

3

Spatial Interactions among Grassland Plant Populations

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3.1 Introduction

The neighborhood perspective on plant interactions discussed in Chapter 2 shows the richness of processes in plant neighborhoods and how difficult it can be to obtain a detailed mechanistic understanding of them. Faced with this dilemma, plant ecologists have sometimes adopted a more phenomenological approach, which integrates over the known (and unknown) mechanisms by which neighbors interact, using a few neighborhood-dependent measures of plant performance. These measures are interaction coefficients, usually thought of as relating to competition between pairs of species.

In multispecies communities, competition coefficients can summarize a lot of information on the effects species have on one another and help ecologists to understand the spatial structures that develop over the course of time. This chapter describes

- how plant ecologists have tried to investigate competition in the field,
- what has been learned about plant competition coefficients from this field work,
- the information available about the structure of matrices of these competition coefficients, and
- how sensitive the outcome of competition is to the initial spatial pattern.

We focus on grassland communities. These communities are almost ideal for studying the significance of spatial pattern for ecological processes because they are patchy and approximately two-dimensional. In fact, the appearance of patchiness is more complicated than it might seem at first. Borders between patches that look well-defined from a distance can turn out to be quite diffuse when viewed more closely. Patches of one species frequently overlap patches of another, and the canopies of different species

can be intimately mixed (Watkins and Wilson 1992; Chapter 4), especially in species-rich communities. It is our impression that patches are more discrete and individuals overlap less in communities of modular organisms that lack roots, such as lichens and bryozoans. The lesson seems to be that if you want to be discrete, life must remain superficial!

One reason for the complexity of spatial structure in perennial grasslands is that, strictly speaking, they are not two-dimensional. Functioning connections in the soil can stretch between ramets (effectively, rooted branches) that appear unconnected above ground; structurally it is better to think of a perennial grassland as a forest buried up to its canopy in soil than as a two-dimensional surface. It is possible that annual communities (Wu and Levin 1994; Moloney and Levin 1996; Rees *et al.* 1996) fit a two-dimensional model better than perennial ones. However, in this chapter we only discuss the latter, and it should be kept in mind that an assumption of two-dimensionality can be no more than a rough approximation to such communities.

3.2 Methods for Measuring Competition in the Field

Definitions of competition tend to be contentious, but we shall use the operational definition that competition is an interaction between neighboring plants in which each suppresses the other's performance (i.e., how well it grows). It is helpful to distinguish between two components of a species' behavior when in competition with neighbors. Each species has an *effect* on its competitor and a *response* to competition from its neighbor (Miller and Werner 1987). The effect on its competitor is actually the same as the competitor's response, so it is enough to measure the responses of both species to determine their interaction. However, competitive effect and response of a single species when it interacts with a neighbor need not be correlated: an interaction may be asymmetric, such that one species exerts a much greater effect than its neighbor. Only when effect and response are both negative is the interaction a genuinely competitive one.

The experimental literature on interactions between herbs, many of which are grassland plants, is voluminous. However, the literature *relevant* to understanding the dynamics of spatial structure in plant communities is quite small for two reasons. First, most grasslands only remain grasslands if they are mown, grazed, or burned. Therefore the majority of the literature, which reports interactions between plant species in pots in glasshouses, ignores important aspects of reality in the field. Second, field experiments often have time scales so short that they deal only with the performance of

individual plants, not with the effects of competition on population dynamics. At the very least, experiments need to be run long enough for some population turnover of plants in the experimental mixture to occur. Otherwise, one must make untested assumptions about how short-term effects of competition upon *performance* translate into longer-term effects upon population *dynamics* and spatial structure.

The standard method for measuring competition between grassland plants in the field is to remove one or more neighbors from around a “target” individual and to observe the target’s response compared with that of a control individual whose neighbors are left in place. Alternatively, plants can be added to the neighborhood around a target; however, in practice this is much more difficult to achieve than neighbor removal, because planting is likely to damage the target’s roots.

