different genotypes with their particular traits to persist (Falster and Westoby, 2003; Nowak and Sigmund, 2004). Also in the research of timing issues, game theory has often been successfully applied (Iwasa and Levin, 1995). Whereas most modeling studies on the selection for traits concentrate on the dynamics at plant or even population level, we explicitly include allocation patterns within a plant as the basis for competition. Plants thus grow on the basis of intrinsic allocation trade-offs. The size and leaf area distribution of a plant and that of neighboring plants during growth explicitly determines a plant's resource capture (Pronk et al., 2007a,b). This puts each plant into a direct game theoretical context. In addition, on a population level, plants on average will change their seed production as the total composition of the vegetation changes and thus the frequency of encounters with other plant types change. This puts the populations in a game theoretical context as well. Plants in our model are competing for light as a single limiting resource.

An important finding of this study is that competing annual plants that differ in the timing of reproduction do not necessarily converge towards a single evolutionary stable strategy without external disturbances. Populations of plants with different strategies are able to generate their own variability and show cyclic behavior. In this self-organizing model vegetation, multiple genotypes differing in their switch to reproduction find temporal opportunities to perform well so that the diversity of genotypes over a period of time is maintained.

## Methods

### The Plant Growth Model

To simulate the fitness and growth of competing plants that switch to reproduction at different moments in time, we used a mechanistic plant growth model. The model is described in detail in Appendix A (see also Pronk, 2004). Only a brief description of the most important features of the model is given here. Parameter settings are given in Table A1 in the Appendix.

Plants grow within a fixed area of ten by ten centimeters, referred to as a cell. Only plants that share such a cell compete (i.e. plants in separate cells do not compete). However, plants are able to disperse their seeds into other cells between growing seasons. Plants are annual and die at the end of the growing season. The growing season is 365 days, with a seasonal course of the light climate, as it would occur in a temperate region (Equation A14).

As we want to compare plants with respect to their timing of the switch to reproduction, other characteristics are held equal amongst plants. Each plant starts with an initial leaf area, root mass and height (Table A1 in the Appendix). All plants have a parabolic distribution of leaf area over their height (Caton et al., 1999; Pronk et al., 2007; Equation A1). Light interception is modeled following Beer's law (Monsi and Saeki, 1953; Equations A5-A7 Appendix) and the light response of photosynthesis is described by a non-rectangular hyperbola (Marchall and Biscoe, 1980; Equation A8). To obtain daily gross photosynthesis per plant, leaf photosynthesis is integrated over canopy depth and over the day (Equation A10). Part of the assimilate pool thus obtained is spent on the maintenance respiration of structural mass (Equation A9).

In the vegetative phase of growth, a plant invests a fixed proportion of its net photosynthetic production in height (i.e. stem mass). When growing in height, the leaves at the base of the plant are discarded while leaves at the top are newly produced, according to the leaf distribution (Equation A1). Whatever of the net photosynthetic production is left after height growth is invested in leaf and root mass, divided between these structures in some constant proportion. If at any time the carbon that is spent for maintenance and height growth exceeds the carbon income, leaf and root mass are shed and the retracted carbon from these leaves and roots is used to make the carbon balance equal to zero. If either leaf or root mass is zero grams or less, the plant is considered dead.

## **The Switch to Seed Production**

The model plants have a clear switch from vegetative growth to seed mass production. After the switch, the plants no longer grow in height or leaf mass, but all available carbohydrates are invested in seeds. Seed production continues to the end of the growing season. All seeds stay on the plant until the end of the growing season. At the start of the new growing season, all old plants are removed, the seeds are redistributed over the cells and germinate. We assume, that switching time is genotype-specific. To evaluate the consequences of the timing of a switch to seed production, we distinguish ten genotypes which differ in their timing of this switch during the simulated growing season (top part of Table 1).

## **Simulations with Isolated Plants**

First we simulate the growth and seed production of plants of the different switch genotypes (Table 1) without competition in a cell, for a single growing season.

**Table 1. Top part of the table: Time step of the switch to the production of seed mass of plant genotypes. The timing of a switch to the production of seed mass is given in days after the start of the simulation. Lower part of the table: Seed output (gram per plant) of plant genotypes (rows) in pair-wise competition. The seed output of the genotype that is the fittest against a particular opponent genotype (columns) is marked in bold.**

| Switch<br>(day) | Type 1<br>5   | Type 2<br>25 | Type 3<br>45 | Type 4<br>65 | Type 5<br>85 | Type 6<br>105 | Type 7<br>125 | Type 8<br>145 | Type 9<br>165 | Type 10<br>185 |
|-----------------|---------------|--------------|--------------|--------------|--------------|---------------|---------------|---------------|---------------|----------------|
|                 | Opponent type |              |              |              |              |               |               |               |               |                |
| Type            | 1             | 2            | 3            | 4            | 5            | 6             | 7             | 8             | 9             | 10             |
| 1               | 1.15          | 1.13         | 1.09         | 0.97         | 0.64         | 0.15          | 0.15          | 0.15          | 0.15          | 0.15           |
| 2               | 1.53          | 1.50         | 1.45         | 1.29         | 0.84         | 0.18          | 0.18          | 0.18          | 0.18          | 0.18           |
| 3               | 2.62          | 2.54         | 2.42         | 2.15         | 1.41         | 0.23          | 0.23          | 0.23          | 0.23          | 0.23           |
| 4               | 5.47          | 5.32         | 5.01         | 4.42         | 3.03         | 0.32          | 0.31          | 0.31          | 0.31          | 0.31           |
| 5               | 10.78         | 10.61        | 10.23        | 9.15         | 6.58         | 2.05          | 0.33          | 0.33          | 0.33          | <b>0.33</b>    |
| 6               | <b>12.37</b>  | <b>12.41</b> | <b>12.49</b> | <b>12.52</b> | <b>10.66</b> | 5.60          | 0.66          | 0.27          | 0.27          | 0.27           |
| 7               | 7.61          | 7.69         | 7.85         | 8.27         | 9.56         | <b>7.96</b>   | 3.22          | 0.23          | 0.20          | 0.20           |
| 8               | 3.53          | 3.56         | 3.64         | 3.85         | 4.58         | 6.86          | 5.06          | 1.50          | 0.14          | 0.14           |
| 9               | 1.30          | 1.32         | 1.34         | 1.42         | 1.69         | 2.66          | <b>5.33</b>   | 2.98          | 0.56          | 0.09           |
| 10              | 0.33          | 0.33         | 0.34         | 0.36         | 0.44         | 0.73          | 1.78          | <b>4.16</b>   | <b>1.50</b>   | 0.14           |

