4. Interspecific competition

Interactions between species

Until now only monocultures have been considered, although, most often populations of different plant species will form plant communities. The individual plants in a natural plant community will typically compete with conspecific plants (intraspecific competition) and with plants belonging to other species (interspecific competition) for the limiting resources (Harper 1977, Goldberg and Barton 1992, Gurevitch et al. 1992).

It is believed that interspecific competition plays an important role in the composition of plant communities, and this has indeed been demonstrated (e.g., Weiher et al. 1998, Silvertown et al. 1999, Gotelli and McCabe 2002). Thus, to understand and possibly to predict the formation of plant communities, the interspecific competitive forces between different plant species have been investigated, often by performing two-species competition experiments (e.g., de Wit 1960, Marshall and Jain 1969, Antonovics and Fowler 1985, Law and Watkinson 1987, Pacala and Silander 1987, Francis and Pyke 1996).

Table 4.1   Different types of interactions between two plant species (after Haskell 1947).

Interaction	Species A	B	Nature of interaction
Competition	-	-	Each species has a negative effect on each other
Parasitism	+	-	Species A exploits species B
Mutualism	+	+	Interaction is favourable to both species
Commensalism	+	0	Species A benefits whereas species B is unaffected
Amensalism	-	0	Species A is inhibited whereas species B is unaffected
Neutralism	0	0	Neither species affect each other

Different plant species have different strategies to obtain their necessary share of the resources in order to grow and reproduce (Grime 2001). Some plant species are of the same functional type, i.e., they compete for the same resources. Other plant species do not compete for the same resources and may have no effect on each other. In some cases the interaction of two species is beneficial for one of the species but has no effect on the other. For example, the early emerging small geophyte *Anemone nemorosa* depends on a dense tree cover of e.g. *Fagus sylvatica* during the summer in order not to be outcompeted by e.g. grasses. In total, two plant species may interact in six qualitatively different ways (Table 4.1).

The nature and strength of interspecific competitive interactions may be investigated by two different approaches: manipulated competition experiments or by censusing coexisting plant populations in a natural plant community. Manipulated plant competition experiments are conducted by measuring size, fecundity, the number of successful descendants, or other measures of ecological success at variable densities and proportions of two or more plant species. There has been an argument in the ecological literature, whether a substitution design (varying species proportions while keeping combined density fixed) or an additive design (increasing the density of one species while keeping the density of the other species fixed) was the best design of a plant competition experiment. This argument is a leftover from the time when plant competition experiments mainly were used to address applied issues in the agricultural sciences. There is no doubt that both types of plant competition designs are equally inferior when plant ecological questions are investigated (e.g. Cousens 1991, Inouye 2001). In the words of Inouye (2001): "The use of substitution and additive designs has largely precluded generating quantitative estimates of the effects of interspecific competition on population dynamics or coexistence, beyond the inference that species do or do not compete." Instead it is recommendable to vary both density and proportion of each species (response surface design) in order to cover a realistic domain of densities and proportions of a natural plant community (Inouye 2001). Hence, the minimum requirement of a two-species competition experiment is three proportions (e.g. 1:0, 1:1, 0:1) at three densities (Fig. 4.1).
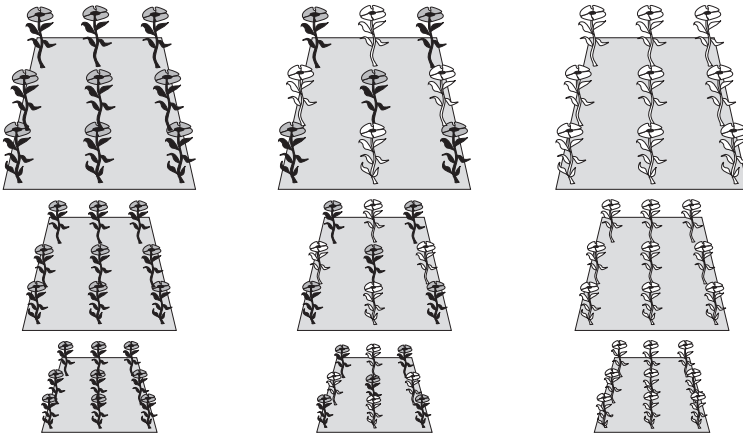

Fig. 4.1   A two-species competition experiment at three proportions (e.g. 1:0, 1:1, 0:1) and at three densities.

The censusing of coexisting plant populations in a natural plant community (e.g. Rees et al. 1996, Freckleton and Watkinson 2001) has the advantage that it is the actual ecological processes which are studied, where manipulated competition experiments often may be criticised for unrealistic growing conditions. The drawbacks of the censusing methodology is that it is often time consuming and work intensive, and that the domain of the data (densities and proportions of the non-manipulated coexisting species) may be inadequate to make useful ecological predictions.

Modelling interspecific competition
The qualitative descriptive terminology of interaction types in Table 4.1 has become standard, and is readily generalised by the well-known Lotka-Volterra quantitative model of species interaction based on competition coefficients (e.g. Christiansen and Fenchel 1977). The concept of competition coefficients may, at least in principle, be developed from the causal factors: time, habitat and resources of the multidimensional niche concept (MacArthur and Levins 1967, Christiansen and Fenchel 1977). However, usually competition coefficients are thought of as parameters in an empirical competition model, which are estimated using standard statistical methodology (e.g. Marshall and Jain 1969, Harper 1977, Firbank and Watkinson 1985, Law and Watkinson 1987, Pacala and Silander 1990, Francis and Pyke 1996, Rees et al. 1996, Damgaard 1998). This statistical approach has been criticised (Harper 1977, Tilman 1988) for contributing little to the understanding of the underlying mechanisms behind the phenomenon of competition and consequently provide only limited predictive power. In some cases the estimation of competition coefficients may even be directly deceptive of the underlying causes of the interaction, e.g., apparent competition (Holt 1977), when a herbivore tends to eat the most common of two plant species.

As discussed previously, two fundamentally different (or complementary) modelling approaches may be taken in the description of the interactions between plant species: The mechanistic – and the empirical modelling approach. While the mechanistic modelling approach, at least in principle, would respond to the just criticism raised by Harper (1977), Tilman (1988) and others, the complexity and stochasticity of the causal relationships underlying the species interaction in a natural plant community are daunting. The dynamics of plant communities are so complex that only simple heuristic mechanistic modelling is realistic at present. If we want to make use of the available exciting plant ecological data on interspecific competition in a quantitative way, we are forced to make use of relatively simple empirical competition models.