A target’s response to the manipulation of its neighbors can be measured in a variety of ways. The most common method is to harvest target plants at the end of the experiment and compare their dry weight with that of control plants (see Box 3.1). This method does not explicitly measure how a target plant’s occupancy of space changes in response to competition from neighbors, even though any increase in plant size due to neighbor removal is likely to mean the plant occupies more space.

If we are interested in how plants compete for space, then it makes sense to measure directly how occupancy of space is affected by competitors. However, a removal experiment is not necessarily the best method for determining this effect. The degree to which a target plant occupies the space left vacant by a neighbor that has been artificially removed is a measure of how well the target invades bare space, but invading bare space is not the same as capturing space from a neighbor. For example, white clover (*Trifolium repens*) is a creeping plant that is good at invading bare ground but poor at invading moderately tall grass (Thompson and Harper 1988). From the point of view of competition for space, what is really of interest is how well white clover can invade other species and how well it resists displacement by other invaders. These questions can be addressed by monitoring the spatial distributions of plants in a community at a fine scale over a long period and calculating species-by-species replacement rates (Law *et al.* 1997), or by experimentally creating interfaces between monospecific patches of different species and recording how plants move across the interface (Silvertown *et al.* 1994).

The advantage of measuring competition in terms of the space neighbors capture from each other is that the spatial consequences of the interaction

Box 3.1 Nonspatial measurement of competition

A variety of models have been used to estimate interspecific competition coefficients from plant performance in nonspatial experiments. If the total weight of plant material reaches an asymptote as density rises, then a simple relationship that often fits experimental data well is the reciprocal yield model (Wright 1981; Spitters 1983). For a mixture of two species i and j , the mean weights w_i , w_j of the plants under competition are

$$\frac{1}{w_i} = B_{i0} + B_{ii} N_i + B_{ij} N_j , \quad (a)$$

$$\frac{1}{w_j} = B_{j0} + B_{jj} N_j + B_{ji} N_i , \quad (b)$$

where B_{i0} and B_{j0} are the reciprocals of mean plant weight when competitors are absent (i.e., have been removed) for species i and j , respectively; B_{ii} and B_{jj} measure intraspecific competition; B_{ij} and B_{ji} measure interspecific competition; and N_i and N_j are the densities of species i and j , respectively. Competition coefficients are generally standardized so that the effect of species j on species i is expressed relative to the effect of species i on itself. Thus, competition coefficients (α , β) can be calculated from Equations (a) and (b):

$$\frac{B_{ij}}{B_{ii}} = \alpha \quad \text{and} \quad \frac{B_{ji}}{B_{jj}} = \beta , \quad (c)$$

where α is the competition coefficient for species j 's effect on species i and β is the competition coefficient for species i 's effect on species j . The effect of one species is the response of the other.

In principle it is straightforward to extend this to a multispecies community, giving a matrix B of all the pairwise responses (and effects). Row i of this matrix describes the different responses of i to its neighbor species; column j gives the different effects of neighbor species j on each species.

are explicit. The main practical problem is that measuring invasion requires clearly demarcated boundaries between species, which can be difficult to engineer between mature plants in the field. There is also an interpretational problem because invading another species across a boundary is not necessarily the same as capturing space at its expense. Even when a species is at equilibrium density in monoculture, physical space exists between shoots that in theory can be penetrated by a smaller neighbor – in effect, this is invasion without displacement of the resident territory holder. If two species are able to interdigitate physically, then an invading species may occupy more space than the resident loses. Only when the competition

coefficient (see Box 3.1) is equal to 1, and species are thus effectively identical to one another, do gains and losses of space balance. Ideally, then, one needs a measure of the space lost by the invaded species (which we term its *displacibility* due to competition) and a measure of that taken by the invader (the invader's *invasiveness*), because the two quantities may not be the same. (The loser's *invasibility*, however, is equivalent to the invader's *invasiveness*.) So few experiments on spatial competition have been conducted (see Section 3.3) that there is not yet a standard way to conduct or analyze this type of experiment; Box 3.2 makes some suggestions on how to proceed.

3.3 Results of Field Experiments

In this section, we look in turn at experiments where the effects of competition were measured in terms of performance and experiments that explicitly measured the effects of neighbors on each other's occupancy of space.