## Simulations with Competing Plants

To simulate the competition between plants that grow up together, we let the different switch genotypes (described in Table 1) grow in pairs within a cell, in every possible combination of genotypes. The seed mass produced by the plants in each pair at the end of the 365-day simulation is put into a ‘pay-off matrix’ (Maynard Smith, 1974; Riechert and Hammerstein, 1983) (see Table 1).

## Calculations on the Frequency Development of Plant Genotypes

Then, we extend the simulations to a situation where all different genotypes have an influence on performance of a genotype, using a replicator equation (Taylor and Jonker, 1978; Nowak and Sigmund, 2004). This can be visualized as an immense arena consisting of very many cells, each with two players. Often these players belong to two different genotypes, and the frequency of the various genotype combinations equals the product of the frequencies of both genotypes in the total seed pool. The success of a switch genotype now depends on its performances against every single switch genotype in the simulated community, and the frequency at which these encounters occur. For this purpose we sum the plant genotype’s seed productions when competing with all the different opponents that are present:

$$P_i = f_i \cdot \sum_j p_{ij} \cdot f_j \quad (1)$$

Here  $P$  is the total pay-off (i.e. seed production) for a plant genotype and  $p_{ij}$  is the pay-off of a plant genotype  $i$  against an opponent plant genotype  $j$ , taken from the pay-off matrix (Table 1). The frequency at which the genotypes are present is  $f$ . The total pay-off is a measure of fitness for the plant genotype.

In addition, we calculate whether the genotype will increase or decrease in frequency  $f$  in the course of years, compared to other genotypes. Each year, the new frequency is the relative contribution of the target plant's previous-year pay-off to the total pay-off of all competing plants in that year:

$$f_{i(t+1)} = \frac{P_{i(t)}}{\sum P_{j(t)}} \quad (2)$$

With each repeated calculation, the relative frequencies of plant genotypes in the community will change and can be followed during simulation years. If the frequency of a genotype falls below a certain frequency ( $10^{-5}$  of the total community size) it is supposed to have gone extinct and its frequency is set to zero. This limit implicitly defines the order of magnitude of the system: ca  $10^5$  cells.

## Reintroduction of Plant Genotypes

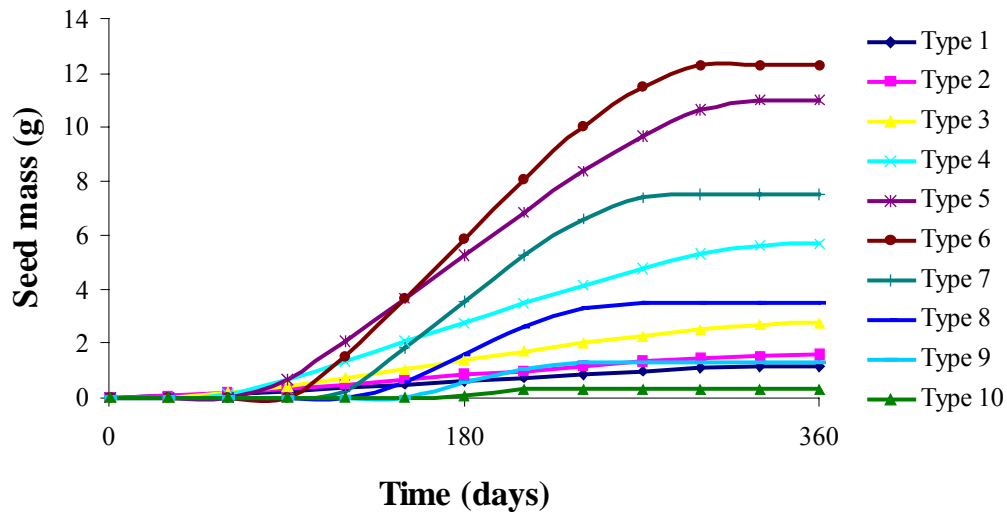
The selective pressure changes with the composition of the community. It is possible that some genotypes have gone extinct before conditions occur that would benefit them. The switch genotype, or genotypes, that finally become dominant are therefore not necessarily evolutionary stable strategies (Maynard Smith, 1982). To investigate this, the estimated threshold frequency of  $10^{-5}$  is removed, allowing each genotype to remain in the vegetation at (infinitely) low frequencies. This can also be seen as a probability that such an 'extinct' genotype re-immigrates into the system. We explore the question whether switch genotypes can successfully re-establish themselves from a low frequency at some point during the development of the simulated community.