Many manipulated competition experiments have been reported using a set of competition indices introduced by de Wit (1960). Unfortunately, the notion of population changes is not easily incorporated into the de Wit competition model (Inouye and Schaffer 1981) and the model is not readily comparable with the classical Lotka-Volterra competition model. Furthermore, the indices in the de Wit competition model lead to statistical difficulties (Connolly 1986, Skovgaard 1986). Instead, it is advantageous to use a generalised single species competition model, where the effect of the individuals of other species is weighted by competition coefficients. In principle all the models in chapter 2 and 3 might be generalised to multiple species using competition coefficients, but here we will mainly discuss the relatively simple class of mean-field models of two competing species. An often used and flexible mean-field two-species competition model is a generalisation of the hyperbolic size-density response function (2.12) (e.g. Firbank and Watkinson 1985, Law and Watkinson 1987, Damgaard 1998).

$$v_1(x_1, x_2) = \left(\alpha_1 + \beta_1(x_1 + c_{12}x_2)^{\phi_1}\right)^{-1/\theta_1}$$
$$v_2(x_1, x_2) = \left(\alpha_2 + \beta_2(c_{21}x_2 + x_2)^{\phi_2}\right)^{-1/\theta_2}$$

(4.1),

where x_i are the densities of plant species i, c_{ij} are the competition coefficients and the other shape parameters are defined as in the single-species case (2.12). The competition coefficient c_{ij} can, analogous to the Lotka-Volterra competition model, be interpreted as the inhibition of species j on species i in units of the inhibition of species i on its own growth. For example, when $c_{ij} = 0$, species j has no effect on the growth of species i; when $c_{ij} = 1$, a plant of species j has the same effect on the growth of species i as a plant of species i; and when $c_{ij} = 2$, one plant of species j has the same effect on the growth of species i as two plants of genotype i. If $c_{ij} < 0$, species j has a positive effect on the growth of species i.

The empirical competition model (4.1) is quite flexible and in many cases the model will be over-parameterised, see the discussion in the single-species case leading to model (2.13). Such a possible over-parameterisation generally decreases the testing power of the model, and it is therefore a standard statistical procedure to test, in this case by a loglikelihood ratio test (Appendix B), whether the model may be reduced by setting e.g. $\theta_1 = \theta_2 = 1$ and $\phi_1 = \phi_2 = 1$.

Example 4.1   Competition between two genotypes of *Arabidopsis thaliana* I

Arabidopsis thaliana is an almost completely self-fertilising winter an-nual (Abbott and Gomes 1989). The selfing breeding systems means that there is limited genetic exchange between *A. thaliana* genotypes on an ecological time scale (Miyashita et al. 1999) and that the eco-logical success or fitness of different *A. thaliana* genotypes may be de-scribed by a plant species competition model (Ellison et al. 1994). That is, when there is no sexual transmission between individual plants, the ecological success of different genotypes may be modelled as if the genotypes where separate species.

In a manipulated competition experiment two *A. thaliana* geno-types (*Nd-1* and *C24*) were grown in an experimental garden in a design similar to Fig. 4.1, i.e., three proportions (1:0, 1:1, 0:1) at three densities (0.025 cm^{-2}, 0.101 cm^{-2}, 0.203 cm^{-2}), and the dry weights were measured after seed setting.

The dry weight data was fitted to competition model (4.1) and af-ter the model was reduced ($\theta_1 = \theta_2 = \phi_1 = \phi_2 = 1$, loglikelihood ratio test with four degrees of freedom, P = 0.36), the posterior distribution of the competition coefficients were calculated assuming an uninforma-tive prior (Fig. 4.2). Based on the 95% credibility intervals (Appendix C) genotype *Nd-1* has a significantly higher negative effect on *C24* than vice versa.
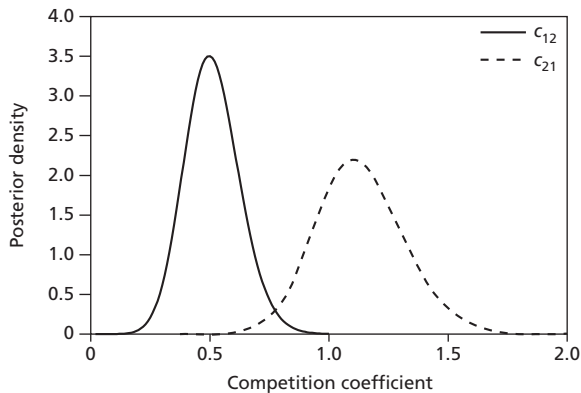

Fig. 4.2   The posterior density distribution of competition coefficients of two *Arabidopsis thaliana* genotypes (1: *C24* and 2: *Nd-1*). The 95 % credibility inter-vals for c_{12} is {0.30 – 0.75} and for c_{21} is {0.80 – 1.52}.

Analogous to the single-species case in Chapter 3, discrete recursive equations of the densities of competing synchronous monocarpic plant populations may be formulated. However, in order to simplify the calculations it will in the following be assumed that the probability of germination, establishment and reaching reproductive age is independent of the seed densities of the competing species and constant, i.e. $p_i(x_{i,0}, x_{j,0}) = p_i$, and the recursive equations will be:

$$x_1(g+1) = p_1\, x_1(g)\big(\alpha_1 + \beta_1(x_1(g) + c_{12}\,x_2(g))^{\phi_1}\big)^{-1/\theta_1}$$
$$x_2(g+1) = p_2\, x_2(g)\big(\alpha_2 + \beta_2(c_{21}x_1(g) + x_2(g))^{\phi_2}\big)^{-1/\theta_2}$$

(4.2),

where the hyperbolic terms are measures of the average fecundity per plant (Hassell and Comins 1976, Firbank and Watkinson 1985, Damgaard 1998). The parameters in competition model (4.1) may be estimated from competition experiments and the population growth of the two species may be predicted using (4.2). To account for the possible effect of density-dependent mortality and if density-independent mortality may be assumed to occur before any density-dependent mortality (see Chapter 3), then plant densities should be censused before the onset of density-dependent mortality. The plants that die due to density-dependent mortality before they are able to reproduce will then be recorded as having a fecundity of zero.