Experiments on effects of neighbors on performance

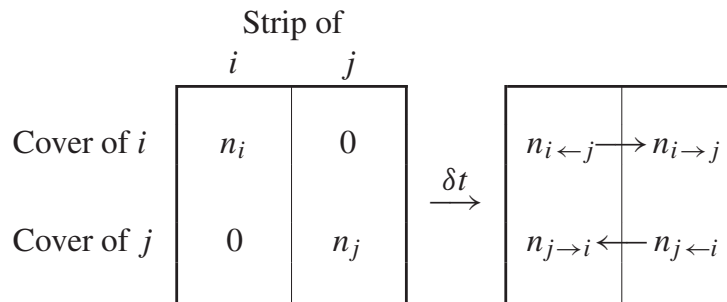
Goldberg and Barton (1992) reviewed field experiments on interspecific competition between plants. Among the 101 experiments they examined, by far the most common (76 cases) test of interaction between species involved removal of neighbors from around a target plant whose growth was then compared with that of control plants. In the other experimental designs, one or more species were planted in the field to manipulate relative or absolute densities of competitors. Some of the studies did not test responses for statistical significance, but 79% of those that did found neighbor presence or abundance to have a negative effect on the target, and 18% found some positive effects on the target.

The commonness of negative interactions is no surprise, as all plants require more or less the same resources and thus compete with one another when in physical proximity. A plant must acquire and hold onto space in order to gain access to resources such as light, water, and the mineral nutrients obtained from soil. Some partitioning of space into different niches might be possible – for example, if plants can divide space by placing their roots at different soil depths or if short species can tolerate conditions in the shade of taller ones – but there seem to be far fewer such niches than there are species in most plant communities.

Nonetheless, neighbors sometimes have positive effects on each other (Box 2.1), and the mechanisms that lie behind such interactions require further study (Callaway 1995). One such mechanism that is potentially

Box 3.2 Measurement of competition through occupation of space

There is not yet a consensus on how spatial competition experiments should be carried out. This box suggests a protocol based on monocultures of species i and j placed side by side so that each can invade the other. The basic arena comprises a strip of each species, and the region of interest is close to the boundary between them.



Here, n_i and n_j are the cover of species i and j , respectively, at the start; after a period δt has elapsed, $n_{i \rightarrow j}$ is the cover of species i in j 's territory and $n_{i \leftarrow j}$ is the cover of i in its original territory (which changes as a result of invasion by j). Two simple measures of the interaction as experienced by species i are as follows:

$$\text{rate of invasion of } i \text{ into } j: \frac{\delta n_{i \rightarrow j}}{\delta t} = \frac{n_{i \rightarrow j}}{\delta t},$$

$$\text{rate of displacement of } i \text{ due to invasion by } j: \frac{\delta n_{i \leftarrow j}}{\delta t} = \frac{n_i - n_{i \leftarrow j}}{\delta t},$$

$$\text{with net rate of change of } i \text{ with } j: \frac{\delta n_{i \rightarrow j} + \delta n_{i \leftarrow j}}{\delta t}.$$

Elaborations on this theme would entail controls for changes in cover that occur irrespective of the presence of the other species and measures expressed per unit cover. Because the spread into each other's territory takes place gradually, the boundary strip in which measurements are made should be made long and thin.

relevant in grasslands (because of the importance of herbivory) is that plant species that are well-defended against herbivores provide refuge for more palatable species growing in their immediate vicinity (Atsatt and O'Dowd 1976). There are some examples of such a mechanism operating with insect herbivores (Pfister and Hay 1988), but the mechanism runs counter to experience in grasslands grazed by vertebrates. Plants that are poisonous to vertebrates, such as ragwort *Senecio jacobaea*, thrive under the heaviest grazing pressures when all their competitors are removed: rabbits simply graze all other plants from around them. Sheep, too, can graze in a

very fine-grained manner, but can the smell of a poisonous plant protect its neighbors from these grazers? An experiment by Launchbaugh and Provenza (1993) suggests that this is unlikely. They found that sheep would not persistently avoid food that smelled aversive if it did not also taste of a toxin. In other words, there is no refuge for a palatable species in the chemical neighborhood of an unpalatable one. Contrary results have been found with woody plants that have physical defenses against herbivory such as spines. Watt (1919) reported that spiny holly and brambles provided refuge from herbivory that facilitated the regeneration of oaks, and Hjalten *et al.* (1993) have described a case where hares attacked birch trees less often when the trees were mixed with less palatable woody species. It is probably too early to rule out the existence of associative defense from vertebrate herbivores among grassland plants because too few field experiments have investigated the combined effects of competition and herbivory in grasslands.