## Results and Interpretation

### Isolated Plants

Plants that switch to seed mass production early have a long period for seed mass production (Iwasa and Levin, 1995). However, these plants have not yet produced much leaf area and gross photosynthetic production is small, resulting in a low production of seed mass. Plants that switch to seed mass production at a very late stage have produced much leaf area and have a large gross photosynthetic production. However, the end of the simulation period is near and the period for seed mass production is short. Secondly, such plants have more leaf area and have a higher degree of self-shading, resulting in more non-productive leaves. Thirdly, being larger, the plant will have high costs of maintenance and not much carbon will

be left to invest in seed mass. As a result, the optimal switch time for isolated plants is somewhere in the middle of the season (see also Iwasa, 2000; Widen, 1991).



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Figure 1. The seed mass production during one simulation year of isolated plants switching to seed mass production at different times. See the top part of Table 1 for a description of the different switch genotypes.

Figure 1 shows the produced seed mass per switch genotype (see Table 2) for isolated plants. Seed mass is highest for a medium switch genotype. The highest seed mass yield is achieved when switching to the production of seed mass at 105 days after the onset of growth (this is switch genotype 6). The further (both earlier or later) the switch is from this 105 days, the more the production of seed mass declines.

### Simulations on Competing Plants

Table 1 shows the pay-offs of the different switch genotypes (rows) in pair-wise competition with opponent switch genotypes (columns). Within a column, the switch genotype that has the highest production of seed mass in competition against a particular opponent switch genotype is indicated in bold lettering.

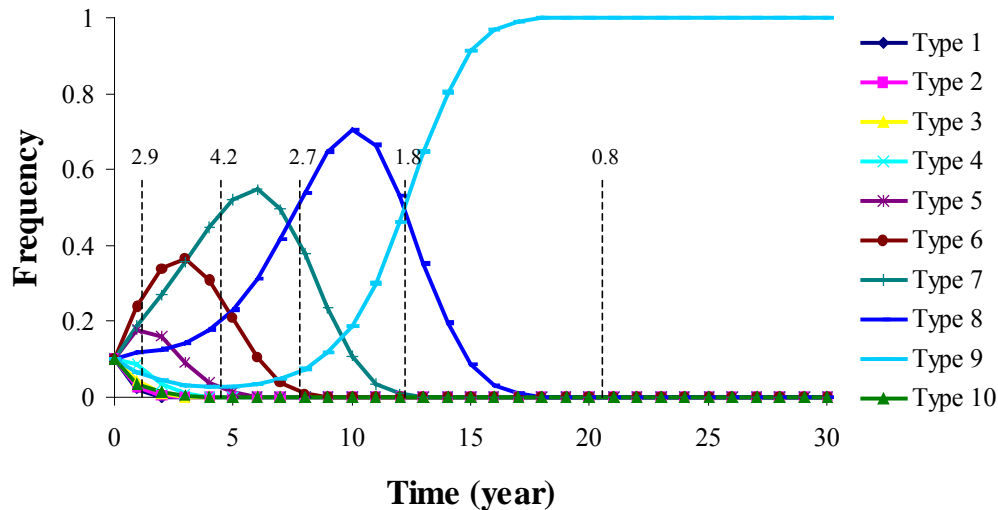
When switch genotypes compete with weakly competitive opponent genotypes such as genotype 1 to 5 (left columns in Table 1), genotype 6 achieves the highest seed mass. Genotype 6 also showed the highest seed mass as a single plant. When switch genotypes have to compete with genotypes that have a later switch (columns more to the right in Table 1), the latter genotypes have a higher seed mass production. This implies that genotypes, above a certain optimal switch, should delay their investment in seed mass slightly when competing with genotypes that are late in the production of seed mass as well.

If a plant starts earlier than its competitor with the production of seed mass, it will become shaded. This obviously has negative effects on its seed production. The early switcher can even become so severely shaded that it cannot intercept enough light to pay for

maintenance. This forces the plant to shed leaves and roots, leading to a further reduction of its ability to intercept light. Consequently, a switch to seed production should be as close as possible to the switch time that gave the highest seed mass in isolated plants, but also later than the switch of the neighboring plant.

### Calculations on the Frequency Development of Plant Genotypes

As the performance of a switch genotype depends on the genotype of the competitor (Table 1) the total pay-off per switch genotype will differ with each change in the overall composition of the community.



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Figure 2. The frequency development of competing switch genotypes. The frequencies of switch genotypes are relative to each other, e.g. the frequencies of all genotypes combined add up to 1 at each point in time. For a description of switch genotypes, see the top part of Table 1. The numbers above the vertical dashed lines in the figure depict the seed mass produced on average per plant in the particular composition at the vertical dashed line.

Figure 2 shows the frequency development over several years (Equations 1 and 1) of switch genotypes 1 to 10 under pair-wise competition (Table 1). It shows that there is an initial shift in dominance during the simulation. Initially, when all plants start with equal frequency, switch genotype 6 is dominant. During the subsequent simulation years, switch genotypes 1 to 5 that start investing in the production of seed earlier (and thus lose from switch genotype 6 in competition) go extinct. Genotype 6 now encounters relatively more late-switching plants, which have a larger competitive vigor. These more competitive genotypes increasingly suppress genotype 6 and its seed production declines. The next genotype, which is genotype 7, invests almost as much in seed mass but has a slightly better competitive vigor than genotype 6. It thus replaces genotype 6. As genotype 6 starts to decline in frequency, genotype 7 encounters more competitive genotypes, and in its turn declines also. As can be seen in Figure 2, genotype 6, 7, 8 and 9 are successively dominant.