Analogous to the single-species case, knowledge on the equilibrium densities may provide valuable information in predicting the future states of the plant community. The recursive equations (4.2) may be solved, $\hat{x}_i = x_i(g + 1) = x_i(g)$, with the equilibria (Damgaard 1998):

$$\hat{x}_1 = 0; \qquad \hat{x}_2 = 0$$

(4.3a),

$$\hat{x}_1 = u_1; \qquad \hat{x}_2 = 0$$

(4.3b),

$$\hat{x}_1 = 0; \qquad \hat{x}_2 = u_2$$

(4.3c),

$$\hat{x}_1 = \frac{u_1 - c_{21}u_2}{1 - c_{12}c_{21}}; \quad \hat{x}_2 = \frac{u_2 - c_{12}u_1}{1 - c_{12}c_{21}}$$

(4.3d),

where $u_i = (\beta_i^{-1}(p_i^{\theta_i} - \alpha_i))^{1/\phi_i}$.

In order to determine when the nontrivial equilibrium (4.3d) degenerated to either equilibrium (4.3b) or equilibrium (4.3c); equilibrium (4.3d) was solved for c_{ij} after setting $\hat{x}_1 = \hat{x}_2 = 0$ ($c_{12}c_{21} \neq 1$) and the following roots were obtained:

$$\breve{c}_{12} = u_1/u_2 \; ; \quad \breve{c}_{21} = u_2/u_1 \tag{4.4}.$$

The Jacobian matrix (see Appendix D) of recursive equation (4.2) at the nontrivial equilibrium (4.3d) has two complicated eigenvalues $\{\lambda_1, \lambda_2\}$. The inequalities $\lambda_1 < 1$ and $\lambda_2 < 1$ can be solved and both has the solution:

$$c_{12} < \breve{c}_{12}; \qquad c_{21} < \breve{c}_{21} \tag{4.5}.$$

The solutions to the inequalities $\lambda_1 > -1$ and $\lambda_2 > -1$ are more complicated and a numerical investigation of the eigenvalues is necessary to determine the stability of a specific equilibrium. Generally, if the curves of the cumulative plant sizes are not to concave (see Fig. 2.6), then the two species will coexist at equilibrium at the equilibrium densities (4.3d) if both species are able to persist when alone (see stability conditions for equilibrium (3.10)) and inequalities (4.5) are fulfilled. In the important case, when $\phi_i = \theta_i = 1$ and $c_{12} > 0$, $c_{21} < 1/c_{12}$, it can be showed that if both $\lambda_1 < 1$ and $\lambda_2 < 1$ then $\lambda_1 > -1$ and $\lambda_2 > -1$ (Damgaard 2004a). When the curves of the cumulative plant sizes becomes sufficiently concave then the nontrivial equilibrium (4.3d) becomes a saddle point and the trajectory of the densities of the two species bifurcates into periodic coexisting densities. For even more concave curves of the cumulative plant sizes the dynamics become chaotic and the two species coexist at densities in the form of a strange attractor (Damgaard 2004a).

Analogous to the continuous Lotka-Volterra competition model, there are four different ecological scenarios when two species compete: coexistence, species 1 will outcompete species 2, species 2 will outcompete species 1, and either species may outcompete the other depending on the initial conditions. In the last case of indeterminate competition the rarer of the two species will generally be outcompeted (but see Hofbauer et al. 2004). These four ecological scenarios may be characterised by a set of inequalities of the competition coefficients similar to (4.5) (Table 4.2).

Table 4.2   The four different ecological scenarios when two species compete (Damgaard 1998).

Ecological scenario	Condition	Equilibrium
Coexistence	$c_{12} < \breve{c}_{12}$; $c_{21} < \breve{c}_{21}$	4.3d
Species 1 will win	$c_{12} < \breve{c}_{12}$; $c_{21} > \breve{c}_{21}$	4.3b
Species 2 will win	$c_{12} > \breve{c}_{12}$; $c_{21} < \breve{c}_{21}$	4.3c
Either species 1 or species 2 will win	$c_{12} > \breve{c}_{12}$; $c_{21} > \breve{c}_{21}$	4.3b or 4.3c

In some applied ecological questions, e.g., risk assessment of genetically modified plants (Damgaard 2002) and the management of natural habitats, it is desirable to be able to predict which of the four different ecological scenarios is most likely. If the competition model (4.2) is reparameterised so that $\breve{c}_{ij} = c_{ij} + \delta_{ij}$, then the signs of δ_{ij} will discriminate between the four ecological scenarios (Fig. 4.3). The four different ecological scenarios may be considered as four complementary hypotheses and the Bayesian posterior probabilities of each hypothesis may be calculated from a manipulated competition experiment, a known and density-independent probability of reaching reproductive age, and a prior distribution of the four hypotheses (Damgaard 1998).
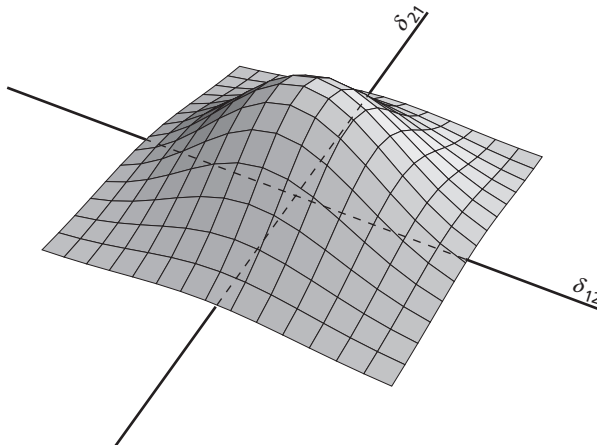

Fig 4.3   The joint posterior distribution of the two competition coefficients ($c_{ij} = \breve{c}_{ij} + \delta_{ij}$) calculated from a hypothetical two-species competition experiment and the recursive equations (4.2) (Damgaard 1998). The volume under the "posterior surface" in the quadrate $\delta_{12} < 0$ and $\delta_{21} < 0$ is equal to the probability that the two species will coexist at equilibrium. Likewise, the volumes in the quadrate $\delta_{12} < 0$ and $\delta_{21} > 0$, or $\delta_{12} > 0$ and $\delta_{21} < 0$, is equal to the probability that either species one, or two, respectively, will outcompete the other species, and the volume in the quadrate $\delta_{12} > 0$ and $\delta_{21} > 0$ is equal to the probability that either species will outcompete the other species.