In view of the fact that most grasslands only continue to exist by virtue of mowing, grazing, or burning, it is important to design field studies of competition so that the effects of these processes can be determined. Yet, in their survey Goldberg and Barton (1992) found only eight studies where competition and herbivory were combined in a factorial design, none of which were performed in grasslands even though both these processes are important in this kind of vegetation. To this list we can add an experiment we carried out in a seminatural grassland at Little Wittenham, England (Bullock *et al.* 1994; Silvertown *et al.* 1994). We outline this experiment in some detail in the next subsection because the experiment deals explicitly with spatial invasion of one species by another and because the results are used in a simulation model described later in this chapter.

Experiments on space occupancy by neighbors

The seven studies we know of that have explicitly looked at mutual invasion between grassland species are listed in Table 3.1. All of them can be improved upon and all leave some important questions unanswered. For instance, a common design, used in more than half the studies, was a hexagonal plot sown as a monoculture and surrounded by a different species on each side. Hexagonal plots were usually closely packed, producing a tessellated arrangement. The problem with this design is that the plots are not statistically independent of each other, and two invaders of a third species may soon begin to interfere with one another. Cellular automaton models (Silvertown *et al.* 1992) suggest that such higher-order interactions among

Table 3.1 Summary of spatial competition experiments on grasses.

Study	No. of species (grasses/dicots)	Design	Invasiveness and invasibility correlated?	Competition transitive?	Ranks altered by treatment?
Thórhallsdóttir (1990b)	5/1	6 × 6 species in hexagonal plots	No	Yes	–
Turkington (1994)	6/0	6 × 6 species in hexagonal plots	Positively in 1 treatment	No	Yes
Wedin and Tilman (1993)	4/0	4/6 possible pairwise combinations	No	Probably	Yes
Marshall (1990)	7/0	1 × 6 species in hexagonal plots	Fourfold range in invasibility among 6 species	–	–
Van Andel and Nelissen (1981)	2/5	Hexagonal plots	No	Cannot tell	–
Stewart and Potvin (1996)	3/1	Mapped plants in mixture	Positively in some treatments	Yes	Yes
Silvertown <i>et al.</i> (1994)	4/0	All species pairwise	No	Yes	Yes

three or more species may be important, but in experiments like those listed in Table 3.1, where interactions are assumed to be pairwise, they could make interpretation difficult.

Our own experiment (Silvertown *et al.* 1994) was designed to avoid the problems of nonindependence and unplanned higher-order interactions and to determine the effect of grazing upon spatial competition. We performed the experiment in a seminatural grassland, examining the mutual invasion of all possible pairs of four perennial grass species. The competition experiment was nested within a replicated sheep grazing experiment that imposed two levels of grazing in each of three seasons of the year (winter, spring, summer), factorially combined in a randomized block design to give eight different field environments (grazing treatments) in each of two replicate blocks. Grazing levels in winter and spring were determined by the presence or absence of sheep. Summer grazing levels were determined by adjusting sheep stocking levels to achieve mean sward heights of 3 cm or 9 cm. The vegetation in the experimental area was dominated by the grasses *Lolium perenne* and *Agrostis stolonifera*, but also contained about a dozen other grasses and a very low percentage cover of some 40 dicotyledonous species. Our mutual-invasion experiment used the grass species *Festuca arundinacea* (A), *Festuca rubra* (R), *Lolium perenne* (L), and *Poa pratensis* (P), in all pairwise combinations, and involved transplanting pairs of small, monoculture turfs into the native grassland so that each pair shared a common boundary over which invasions could occur. Over a year later, we counted the number N_{ij} of tillers of each species i that had invaded the neighboring turf of species j . Net invasion rates were calculated for each permutation of species i, j as $N_{ij} - N_{ji}$. (In the absence of more detailed information, these net rates assume that i 's gain in tillers in j 's neighboring turf is equal to j 's loss.) The rates are shown in Figure 3.1.