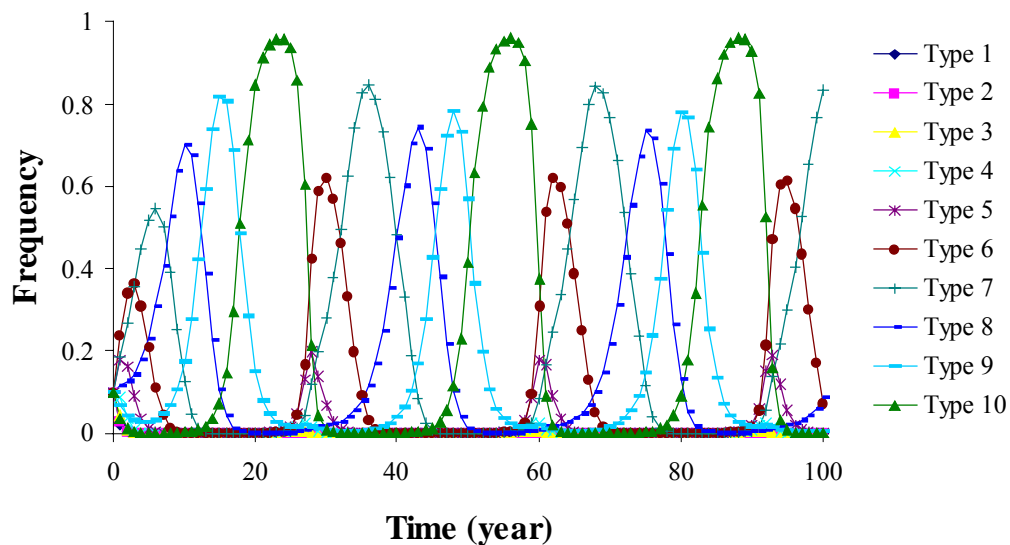


Genotype 10 has gone extinct already at the beginning of the simulations because of its relatively small seed production. The genotype that eventually becomes all dominant is genotype 9. This genotype 9 switches to seed mass production at day 165.

In our results we see a clear succession from the switch genotype that has the highest fitness in isolated plants, towards genotypes that switch later. In Figure 2 the average seed production per plant during the frequency development is indicated. Initially, the average seed production increases slightly. This is because the very early switch genotypes go extinct. These genotypes produce a low amount of seed because they start allocation to reproduction before they have produced sufficient leaf area, and additionally are suppressed by all other genotypes. After the initial increase, the average seed production gradually decreases again to a low level. This is because the later switch genotypes that become dominant produce a very low amount of seed, as a result of their late switching time. The seed production of the final population thus is lower than in earlier stages of the succession and may even reach values which are insufficient for self-replacement of the remaining genotype (Fig. 2).

### Reintroduction of Plant Genotypes

Figure 3 shows that, when formerly extinct switch genotypes are allowed to re-establish from a low frequency, the abundance of switch genotypes shows a regular pattern of switch genotypes decreasing and increasing in frequency in the course of years. Apparently, there are cyclic opportunities for the reintroduction of switch genotypes (Figure 3).



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Figure 3. The frequency development of competing switch genotypes, when reintroduction of switch genotypes is allowed. The frequencies of switch genotypes are relative to each other, e.g. the frequencies of all genotypes combined add up to 1 at each point in time. See the top part of Table 1 for a description of the switch genotypes.

In the previous simulation, genotype 10 plants were already extinct, but with reintroduction they can make a re-entry at the point when genotype 8 and 9 are most abundant (Figure 3). The plants of genotype 10 slowly exclude the plants of genotype 9. However, plants of genotype 10 grow vegetative for such a long period of time, that by the time they become reproductive they spend most of their photosynthetic production on maintenance of vegetative biomass. Genotype 10 already produces very little seed mass, and even less when competing against another plant of genotype 10 (see Table 1). Therefore, as the frequency of genotype 10 increases, the seed production lessens. Against plants of genotype 8 or 9 it performed better, for the counter-intuitive reason that these genotypes hamper its growth, which resulted in the plant being further from steady state as the switch to reproduction occurs. Genotype 5 has a comparable seed mass production to genotype 10 when competing against it (see Table 1) and a better seed mass production when it encounters con-specifics. As it increases in frequency, its overall seed production increases (Figure 3). Because genotype 5 is present, genotype 6 can perform well. Genotype 6 is followed by genotype 7, 8, 9, and 10, and the cycle, as explained in the case without reintroduction, repeats itself.

So far, we have taken only 10 genotypes that differed 20 days from each other in their switch to the production of seed mass. If the genotypes are taken closer together, even more genotypes can coexist in a cyclic manner (results not shown). The ability of genotypes to invade and exclude other genotypes also can be calculated formally. Appendix B gives a formal calculation for the possibilities for any switch genotype to invade the population of another switch genotype and/or to exclude that switch genotype.

## Conclusion

In this paper, the aim was to investigate the adaptive values of different seed investment strategies for annual plants under competition and to find whether they could coexist at equilibrium or non-equilibrium. Initially, we found a shift towards delayed reproduction over the course of subsequent growing seasons. With the shift to delayed reproduction, we also found a classic example of a ‘tragedy of the commons’ as introduced by Hardin (1968). In a simulated community where all genotypes were present initially, there was a clear succession from highly fecund genotypes (that switch early) towards a community consisting of genotypes that switched later and, as a consequence, produced an excessive vegetative mass (Donald, 1968; Kawecki, 1993; Zhang et al., 1999) at the disadvantage of seed production. It is known that strong selection for growth is in general one of the key processes causing delayed reproduction (Rees and Rose, 2002). In other studies, selection for growth was also found for separate plant traits rather than whole plant size. For instance, Gersani et al. (2001) showed a tragedy of the commons for plants competing for root-space (and thus nutrients and water). Schieving and Poorter (1999) showed that species should increase specific leaf area in a competitive game, at the expense of carbon gain.