Example 4.2   Competition between two genotypes of *Arabidopsis thaliana* II

Assume that the two genotypes of *Arabidopsis thaliana* (*Nd-1* and *C24*) investigated in example 4.1 are the two only genotypes in the *A. thaliana* population and that the density of *A. thaliana* is not controlled by other species. Similar to example 3.1, assume that mortality is high and density-independent, and furthermore that both genotypes have the same probability of reaching reproductive age.

The fecundity was estimated from the dry weight data by linear regressions. The two genotypes differed significantly in the way they converted biomass at the end of the growing season into fecundity; genotype *C24* produced relatively more seeds per biomass (Damgaard and Jensen 2002). The Bayesian posterior probabilities of each ecological scenario was calculated assuming that the different ecological scenarios were equally probable (uninformative prior distribution) (Table 4.3). Depending on the probability of germination, establishment and reaching reproductive age either "coexistence of the two genotypes" or "genotype *C24* would outcompete *Nd-1*" was the predicted most likely long-term ecological scenario.

Table 4.3   Predicted probabilities of the four different ecological scenarios when two genotypes of *Arabidopsis thaliana* (*Nd-1* and *C24*) compete against each other at different probabilities of germination, establishment, and reaching reproductive age.

Ecological scenario	$p_1=p_2=0.005$	$p_1=p_2=0.001$	$p_1=p_2=0.0005$
Coexistence	0.34	0.57	0.71
Genotype *Nd-1* will win	0	0.001	0.003
Genotype *C24* will win	0.66	0.43	0.28
Either genotype will win	0	0	0.001

In the single-species case, it was discussed that the probability of germination, establishment and reaching reproductive age in a natural habitat is a critical and variable factor in predicting population growth and equilibrium densities (Crawley et al. 1993, Stokes et al. 2004). However, as suggested in Table 4.3, the predicted probabilities of the four different ecological scenarios when two species compete against each other are less sensitive to variation in the absolute value of the establishment probabilities. It is the relative differences between the establishment probabilities, the fecundities and the competitive abilities of the two

Example 4.3   Competition between *Avena fatua* and *Avena barbata*

Assume that the densities of *Avena fatua* and *Avena barbata* are controlled by each other through competitive interactions and not by other species, and furthermore that the probabilities of reaching reproductive age are density-independent and known.

The fecundities of the two *Avena* species were estimated in a competition experiment of five proportions at six densities (Marshall and Jain 1969). The Bayesian posterior probabilities of each ecological scenario were calculated assuming that each of the ecological scenarios was equally likely to occur (uninformative prior distribution) (Table 4.4).

Ecological scenario	$p_1 = p_2 = 0.25$
Coexistence	0.186
A. fatua will win	0.671
A barbata will win	0.001
Either species will win	0.142

Table 4.4 Predicted probabilities of the four different ecological scenarios when *Avena fatua* and *Avena barbata* compete against each other (Damgaard 1998).

The species distribution of *Avena fatua* and *Avena barbata* was observed in a number of natural plant communities in two regions in California (Marshall and Jain 1969). Interestingly, the predicted probabilities correspond with the observed distribution of the two plant species in the Mediterranean warm summer region, whereas the observed competitive interactions do not explain the observed plant distribution in the Mediterranean cool summer region (Fig. 4.4).
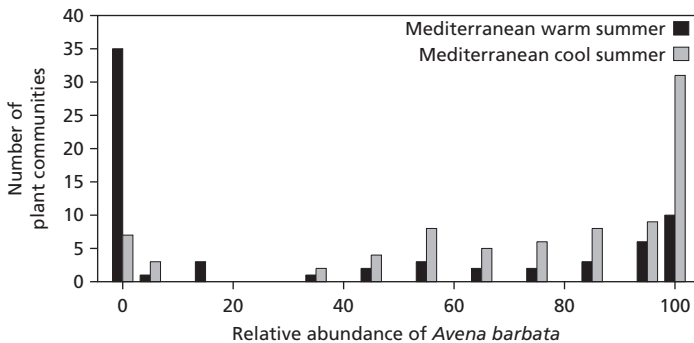

Fig. 4.4   **The species distribution of *Avena fatua* and *Avena barbata* in two regions in California.** Figure after Marshall and Jain (1969).

species, which mainly determine the fate of the competitive interaction (Damgaard 1998). Consequently, the predictions based on the competitive interactions between two species may therefore be less variable from year to year than estimating the population growth of each species separately.

Similar to the single-species case the predicted equilibrium state of the plant community is independent of the age structures in the seed bank. At equilibrium, the age structures in the seed bank will also be at equilibrium and a fixed number of seeds will germinate from each age-class and species in the seed bank each year (Damgaard 1998).

Ecological predictions will always have to be taken with some scepticism; it is an open question how well the predicted probabilities of the different ecological scenarios obtained from a short-term competition experiment will reflect actual long-term ecological processes in a natural plant community (Kareiva et al. 1996). The realism will to a large extent be determined by the design of the competition experiment, since the predicted probability will never be better than the competition experiment. If a key factor determining the competitive output between two plant species is not included in the experiment, then the predicted probabilities will most likely be erratic and misleading.

Manipulated experiments necessarily reduce the ecological complexity, and extrapolation from such experiments to long-term ecological scenarios can only be made with uncertainty. The predicted probabilities of the different ecological scenarios depend critically on a number of abiotic and biotic factors that for practical reasons often are kept fixed in manipulated experiments. The competitive ability may vary with the physical environment, e.g., temperature, nutrition and water availability (Clauss and Aarssen 1994). Species may also perform differently in competition with other plant species (Abrams 1996, Rees et al. 1996). Nevertheless, when confronted with a complex system, it is common scientific methodology to reduce the complexity of the system by ignoring some processes, to obtain manageable information, which is expected to be relevant in understanding the full system. Furthermore, quantitative ecological predictions are in demand in applied ecology, e.g., risk assessment of genetically modified plants and the management of natural habitats, and more generally to advance the scientific field of plant ecology (Keddy 1990, Cousens 2001).

In the above discussion of the equilibrium states of two competing plant species, it is implicitly assumed that the environment where the plant species are competing is approximately constant or slowly changing on an ecological time scale. However, in some ecosystems,

e.g., competing algae species, the species composition may have a large effect on the environment; in the algae case the amount of abiotic essential resources is altered. In such ecological systems more complicated dynamics, analogous to a predator-prey system of interaction, may be a more relevant description of the system (Huisman and Weissing 2001).