In so far as it is possible to generalize from this ragbag of experiments, three main results emerge. First, there is no clear tendency for the invasiveness and invasibility to be correlated (Table 3.1). The rare cases where there is a positive correlation suggest the existence of a gradient in mobility between species from the “stay-at-homes” (neither invasive nor invisable) to the “tramps” (invasive and invisable).

Second, competition is typically transitive, meaning that it is possible to rank the species by their net invasion rates in a strict pecking order. For example, in our experiment, the spring-grazed, 3-cm treatment shown in Figure 3.1 has the following pecking order of net invasion rates: $L > R > A > P$.

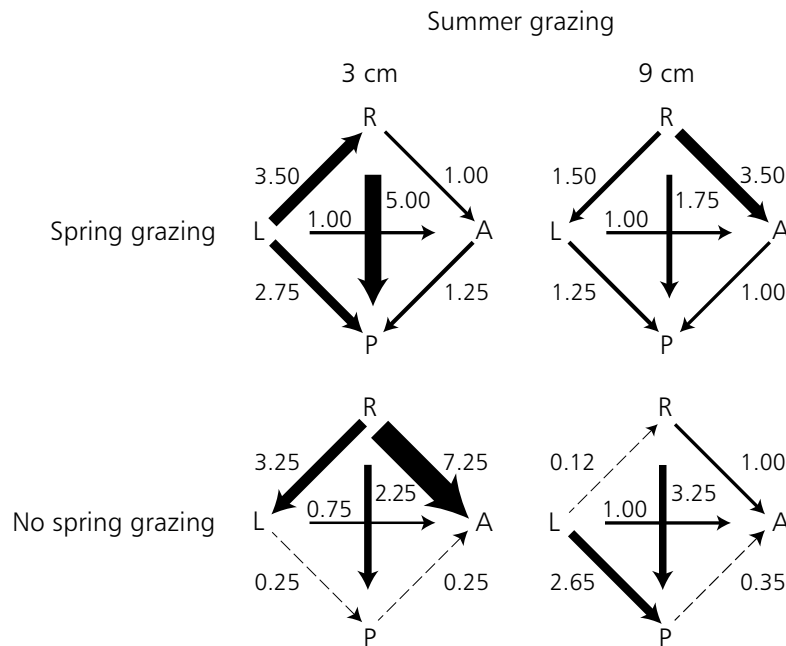


Figure 3.1 Net rates of tiller invasion between all pairwise combinations of four grass species under four different grazing regimes in a seminatural grassland. Abbreviations: A = *Festuca arundinacea*; R = *Festuca rubra*; L = *Lolium perenne*; P = *Poa pratensis*. Source: Silvertown *et al.* (1994).

Third, the rank a species has in a transitive competitive hierarchy depends on the grazing treatment. This is true, for instance, in our own experiment (Figure 3.1). Analysis of variance of square-root transformed tiller counts identified a significant interaction between spring and summer grazing treatments affecting invasion rates. For example, Figure 3.1 shows that net invasion rates between L and R were reversed by spring and summer grazing treatments.

Caveats

Clonal plants (see Box 2.2) vary greatly between and even within species in the degree to which they invade the space around them. Lovett Doust (1981) introduced the terms “guerilla” for plants that send out long stolons and “phalanx” for those that place new ramets near the parent. There is a continuum of variation between these two extreme types of clonal morphology.

It might seem inevitable that such differences in morphology will have major consequences on space capture in the field. But the following example of two herbs suggests that matters are not necessarily so simple. Schmid and Harper (1985) compared the responses of a phalanx species (*Bellis perennis*) and a guerilla species (*Prunella vulgaris*) to the presence

Table 3.2 Competition matrix for five species in a weedy old-field community. Numbers given are growth of target species over a season in pairwise mixture relative to growth of target in monoculture. *Source:* Miller and Werner (1987).