When we allowed the different switch genotypes to be reintroduced after extinction, we found stable cyclic species replacement patterns. Cycles were caused by the succession from early to late switch genotypes that in turn could be reinvaded by the early switch genotypes. These cyclic patterns were generated not by external factors, but by the process of competition itself. The strongest competitor invested in vegetative growth for such a long period of time that it could produce only a small amount of seeds. A switch genotype that

switched to seed production earlier in the season, made relatively more seed and was able to increase its frequency compared to the strongest competitor. Thus, as the composition of plants developed, the circumstances for growth changed. Switch genotypes that were excluded earlier in community development were able to re-enter the community.

Empirical evidence for the occurrence of large-scale fluctuations in species composition such as we found in our model study, will not be easy to trace in real plant communities. However, it is clear that populations often show cyclic or chaotic behavior rather than converging to a stable equilibrium (Kendall et al., 1999; Nowak and Sigmund, 2004) and that this also applies to plant populations (Bauer et al., 2002). Silvertown et al. (2002) for instance, argue that cyclic fluctuations might be common phenomena in herbaceous plant communities, even those otherwise thought to be stable. They put forward the ‘Park Grass experiment’ (van den Bergh, 1979; Tilman, 1996) which is a long-term experimental set of equilibrium plant communities. Although monitoring showed the gross composition of the vegetation was at equilibrium over a 60-year period, annual records showed that individual species exhibited a range of dynamics. Because long-term records are not available for most other experimental sites, these cycles or the chaotic behavior would go undiscovered.

For plants, seasonality or drought are among the recorded mechanisms that can cause oscillations. Also, oscillations can be caused by density dependent effects that affect life-history traits, such as overcompensation (Crone and Taylor, 1996; Bauer et al., 2002). Overcompensation can, theoretically, cause a stand of two coexisting plant species to oscillate (Damgaard, 2004). Furthermore, oscillations can be caused by delayed feedback mechanisms such as can occur in plant – nutrient interactions (Daufresne and Hedin, 2005).

While the occurrence of periodically cycling populations has been documented (Kendall et al., 1999), there has not been much evidence whether these cycles can permit coexistence of populations of species that would otherwise exclude each other. Huisman and Weissing (1999) found that species may coexist by oscillating patterns on the basis of competition for three different resources, in their model for well-mixed plankton species. An additional species also found opportunity to grow within these cycles.

Our simulation model results show that the coexistence of plants can be a consequence of the oscillatory behavior of different genotypes. This exemplifies that cycling populations are not necessarily restricted to multi-resource systems (Huisman and Weissing, 1999) but can also occur in systems where individuals compete for light as a single resource. We propose that a simple life-history trade-off between growth and reproduction, mediated by competition, can in theory generate oscillatory dynamics within a plant community that maintain diversity, even without an environmental trigger. Of course, although model results can give clues to what the mechanisms behind plant growth and competition are, only the confirmation or rejection of these clues in an experimental setting will be conclusive. Because the assumptions for the individual plant growth in this model are explicitly formalized, they can be tested and falsified. Phenotypic or genetic manipulations, or the comparison of closely related plant genotypes that differ slightly in the expression of their traits, will give the best system to test model predictions.

Obviously, the model results may be partly determined by its simplicity and rigidity. Thus, the population is conceived as a collection of cells with competition restricted to just two plants per cell and a mean-field approach to the distribution of seeds at the beginning of each new growing season. We suggest, however, that the presence of genotypes with only

very few seeds can be interpreted as probabilities of re-entry of extinct genotypes rather than presence at extremely low densities.

Another restriction in our analysis is the uniform distribution of seeds over the cells. A Poisson distribution over the cells would be more realistic, but would make it far more difficult to determine the frequencies of competing genotype pairs (cf. Geritz (1995), who introduces simplicity in a different way, i.e., by allowing only the largest seed in a cell to survive).

Furthermore, the conditions of the model are highly determinate and so, the strategies are discrete, without stochasticity or mutational drift. Studies explicitly comparing games with discrete and continuous strategies suggest, that the results may be qualitatively different (e.g., Maynard Smith, 1974; Bishop and Cannings, 1978), and that continuous strategies may lead to one stable equilibrium in games that allow several coexisting strategies if these are discrete (e.g., Broom et al., 2005). It would be fascinating to test, whether introduction of stochasticity or evolutionary change in switching dates of our strategies would similarly turn our oscillating system into a system with one stable equilibrium strategy. We expect, however, that oscillations will be maintained because of a defining characteristic of our system: selection will favour later-switching genotypes until the winning genotype has so little time left for seed production, that it can no longer produce sufficient numbers of seeds to fill all cells, after which an earlier-switching genotype can re-immigrate.