Modelling spatial effects

Often plant species are non-randomly distributed among each other (Dieckmann et al. 2000). The non-randomness may be due to historic establishment events of a primarily stochastic nature or as an effect of competitive interactions in previous generations, and the spatial processes of plants have theoretically been shown to affect the structuring of plant communities (Bolker and Pacala 1999). There has been a recent trend within the scientific community to explain various general ecological phenomenons by spatial effects and new hypotheses on the role of space in ecological processes have been developed (Tilman and Kareiva 1997, Dieckmann et al. 2000). Unfortunately, the theoretical investigation of the often-complicated spatial effects shows a history of being prone to erroneous interpretations (Pacala and Levin 1997). For example, in an often-cited paper Tilman (1994) showed that an arbitrarily large number of competing species can coexist in a spatially structured habitat, but later this effect has been shown to be due to an overly simplified competition model rather than to spatial structure (Adler and Mosquera 2000).

It is possible to generalise the empirical models developed for the single-species case using competition coefficients and test different ecological hypotheses with plant ecological data. However, only a few empirical studies have actually used such models to explain the effect of space on interspecific competition (Pacala and Silander 1990, Coomes et al. 2002) and these studies have not demonstrated a significant effect of space on interspecific competition between two pairs of annual species.

The importance of spatial effects in interspecific competition and the structuring of plant communities have until now mainly been examined by heuristic models. Analogous to the single-species case (equations 3.16 and 3.17), the spatial covariance of two species ($C_{11}(r)$, $C_{22}(r)$, and $C_{12}(r)$) as a function of the distance, r, at which it is measured, and the average spatial covariance

$$\bar{C}_{ij} = \int (U_{ij} * D_i)(r) C_{ij}(r) \, dr \tag{4.6},$$

(Bolker and Pacala 1999, Bolker et al. 2000), may be defined in the two-species case. Comparable to the single-species case, a set of differential

equations describing the changes in mean densities and average covariances in a spatial explicit model of plants with a simplified life history may be formulated and the invasion criteria of an invading species may be calculated. In this way the invasion criteria of different spatial plant strategies have been investigated (Bolker and Pacala 1999).

In the discrete hyperbolic competition model (equation 4.1) the plants are implicitly assumed to be randomly dispersed, however, the notion of the average spatial covariance may be integrated into the competition model (Bolker and Pacala 1999, Damgaard 2004b):

$$v_1(x_1,x_2) = \left(\alpha_1 + \beta_1\ (x_1 + \bar{C}_{11}/x_1 + c_{12}(x_2 + \bar{C}_{12}/x_2))^{\phi_1}\right)^{-1/\theta_1}$$
$$v_2(x_1,x_2) = \left(\alpha_2 + \beta_2\ (c_{21}(x_1 + \bar{C}_{12}/x_1) + x_2 + \bar{C}_{22}/x_2)^{\phi_2}\right)^{-1/\theta_2}$$

(4.7),

where $x_i + \bar{C}_{ii}/x_i$ is the average density of species i in the vicinity of species i, and $x_i + \bar{C}_{ii}/x_i$ is the average density of species i in the vicinity of species j (Bolker and Pacala 1999). Assuming that the average spatial covariance at equilibrium is known, it is possible to calculate the predicted probabilities of the different ecological scenarios as explained previously.

A special issue of spatial covariance is that many manipulated plant competition experiments for practical purposes often are arranged in a non-random spatial design, i.e. a grid design, a row design, or a honeycomb design. Non-random spatial designs have consequences for the analysis of competition experiments that need to be clarified in order to interpret the results (Mead 1967, Fortin and Gurevitch 2001, Stoll and Prati 2001, Damgaard 2004b). A regular spatial design in manipulated competition experiments decreases the variation in size and weight among conspecific plants since the species composition and density of the neighbourhood in most designs are held constant and less variable than in a random spatial design. Such a decrease in variation increases the likelihood of detecting a difference in the competitive ability of different plant species, which in many cases may be a motivating factor for choosing a non-random design. It could be argued that a reduction in experimental variation in many cases would be beneficial since the objective of many experiments is to detect mean differences rather than describing the variation. However, for a deeper understanding of the competitive forces and in order to predict different ecological scenarios, it is necessary to estimate different parameters of interests in a competition model. The problem with using a non-random design is that the data from plant competition experiments usually are analysed in mean-field competition models, which implicitly assume that plants interact

Example 4.4   Competition between two genotypes of *Arabidopsis thaliana* III

The two genotypes of *Arabidopsis thaliana* (*Nd-1* and *C24*) investigated in examples 4.1 and 4.2 were grown in a lattice grid design and in the mixed treatment the genotypes were arranged in a chessboard pattern. The spatial covariance can be calculated from such a regular spatial pattern by using the probability of site occupancy for each plant species and the conditional probabilities of two plants being the same plant species and different plants species (Damgaard 2004b).

There is no dispersal in the competition experiment and the average spatial covariance may be calculated with respect to a known competition kernel (equation 4.6). However, since there is no prior knowledge on the spatial scale of the interaction distance and the functional shape of the competition kernel a sensitivity analysis of different spatial scales and functional shapes was made (Table 4.5). The parameters of interest and especially the predicted most likely ecological scenario depended strongly on the mean interaction distance of the competition kernel, whereas the functional shape of the competition kernel was less important (Table 4.5). Since the actual competition kernel among *A. thaliana* plants is unknown it is difficult to interpret the consequences of the results in Table 4.5, except that neglecting the effect of spatial covariance in non-randomly designed competition experiments may affect the inferred conclusions (Damgaard 2004b).

Table 4.5 Estimation of parameters of interest from a competition experiment between two *A. thaliana* genotypes (1: *C24* and 2: *Nd-1*) under field conditions with and without including spatial covariance (mean-field) using equation (4.7). The competition kernel at various mean interaction distances was assumed to be either a two-dimensional exponential -, Gaussian -, or Bessel distribution with the dimension of the scale parameter in cm. The competition kernel is expected to differ among species, i.e., $U_{11} \neq U_{22} \neq U_{12} \neq U_{21}$, but since the two *A. thaliana* genotypes belong to the same species it is here assumed that $U = U_{11} = U_{22} = U_{12} = U_{21}$.