Target species	Neighbor species				
	<i>Ambrosia</i>	<i>Agropyron</i>	<i>Plantago</i>	<i>Trifolium</i>	<i>Chenopodium</i>
<i>Ambrosia artemisiifolia</i>	1.00	0.94	1.03	1.02	1.04
<i>Agropyron repens</i>	0.37	1.00	0.86	0.95	1.16
<i>Plantago lanceolata</i>	0.23	0.36	1.00	1.08	0.73
<i>Trifolium repens</i>	0.22	0.27	0.67	1.00	0.90
<i>Chenopodium album</i>	0.08	0.16	0.43	1.15	1.00

or absence of the other. In mixture there was evidence of a slight but significant difference in density-dependent growth (number of modules per plant) of the species, with *Bellis* favored at high densities and *Prunella* favored at low densities. In the light of such a difference, one might expect the planting arrangement of species to influence interspecific competition between them, but no such influence was found. This suggests that slight differences in how species capture space may have undetectable consequences in the field, where many other factors impinge upon interactions between species. The species differed in how they recolonized bare ground, with *Prunella* doing so almost exclusively by clonal growth and *Bellis* recolonizing twice as many gaps by establishment from seed as by clonal growth (Schmid 1985). The colonization of gaps is a significant spatial process in grasslands, but beyond the scope of this chapter.

3.4 Competition Matrices

Competition matrices provide a convenient summary of the information on pairwise interactions (including competition) obtained by field experiments (Box 3.1). An example of such a matrix is shown in Table 3.2; this matrix is based on five species at an early stage of succession in an old-field community (Miller and Werner 1987). The information in such matrices plays an important part in spatio-temporal modeling of communities, because it is these interactions that couple the dynamics of different species. Depending on the structure of the matrices, we may find spatial patterns developing that are homogeneous or heterogeneous in space, including exotic kinds of behavior such as the spirals described in Chapter 10. It is important for theoretical work to be properly informed about what is known (and not known) empirically about these matrices.

Competition matrices are few, and complete matrices for whole communities are unknown. However, the pairwise field competition experiments

in the literature might be representative of the interactions one would find more widely within a single community. In any case, this is all the information there is to go on at present. Sparse though the data are, two features of competition matrices stand out: their transitivity (Shipley 1993) and the lack of difference between intra- and interspecific interaction strengths.

Transitivity

A competition matrix is transitive if each species can be unambiguously assigned a rank in a competitive hierarchy. Keddy and Shipley (1989) and Shipley (1993) surveyed studies where several species were combined in pairwise competition experiments and concluded that transitivity was the rule. However, Goldberg (1997) pointed out that this survey did not distinguish between hierarchies of effect of competition (ranking down the columns of the matrix) and hierarchies of response (ranking across the rows of the matrix). She surveyed field and non-field experiments, testing for concordance in the hierarchies of effects and responses. Under standardized environmental conditions, 80% of response hierarchies (12/15 cases) and 66% of effect hierarchies (14/21 cases) showed evidence of consistent transitivity; these findings are in approximate agreement with those of other authors. (The matrix in Table 3.2, for example, has consistent hierarchies, both for response and effect.) But hierarchies often changed from one environment to another: 41% of response hierarchies (9/22) and 50% of effect hierarchies (7/14 cases) were contingent upon environmental conditions.

One reason why transitive competition is important is that, in an unvarying environment, it should lead to the exclusion of all other species by the topmost species in rank. This is in contrast with intransitive networks of the form $A > B$, $B > C$, $C > A$, etc., in which coexistence of the species may be possible (Karlson and Jackson 1981). How plant species come to coexist is a long-standing issue in ecology (Silvertown and Law 1987), and it is evident that the transitivity of competition matrices does not help to resolve it. However, it may be premature to reach firm conclusions: the mosaic cycles described in Chapter 4, in which there is a cyclic sequence of states within patches of vegetation, although not quantified to the level of competition matrices, appear to be driven by intransitivities.