## Acknowledgements

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## Appendix A. The Model

### 1. Shape of the Model plant

A plant is confined to grow in a predetermined surface area, referred to as a cell. More than one plant can inhabit this cell. Each plant has a specified smooth distribution of infinitesimally small leaf elements over its height. The leaf area distribution in leaf area per unit height  $\lambda(h)$  per cell basal area is described as (Caton et al., 1999):

$$\lambda(h) = p_0 \cdot \frac{L_t}{h_{pt}} \cdot \left( \frac{h}{h_{pt}} \right)^{p_1} \cdot \left( 1 - \frac{h}{h_{pt}} \right)^{p_2} \quad (\text{A1})$$

in which  $h_{pt}$  is the height of the plant at time  $t$ ,  $L_t$  is the total leaf area of the plant at time  $t$ ,  $h$  is the height at which the leaf density is calculated and  $p_0$ ,  $p_1$ ,  $p_2$  are shape parameters. Here, the shape parameter  $p_0$  is given in terms of  $p_1$  and  $p_2$  by the integral:

$$p_0 = \frac{1}{\int_0^1 dx \cdot x^{p_1} \cdot (1-x)^{p_2}} \quad \text{with } x = \frac{h}{h_{pt}} \quad (\text{A2})$$

By changing the shape parameters  $p_1$  and  $p_2$  different leaf area distribution curves can be achieved.

The relation between height  $h_{pt}$  and stem volume  $S_t$  at time  $t$  is given by a standard allometric equation (Stearns, 1992). In this equation,  $\alpha$  and  $\beta$  are constants.

$$S_t = \alpha \cdot h_{pt}^\beta \quad (\text{A3})$$

Although a root system is present in the model plant, it merely acts as a carbon sink for the carbohydrates from photosynthesis. The root mass is a linear function of the leaf area:

$$R_t = \sigma \cdot L_t \quad (\text{A4})$$

Here  $\sigma$  is a constant factor depicting the ratio between leaf area and root mass.

## 2. The Light Climate within the Vegetation

We assume a light climate in the vegetation cell in which the photons flow vertically downward. At each depth  $h$  the interception of light by the plants is modeled by Beer's law (Monsi and Saeki, 1953). The horizontal light intensity  $i_h(h)$  is given for each height  $h$  in the cell:

$$i_h(h) = i_h(h_v) \cdot \exp \left[ - \int_h^{h_v} \sum_{j=1}^n dh \cdot \lambda_j(h) \cdot \cos \alpha \cdot a \right] \quad (\text{A5})$$

where  $i_h(h_v)$  is the horizontal light intensity above the vegetation and  $h_v$  is the height of the vegetation. The light intensity  $i_h(h_v)$  over a season is described further on.  $\cos \alpha$  is the leaf inclination and  $a$  is the absorption coefficient of leaves. For simplicity, we take these parameters equal for all plant genotypes. The rate of photon absorption for the leaf elements at height  $h$  is calculated from the light climate at height  $h$ , the leaf inclination and absorption coefficient of a plant. It is given by

$$i_{al}(h) = i_h(h) \cdot \cos \alpha \cdot a \quad (\text{A6})$$

## 3. Leaf and Plant Photosynthetic Rates

The leaf photosynthetic rate is calculated on the basis of a non-rectangular hyperbolic relation between maximum photosynthetic capacity, light interception and quantum yield (Marchall and Biscoe, 1980). Leaf photosynthetic rate is given as:

$$P_{gl}(h) = P_{ml} \cdot \frac{(1+x) - \sqrt{(1+x)^2 - 4 \cdot \theta \cdot x}}{2 \cdot \theta} \text{ with } x = \frac{\Phi \cdot i_{al}(h)}{P_{ml}} \quad (\text{A7})$$

Here  $P_{ml}$  is the photosynthetic capacity of the leaves,  $\Phi$  the quantum yield per unit absorbed light,  $\theta$  a curvature factor and  $i_{al}(h)$  is the rate of photon absorption of the leaves at height  $h$  (see 2.4). For reasons of simplicity, we assume that capacity  $P_{ml}$ , quantum yield  $\Phi$  and curvature  $\theta$  do not vary with height or time.

For each plant the total photosynthetic rate is given by the integral over the plant's height, of the leaf photosynthetic rate times the leaf area. This gross photosynthesis is in  $\mu\text{mol}$  carbon per unit time.

$$P_g = \int_0^{hp} dh \cdot P_{gl}(h) \cdot \lambda(h) \quad (\text{A8})$$

#### 4. Carbon Balance and the Allocation Program

The growth of plant organs brings about carbon costs. These costs are balanced at any time by the carbon production rate of the plant. Firstly, the plant allocates carbon to account for maintenance costs.

$$P_n = P_g - R_m \text{ with } R_m = r_{ml} \cdot c_l \cdot L + r_{ms} \cdot c_s \cdot S + r_{mr} \cdot c_r \cdot R \quad (\text{A9})$$

$R_m$  is the maintenance rate and is based on the weights of the plant parts. The parameters  $r_{ml}$ ,  $r_{ms}$ ,  $r_{mr}$  are the maintenance respiration rates in gram carbon per unit carbon mass per unit time. The conversion factor  $c_l$  is in g carbon per  $\text{m}^2$  leaf,  $c_s$  is in g carbon per volume stem,  $c_r$  is in g carbon per gram roots. After maintenance, plants invest the net photosynthetic production in the growth of their vegetative parts or, if they are in reproductive mode, invest it in seed mass.