There is no prior knowledge on the equilibrium spatial distribution of the two *A. thaliana* genotypes and therefore it is assumed that the genotypes at equilibrium are randomly dispersed, but it is possible to generalise this assumption. The establishing probabilities for both genotypes were set to 0.001 (Damgaard 2004b). Note that, based on the same set of experimental data, the predicted outcome of competition between two *Arabidopsis thaliana* genotypes can vary between (almost certain) coexistence and (almost certain) exclusion of one genotype, depending on the assumptions made about the spatial scale of competition between the plants. The predicted outcome of competition depended strongly on the mean interaction distance of the competition kernel, whereas the functional shape of the competition kernel was less important.

		Max. likelihood:		Predicted probabilities of ecological scenarios:			
		c_{12}	c_{21}	Co-existence	Only C24	Only Nd-1	Either
Mean interaction distance = 1							
exponential	$\lambda = 2$	1.240	0.491	0.438	0.562	0	0
Gaussian	$\delta = 2/\pi$	1.107	0.498	0.528	0.471	0.0002	0.0004
Bessel	$\lambda = \pi/2$	1.094	0.522	0.461	0.539	0	0
Mean interaction distance = 2							
exponential	$\lambda = 1$	1.104	0.602	0.175	0.824	0	0
Gaussian	$\delta = 8/\pi$	1.102	0.656	0.148	0.852	0	0
Bessel	$\lambda = \pi/4$	1.199	0.667	0.213	0.787	0.0003	0
Mean interaction distance = 20							
exponential	$\lambda = 0.1$	1.082	0.401	0.678	0.320	0.001	0.001
Gaussian	$\delta = 800/\pi$	1.078	0.425	0.800	0.200	0.001	0
Bessel	$\lambda = \pi/40$	1.155	0.460	0.673	0.325	0.001	0.0003
Mean interaction distance = ∞							
mean-field		1.114	0.501	0.572	0.427	0.0007	0.0002

with other plants in a random way. It is therefore suggested that plants in manipulated competition experiments should be placed randomly, so that the design of the competition experiment is in agreement with the model used in the analysis (e.g. Damgaard 2004b).

Environmental gradients

The abiotic and biotic environment in which most plant interactions take place is highly variable across space and time. It has long been recognised that temporal and spatial variation in the environment is a major force that may influence the outcome of interspecific plant competitive interactions and plant community structures (Tilman 1988, Grime 2001). However, this important notion has only recently begun to influence the theoretical population dynamic models of species interaction (Chesson 2003).

The nature of the spatial and temporal environmental variation also varies and different modelling approaches may be used depending on the studied environmental variation (e.g. Rees et al. 1996, Bolker 2003), but here we will focus on the modelling of a spatial environmental gradient. An environmental gradient may be defined as a set of locations that vary with respect to one or more environmental factors and where the environment of each location is approximately constant or slowly changing on an ecological time scale. Different theoretical hypotheses on the expected effect of various environmental gradients have been developed and investigated in a number of empirical studies. For an introduction to the various hypotheses and the empirical work see e.g. Tilman (1988), Greiner La Peyre et al. (2001), and Grime (2001).

Often studied environmental gradients are specific abiotic stress factors like water availability, salinity, nitrogen availability, heavy metal concentration etc., but also the effects of general productivity (a summary indicator of plant growth) has been investigated. However, in some cases biotic factors may be assumed to be sufficiently constant on an ecological time scale to be modelled as an environmental gradient, e.g., the effect of shading trees on herbaceous plants and the effect of general herbivores and pathogens (Damgaard 2003b).

The growth and competitive interactions of two plant species along an environmental gradient may be adequately described by a generalisation of the discrete hyperbolic competition model (4.1), where it is assumed that the plants are effected by the level (h) of a specific environmental factor,

$$v_1(x_1, x_2, h) = \left(f_{\alpha_1} + f_{\beta_1} (x_1 + f_{c_{12}} x_2)^{\phi_1} \right)^{-1/\theta_1}$$
$$v_2(x_1, x_2, h) = \left(f_{\alpha_2} + f_{\beta_2} (f_{c_{21}} x_1 + x_2)^{\phi_2} \right)^{-1/\theta_2}$$

(4.8),

by some functions $f_z = f_z(z_0, h)$, where $h \geq 0$ and $f_z(z_0, 0) = z_0$ (Damgaard 2003b). The functions f_z that capture the effects of the environmental factor are of course generally unknown and depend on the environmental factor. There may exist prior knowledge, which will aid in choosing the right functional relationship. Alternatively, if competition experiments are made at several different levels of the specific stress, then the functional relationship may be chosen by likelihood ratio tests or by the use of e.g. the Akaike information criterion of different candidate functions. The exponentially decreasing function, sigmoid dose – response function, or the linear function will in many cases be natural candidate response functions, and these response functions may be used interchangeably in the outlined methodology. For simplicity, it is here assumed that within a certain limited range of the stress level, the stress affects the competitive interactions and the reproductive fitness of the susceptible plant species linearly, i.e.,

$$v_1(x_1, x_2, h) = \left(\alpha_{1,0} + \alpha_{1,1}h + (\beta_{1,0} + \beta_{1,1}h)(x_1 + (c_{12,0} + c_{12,1}h)x_2)^{\phi_1}\right)^{-1/\theta_1}$$

$$v_2(x_1, x_2, h) = \left(\alpha_{2,0} + \alpha_{2,1}h + (\beta_{2,0} + \beta_{2,1}h)((c_{21,0} + c_{21,1}h)x_1 + x_2)^{\phi_2}\right)^{-1/\theta_2}$$

(4.9).