Intra- versus interspecific competition

The relative magnitude of interactions within and between species is also important in the context of species coexistence. In Lotka–Volterra competition models, the coexistence of competitors is expected if intraspecific

competition is stronger than interspecific competition, particularly when species are aggregated. Yet, there is no clear indication of diagonal dominance in competition matrices. A lack of diagonal dominance is evident, for example, in Table 3.2: growth is in some cases much more limited by heterospecifics than conspecifics. This is in agreement with Goldberg and Barton's (1992) conclusion that "The very limited field evidence available for coexisting species thus suggests that conspecifics do not usually compete more strongly than heterospecifics."

Competition matrices determined from traits of species

Faced with the great difficulty of estimating competition matrices from manipulation experiments in the field, it would obviously be helpful to find other ways to proceed. Ultimately, one might hope to specify the structure of the competition matrix simply from knowledge of the relevant traits of the species in the community, but we are some way from being able to do so at the moment. Indeed, the first question to ask is whether it is reasonable to expect to be able to predict competitive outcome from species' traits (Goldberg 1997). Recent progress in the study of plant life histories suggests a qualified "yes" in answer to this question. Evidence is accumulating that life-history variation in plants has a single major axis with many traits correlated with lifespan (Silvertown *et al.* 1993; Condit *et al.* 1996; Franco and Silvertown 1996; Grime *et al.* 1997). If many important traits are strongly correlated with one another, the likelihood that they will include traits that influence competitive outcome is great, because competitive ability has important effects on fitness. If life-history traits including those influencing competitive ability have a simple correlation structure, then predicting competitive outcome should only require knowledge of a limited number of trade-offs.

Two obvious qualifications that could prevent the use of traits to predict competitive outcome are that (1) species are genetically variable for traits that affect competitive ability and (2) the fitness conferred by any trait is environment dependent. If trait correlations within species are the same as trait correlations between species, then the first problem can be circumvented simply by treating genotypes rather than species as the taxonomic unit. The second problem cannot be circumvented but can be accommodated by defining how the fitness of traits changes along environmental gradients.

A study by Sugiyama (in press) is interesting in this context. Sugiyama investigated how varietal differences within three species of grasses

(18 cultivars of *Dactylis glomerata*, 15 cultivars of *Lolium perenne*, 5 cultivars of *Festuca arundinacea*) influenced the outcome of competition against a standard cultivar of another species. When the cultivars were grown in monoculture, no differences among cultivars in yield per unit area were found. Although the cultivars differed in mean tiller densities, such differences were counterbalanced by tiller weights so that the yields were the same. However, when the cultivars were grown in interspecific mixture with a standard cultivar of another species, they varied hugely in their final yields. After two years in mixture with *Festuca*, the yield of *Dactylis* cultivars varied from 40–84% of the total yield of the mixture, and the yield of *Lolium* cultivars in mixture with *Dactylis* varied from 54–90%. *Festuca* also showed large differences in proportion of final yield among five cultivars (11–43%). In all three species there was a significant relationship between the mean tiller weight of cultivars and the relative contribution of that species to the yield of the mixture. However, the form of the relationship was different in each species: in *Lolium* it was linear and positive, in *Dactylis* it was parabolic with a maximum at 120 mg mean tiller weight, and in *Festuca* it was parabolic with a maximum at 50 mg tiller weight.

The differences Sugiyama observed between species could be explained in terms of two relationships involving tiller size: (1) regrowth after defoliation and (2) competitive ability. Defoliation took the form of periodic clipping of the plots. Regrowth after defoliation declines with tiller size, but competitive ability increases with tiller size. Under light clipping and high soil fertility, cultivars with large tillers were favored, but a complete competitive reversal (favoring small tillers) was achieved by Sugiyama and Nakashima (1995) through heavy clipping or low soil fertility. This work is the most convincing demonstration that we know of that competitive outcome might be predicted from the traits of the species concerned.