The carbon balance we use in the model is according to the following set of rules: 1. The consumption of carbon should be, at any time, equal to the carbon gain from net photosynthesis  $P_n$ . 2. Height growth rate  $dh_p/dt$  is always non-negative. 3. Leaf area rate  $dL/dt$  can be either positive or negative. If the carbon balance at any moment is negative, because the plant consumes more carbon than comes from photosynthetic production, leaf area is shed and carbon from this leaf area is used to account for the shortage. If the carbon balance is positive, leaf area is produced. 4. If the leaf area is equal to zero, the plant is considered dead. The carbon balance is applicable for any specific allocation program the plant may follow.

$$P_n = [\dots] \frac{dL}{dt} + \left[ (c_s + r_s) \frac{dS}{dh_p} + (c_l + r_l) \int_0^{hp} dh \cdot \text{POS} \left( \frac{d\lambda}{dh_p} \right) - c_{rl} \int_0^{hp} dh \cdot \text{NEG} \left( \frac{d\lambda}{dh_p} \right) \right] \frac{dh_p}{dt} \quad (\text{A10})$$

In case of a positive leaf production rate ( $dL / dt > 0$ ) or a negative leaf production rate ( $dL / dt < 0$ ) we write for the leaf production rate, respectively:

$$[(c_l + r_l) + \sigma(c_r + r_r)] \frac{dL}{dt} \text{ or } [-(c_{rl} + \sigma \cdot c_{rr})] \frac{dL}{dt} \quad (\text{A11})$$

In these equations A10 and A11,  $c_l$ ,  $c_r$ ,  $c_s$ ,  $c_f$  are the structural carbon imbedded in leaves, roots, stem and seed respectively. Parameters  $r_l$ ,  $r_r$ ,  $r_s$  and  $r_f$  are the growth respiration with leaf growth, root growth and stem growth. If a plant grows in height  $h_p$  with rate  $dh_p / dt$  this requires costs for the breakdown and production of leaves to maintain the crown shape as dictated by the parameters  $p_1$  and  $p_2$  in Equation A1. *POS* ( $d\lambda / dh_p$ ) and *NEG* ( $d\lambda / dh_p$ ) respectively depict the leaf area that is produced with growth in height and the leaf area that is cast away with growth in height. Parameters  $c_{rl}$  and  $c_{rr}$  depict the carbon that can be retrieved if leaves and roots, respectively, are cast away.

The investment in stem is always a fixed fraction of  $P_n$ . The actual height growth  $dh_p / dt$  is calculated from the relation between stem volume and height, net photosynthesis  $P_n$  and the allocation of carbon to height growth  $a_s$ .

$$\frac{dS}{dt} = f(P_n) = \frac{a_s \cdot P_n}{c_s} \text{ and as } \frac{dh_p}{dt} = \frac{f(P_n)}{dS / dh_p}$$

the height growth can be written as

$$\frac{dh_p}{dt} = \frac{(a_s \cdot P_n) / c_s}{\alpha \cdot \beta \cdot (h_p)^{\beta-1}} \quad (\text{A12})$$

The denominator of the equation is the allometric height-volume relation, derived from Equation A3.

In conclusion, two state variables determine the state of the plant when it is not in reproductive mode. They are total leaf area  $L$  (with associated roots) and total height  $h_p$ . The allocation to the latter is an imposed control; it determines the strategy of the plant. It is a fraction of the net photosynthetic production. In contrast, the allocation to the leaf area and roots can be determined from the carbon balance as written in Equation A10 and A11.

After the plant switches to seed production, all of the net photosynthetic production goes to the production of seed. If net photosynthesis is negative or zero, the allocation rate to seed is zero.

$$\frac{dF_m}{dt} = P_n \quad (\text{A13})$$

Here  $F_m$  is the seed mass that is produced. It is assumed that maintenance of current biomass is a priority. This is paid from net photosynthetic production. This means the plant is able to maintain its shape when it has switched to seed mass production. Leaf area and

consequent light interception changes only if the plant is forced to shed leaf area as a result of a negative carbon balance, caused by a diminishing light climate.

## 5. The Seasonal Light Climate

We assume a seasonal fluctuation in the yearly light climate, as we would expect it to occur in a temperate region (Kirschbaum, 1999):

$$\text{Daily Incidence } I_{veg} = I_{mean} + I_{amp} \cdot \sin \left[ \Pi \cdot \left( \frac{t - 0.5 \cdot \text{year} + 0.25 \cdot \text{year}}{0.5 \cdot \text{year}} \right) \right] \quad (\text{A14})$$

Here  $I_{veg}$  is the daily incident light above the canopy at day  $t$  in the simulation year,  $I_{mean}$  is the mean incident light above the canopy during a year and  $I_{amp}$  is the amplitude of the fluctuation in incident light.

**Table A1. Parameters settings. Some parameters have been taken as an approximate average of several literature sources. Sources of the parameters: 1. Poorter (1991) 2. Goudriaan and Van Laar (1994) 3. Anten and Hirose (2003) 4. Calibrated parameters (this study) 5. Caton et al. (1999) 6. Kastner-Maresch and Mooney (1994) 7. Kirschbaum (1999) 8. Lieth and Reynolds (1988)**

| Symbol   | Unit                                      | Value      | Source |
|--|---|------------|--------|
| L (initial)                                      | m <sup>2</sup>                            | 0.00165    | 1      |
| H (initial)                                      | m   | 0.01       | 1      |
| c <sub>s</sub>                                   | g C/ m <sup>3</sup>                       | 0.000045   | 4,1    |
| c <sub>i</sub>                                   | g C/ m <sup>2</sup>                       | 15         | 1,2    |
| c <sub>r</sub>                                   | g C/ g mass                               | 0.45       | 1      |
| σ  | g C root/ m <sup>2</sup> leaf             | 7.5        | 1,6    |
| α, β   | -   | 0.018, 1.4 | 4      |
| p <sub>0</sub> , p <sub>1</sub> , p <sub>2</sub> | -   | 30, 2, 2   | 4      |
| P <sub>ml</sub>                                  | μmol CO <sub>2</sub> / m <sup>2</sup> / s | 16         | 3      |
| cos α  | -   | 0.5        | 2      |