Assuming a density-independent and constant probability of reaching reproductive age the discrete recursive equations of the densities of two competing synchronous monocarpic plant populations is:

$$x_1(g+1) = p_1\, x_1(g)\, v_1(x_1(g), x_2(g), h)$$

$$x_2(g+1) = p_2\, x_2(g)\, v_2(x_1(g), x_2(g), h)$$

(4.10),

where $v_i(x_1(g), x_2(g), h)$ is a measure of the average fecundity per plant. The recursive equations have the following equilibrium solutions:

$$\hat{x}_1 = 0; \qquad\qquad \hat{x}_2 = 0 \qquad\qquad (4.11a)$$

$$\hat{x}_1 = u_1; \qquad\qquad \hat{x}_2 = 0 \qquad\qquad (4.11b)$$

$$\hat{x}_1 = 0; \qquad\qquad \hat{x}_2 = v \qquad\qquad (4.11c)$$

$$\hat{x}_1 = \frac{u - f_{c_{12}}(h)v}{1 - f_{c_{12}}(h)f_{c_{21}}(h)}; \qquad \hat{x}_2 = \frac{v - f_{c_{21}}(h)u}{1 - f_{c_{12}}(h)f_{c_{21}}(h)} \qquad (4.11d)$$

where $u = \left(\dfrac{p_1^{\theta_1} - (\alpha_{1,0} + \alpha_{1,1}h)}{(\beta_{1,0} + \beta_{1,1}h)}\right)^{\phi_1^{-1}}$, $v = \left(\dfrac{p_2^{\theta_2} - (\alpha_{2,0} + \alpha_{2,1}h)}{(\beta_{2,0} + \beta_{2,1}h)}\right)^{\phi_2^{-1}}$, and $f_{cij}(h) = c_{ij,0} + c_{ij,1}h$

(Damgaard 2003b). A local linear stability analysis of the recursive equation (4.10) at the different equilibria (4.11 a-d) can be made. The eigenvalues are too complicated to be of general use, but they can be calculated numerically in specific cases, so that the stability properties of the different equilibria may be known.

If species 1 is more tolerant to the environmental factor than species 2, then the condition when species 1 will outcompete species 2 can be found by rearranging the equations after setting the nontrivial equilibrium (4.11d) equal to (4.11b) (Damgaard 2003b):

$$f_{c_{21}}(h) > \frac{v}{u}$$ (4.12).

Plant – herbivore and plant – pathogen interactions

Above the effect of a relatively constant environmental factor on plant competition was discussed and it was argued that general herbivores or pathogens for modelling purposes might be considered to be relatively constant environmental factors. However, if the herbivore or pathogen (in the following called a parasite) has one or more of the investigated competing plant species as the most important host plant, then the density of the parasite is controlled by the density of the host plants. That is, any changes in host plant size or density due to either competition, herbivory or disease will affect the density of the parasite.

The population growth of two competing plant species and a specific parasite may be modelled by recursive equations:

$$x_1(g + 1) = p_1 \, x_1(g) \, v_1(x_1(g), x_2(g), h(g))$$

$$x_2(g + 1) = p_2 \, x_2(g) \, v_2(x_1(g), x_2(g), h(g))$$ (4.13),

$$h(g + 1) \ = f(x_1(g), x_2(g), h(g))$$

where $f(x_1(g), x_2(g), h(g))$ describes the density of the parasite as a function of the densities of the two plant species and the parasite at the previous plant generation. Depending on the parasite life history and especially the generation time, likely candidate functions of $f(x_1(g), x_2(g), h(g))$ are various empirically fitted standard discrete population growth models, a Nicholson-Bailey type of model, and others (Hudson and Greenman 1998). Some parasite species tend to concentrate on a single food source and in some cases a population of parasites will switch between the two

competing species as the preferred food source depending on the plant densities. Such a system of an optimal foraging parasite stabilises the system so that local extinction events will become less likely (Krivan 1996, Krivan and Sidker 1999). Most models describing the population growth of two competing plant species and a specific parasite will face mathematical problems; in many cases only numerical methods will be available to find possible stable equilibria and this complicates the calculations needed to make ecological predictions using Bayesian statistics.

The complicated subject of how another trophic level affect the interaction of species is a classic ecological question and has been studied extensively both theoretically and empirically. It is out of the scope of this monograph to examine the subject in any detail. Here it will suffice to mention that depending on how the parasite affect the competing plant species, the parasite may either enhance or disrupt the likelihood that the two plant species coexist at equilibrium (Yan 1996, Hudson and Greenman 1998).

Plant strategies and plant community structure

Most plant communities are dynamic with continuous local disturbances followed by a relatively long succession process, where plant species have to be able to re-colonise a local area (Rees et al. 2001). Early-successional plant species typically have a series of correlated traits, including high fecundity, long-distance dispersal, rapid growth when resources are abundant and slow growth and low survivorship when resources are scarce. Late-successional species usually have the opposite traits, including relatively low fecundity, short dispersal distances, slow growth, and an ability to grow, survive, and compete under resource-poor conditions (Grime 2001, Rees et al. 2001). It has been hypothesised that much of the plant species diversity among plant communities is controlled by a trade-off between the ability to colonise new habitats and the ability to compete for resources. In plant communities there tend to be considerably more small seeded plant species than large seeded plant species suggesting, in concert with some seed addition experiments, that many plant species are limited by their ability to colonise new habitats (Rees et al. 2001).

As discussed above, the invasion criteria of different spatial plant strategies of plants with a simplified life history may be investigated by describing the changes in mean densities and average covariances in a spatial explicit model (Bolker and Pacala 1999). If plant species are divided into long-distance (globally) dispersing species and short-distance (locally) dispersing species, then only three different spatial strategies may invade under the assumption that the resident species has a slight competitive advantage (Table 4.6).

Example 4.5   Competition between two genotypes of *Arabidopsis thaliana* IV

Assume again that the two genotypes of *Arabidopsis thaliana* (*Nd-1* and *C24*) investigated in example 4.1 and 4.2 are the two only genotypes in the *A. thaliana* population and that the density of *A. thaliana* is not controlled by other plant species. Furthermore, assume that mortality is high and density-independent and that both genotypes have the same probability of reaching reproductive age.

One of the pathogens known to attack natural *A. thaliana* populations is the biotrophic oomycete *Peronospora parasitica* (Holub et al. 1994). The pathogen causes downy mildew, but the effects of the disease in natural plant communities are unknown. The pathogen *P. parasitica* grows on a wide range of crucifers (Dickinson and Greenhalgh 1977) and may be considered a generalist and it is here assumed that the local population size of the pathogen is constant on an ecological time scale. Genotype *Nd-1* is susceptible to *P. parasitica* isolate *Cala2*, and genotype *C24* is resistant to the isolate (Holub and Beynon 1997).

The competition experiment described in Example 4.1 was repeated in the greenhouse both in the absence of the pathogen and where each seedling was infected with about hundred *P. parasitica* (*Cala2*) conidia (Damgaard and Jensen 2002). The fecundity was estimated from
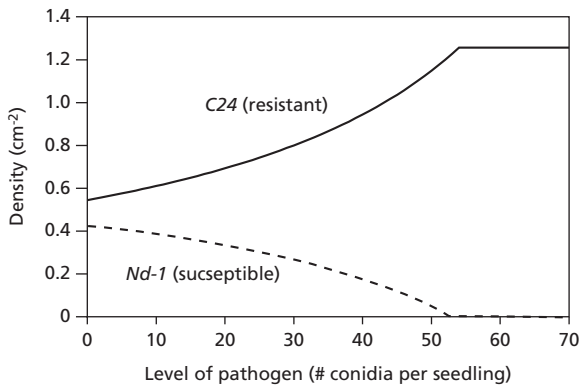

Fig. 4.5   Stable equilibrium densities (equilibrium 4.11d) of *A. thaliana* genotypes as a function of the pathogen level (h, measured in number of *P. parasitica* conidia per seedling) calculated using the maximum likelihood estimates of the competition model (Table 2) . The probabilities of reaching reproductive age were assumed to be 0.001.

dry weight data by linear regressions and fitted to competition model (4.9) with some a priori constraints on the parameter space since the disease had no effect on genotype *C24* (Damgaard 2003b). This experimental design is the minimum design required for applying the model. It would be beneficial to include more densities and proportions of the two species, and to include more levels of the pathogen (presence vs. absence data can hardly be described as a gradient). Nevertheless, the maximum likelihood estimates of parameters were used to predict the densities at equilibrium of the two *A. thaliana* genotypes as a function of the level of the pathogen (Fig. 4.5).

The statistical uncertainty of the estimated pathogen level when the susceptible genotype is just outcompeted at equilibrium was investigated using inequality (4.12) and Bayesian statistics (Fig. 4.6) and it is apparent that the degree of uncertainty of the pathogen level is high. A considerable part of the posterior distribution is outside the domain of the data (0-100 conidia per seedling) and the lack of certainty is probably due to the fact that there was only two pathogen treatments in the competition experiments. The results should therefore be interpreted with care.
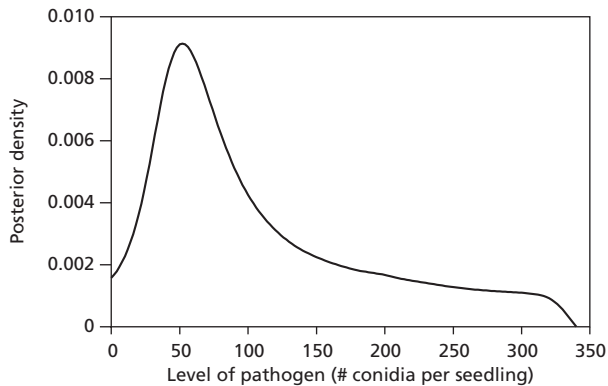

Fig. 4.6   Posterior distribution of the pathogen level (measured in number of *P. parasitica* conidia per seedling) when the susceptible *A. thaliana* genotype (*Nd-1*) is outcompeted by the resistant genotype (*C24*) assuming an uninformative prior distribution. The probabilities of reaching reproductive age were assumed to be 0.001.

Table 4.6 The invasion criteria of the four possible scenarios between an invading and a resident species with two possible scales of dispersing. Only three different strategies may invade if it is assumed that the resident species has a competitive advantage (Bolker and Pacala 1999).

		Resident species	
		Globally dispersing	Locally dispersing
Invading species	**Globally dispersing**	The probability that the invading species succeeds is adequately described by the mean-field model approximation.	A plant with a *colonisation strategy* may invade if the resident species has a clumped distribution.
	Locally dispersing	Both an *exploitation strategy*, where plants quickly exploits the limiting resource, and a *tolerance or phalanx strategy*, where plants are benefited in the inter-specific competitive interactions by an increase in the local density of conspecific plants, may invade.	The invading species may be present in local patches.

The three spatial strategies in Table 4.6, which may invade a habitat even if they are competitively inferior to a resident species, should not be confused with the CSR classification of plant strategies due to Grime (2001). In the CSR classification, it is assumed that the ecological success of different plant species in a habitat mainly is explained by the intensity of disturbance and the general productivity in a habitat (Table 4.7).

Table 4.7 The CSR classification of plant strategies (from Grime 2001). A plant species may have a variable amount of one of the three primary strategies which may de depicted in a De Finetti diagram (Grime's triangle).

	Productivity	
Intensity of disturbance	High	Low
Low	*Competitors*	*Stress-tolerators*
High	*Ruderals*	No viable strategy

In plant ecological research, the diversity of specific plant communities is often a central scientific question and predicting plant community structures by searching for possible community assembly rules since long has been a research goal in plant ecology. At least three research paths have been followed:

1) Either to test whether the species composition deviates from a specified null-model where species are assumed to be independent of each other (Conner and Simberloff 1979, Rees et al. 1996, Wilson et al. 1996).

2) To explain the species composition pattern by the ecology of different species groups (Weiher et al. 1998). If two plants species compete for the same limiting resources in a similar way, they are said to belong to the same functional type, which is a plant ecological term analogous to the guild or niche concept in the animal literature. The classification of plant species to functional types may be done by comparing either morphological and life history traits (e.g. Tilman 1997, Hooper 1998, Weiher et al. 1998), or the positions in the CSR classification or another strategy classification system (e.g. Westoby 1998). One hypothesis of a possible assembly rule of plant communities that has been tested is that the proportions between different functional types are constant (e.g. Wilson et al. 1996, Weiher et al. 1998, Symstad 2000).

3) Or analysing the stability properties of community matrices (Roxburgh and Wilson 2000b, a), which are matrices of the competition coefficients of n competing species:

$$C = \begin{pmatrix} 1 & c_{12} & c_{13} & \cdot & c_{1n} \\ c_{21} & 1 & c_{23} & \cdot & c_{2n} \\ \cdot & \cdot & \cdot & \cdot & \cdot \\ c_{n1} & c_{n2} & c_{n3} & \cdot & 1 \end{pmatrix} \quad (4.14),$$

and similar approaches (e.g. Law and Morton 1996).

As discussed previously, good quantitative predictions of the future states of plant communities are highly in demand (e.g. Keddy 1990). However, it is discouraging that the ecological conclusions typically reached when the above methods are tried on actual cases are very general and unspecific on answering questions such as what will happen and when will it happen. There is still a lot of work to do!