**Table A1. Continued**

| Symbol                   | Unit                                     | Value  | Source |
|--------------------------|--|--------|--------|
| $\Phi$                   | $\mu\text{mol CO}_2/\mu\text{mol ppfd}$  | 0.05   | 3      |
| $\theta$                 | -  | 0.7    | 3,8    |
| $r_s, r_l, r_r$          | $\text{g C}/\text{g C}$                  | 0.213  | 2,8    |
| $r_{ms}, r_{ml}, r_{mr}$ | $\text{g C}/\text{g C plant}/\text{day}$ | 0.0235 | 2,5    |
| $c_{rl}, c_{rr}$         | $\text{g C}/\text{g C}$                  | 0.6    | 4      |
| $I_{\text{amp}}$         | $\mu\text{mol}/\text{m}^2/\text{s}$      | 1360   | 7      |
| $I_{\text{mean}}$        | $\mu\text{mol}/\text{m}^2/\text{s}$      | 1700   | 7      |
| Day length               | $\text{s}/\text{day}$                    | 25200  | 4      |

## Appendix B. Invasion and Coexistence

The possibility for a pair of plant genotypes to coexist, invade each other or exclude each other can be calculated as followed.

We consider a pair of competing genotypes '1' and '2'. The seed production 'A' of genotype 1 will be different depending on whether it is competing against conspecific plants ( $A_{11}$ ) or heterospecific plants ( $A_{12}$ ), this also applies to the other genotype ( $A_{22}$  and  $A_{21}$ ). Examples of such seed productions can be found in the lower part of Table 2.

The frequencies 'x' of the two genotypes add up to unity. The frequency of genotype 2 can thus be expressed in terms of the frequency of genotype 1:

$$x_2 = 1 - x_1 \quad (\text{B1})$$

Because the total produced seed mass 'S' of the pair-wise competing genotypes is dependent on the frequency of the heterospecific and the conspecific plants we write:

$$S_1 = x_1(A_{11} \cdot x_1 + A_{12} \cdot x_2) = x_1(A_{11}x_1 + A_{12}(1 - x_1)) \quad (\text{B2})$$

$$S_2 = x_2(A_{22} \cdot x_2 + A_{21} \cdot x_1) = (1 - x_1)(A_{22}(1 - x_1) + A_{21}x_1) \quad (\text{B3})$$

The frequency at the next time step for genotype 1 can be written as the produced seed mass ( $S_1$ ) divided by the total produced seed mass for both genotypes ( $S_1 + S_2$ ):

$$x_1^+ = \frac{x_1(A_{11} \cdot x_1 + A_{12} \cdot (1 - x_1))}{x_1(A_{11} \cdot x_1 + A_{12}(1 - x_1)) + (1 - x_1) \cdot (A_{22} \cdot (1 - x_1) + A_{21} \cdot x_1)} \quad (\text{B4})$$

The sign of  $x_1^+ - x_1$  determines the increase or decrease of genotype 1. If  $x_1^+ - x_1$  is positive, genotype 1 will increase in frequency. If it is negative, it will decrease in frequency.

$$x_1^+ - x_1 = \frac{x_1(A_{11}x_1 + A_{12}(1 - x_1)) - x_1(x_1(A_{11}x_1 + A_{12}(1 - x_1)) + (1 - x_1)(A_{22}(1 - x_1) + A_{21}x_1))}{x_1(A_{11}x_1 + A_{12}(1 - x_1)) + (1 - x_1) \cdot (A_{22}(1 - x_1) + A_{21}x_1)} \quad (\text{B5})$$

The numerator of the formula will determine the sign of the change in frequency. To clean up the formula (B5), we multiply all terms by  $A_{22}/A_{22}$  and by doing so scale the pay-off to  $A_{22}$  so that

$$\alpha = A_{11}/A_{22} \quad \beta = A_{12}/A_{22} \quad \gamma = A_{21}/A_{22} \quad (\text{B6})$$

This gives:

$$x_1^+ - x_1 = \frac{x_1(x_1 - 1) \cdot (\alpha x_1 + \beta(1 - x_1) - (1 - x_1) - \gamma x_1)}{[\dots]} \quad (\text{B7})$$

If the sign of the formula is positive near  $x_1 = 0$ , it means a genotype 1 is able to invade a population consisting of the competitor genotype 2. If the sign is negative near  $x_1 = 1$ , it means a population of the genotype 1 can be invaded by a competitor of genotype 2.

We can derive what the conditions in pair-wise competition are for either genotype 1 to win, genotype 2 to win, or to get a stable or unstable coexistence of the genotypes.

There is an unstable coexistence if  $\beta - 1 < 0$  near  $x_1 = 0$  and  $\alpha - \gamma > 0$  near  $x_1 = 1$

There is a stable coexistence if  $\beta - 1 > 0$  near  $x_1 = 0$  and  $\alpha - \gamma < 0$  near  $x_1 = 1$ .

Genotype 1 cannot invade if  $\beta - 1 < 0$  near  $x_1 = 0$  and  $\alpha - \gamma < 0$  near  $x_1 = 1$

Genotype 1 cannot be invaded if  $\beta - 1 > 0$  near  $x_1 = 0$  and  $\alpha - \gamma > 0$  near  $x_1 = 1$

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