Aarssen (1983) suggested that genetic variation for competitive ability within species might lead to intransitive competitive relationships between species and thus provide a mechanism for coexistence. We know of no formal theoretical model of this mechanism, so it is not clear under what assumptions it would work. However, clearly one necessary condition is that competitive ability should vary greatly among genotypes, and Sugiyama's experiments as well as much earlier work (Charles 1964) suggest that it does. It is not so clear, however, whether there is sufficient genetic variation for competitive ability *within* neighborhoods (Taylor and Aarssen 1990), although if grassland plants are very mobile it is possible that the genotypic composition of neighborhoods changes with time.

Box 3.3 Estimation of transition matrices from an invasion experiment

Numbers of tillers N_{ij} of each species i invading each other species j were determined from a field experiment in a seminatural grassland described in Section 3.3. Tillers of the four species in the experiment were of different sizes and occupied different amounts of space, so values of N_{ij} were converted to the proportion of space occupied by species j taken by species i using the formula

$$a_{ij} = N_{ij} (Cn_i)^{-1} ,$$

where n_i is the density of tillers of species i in monoculture as determined at the start of the experiment and C is the area available for invasion, which we estimated to be a strip 10 mm wide and 80 mm long along the turf border. Note that this conversion from N_{ij} to a_{ij} assumes that the space occupied by species i must be equal to the space lost by species j , though this assumption is not necessarily correct (see Section 3.2). Values of a_{ij} for all i, j formed the elements of a transition matrix A of dimension (4,4) summarizing spatial interactions (replacements) between species sharing a common border. Elements (a_{ii}) in the leading diagonal of this matrix were set to 1.

The competitive relationships among the four species were transitive in all five transition matrices representing different patterns of grazing. That is, in each case the species could be unambiguously ranked in terms of the proportion of available area captured from each other in one iteration of the model with a random starting arrangement. These hierarchies are shown at the bottom of Table 3.3 and are different from those in Figure 3.1 [which are based on tiller numbers given by Silvertown *et al.* (1994)] because of the transformation of tiller numbers into proportion of area captured necessary for the model.

3.5 Community Consequences of Spatial Interactions

The transitivity of competition matrices that emerges from field experiments might be thought to imply that the highest-ranking species in a competitive hierarchy should always displace those of lower rank from the community. However, this ignores spatial structure: once the spatial component of community dynamics is taken into account, it is not so obvious that the highest-ranking species has an immediate advantage. The aggregation of species, and their pattern of juxtaposition, may radically alter the outcome of competition over the medium term (Silvertown *et al.* 1992).

Below, we show that the initial spatial configuration of a community matters greatly for the dynamics of communities with transitive

competition matrices. We do this by means of a cellular automaton model, in which the transition probabilities of cell states are given by the results of our spatial invasion experiment, described in Section 3.3 and Figure 3.1.

A cellular automaton model

The model was based on a lattice of 40×40 square cells, with synchronous updating and a von Neumann (four-cell) neighborhood. Because it is more realistic to think of a finite spatial region for the patchy environments and communities found in nature, we used absorbing boundaries instead of the periodic boundaries often used in the theoretical literature.

At any time t a cell could be occupied by one of the four species in Figure 3.1. At time $t + 1$ the species in a cell had a chance of being randomly invaded and replaced by one of the neighbors present at time t in one of the four immediately adjacent cells. Replacements of one species by another occurred according to transition probabilities derived from invasion rates measured in the field experiment (see Section 3.3 and Box 3.3). Five transition matrices were used: an overall matrix based on mean invasion rates across the whole grazing experiment and transition matrices based on invasion rates in each of the four combinations of spring and summer grazing (Figure 3.1).

To provide some contrasting initial spatial patterns, we aggregated the species into monospecific bands and placed the bands in each of the 12 possible orders shown in Table 3.3; we also used a spatially random initial configuration. Each species started with the same total abundance of 400 cells regardless of the initial pattern. For each of these 13 patterns and 5 transition matrices, we ran 10 realizations of the cellular automaton model to predict the composition of the community after 500 iterations (notionally 500 years).

Effects of initial spatial configuration

For all five matrices, random initial arrangements of competitors led to the rapid extinction of all species except the first in rank (Table 3.3). In contrast, when species were initially aggregated in bands, the outcome depended strongly on how the bands were ordered. Replicate runs were reasonably consistent, thus by comparing how the survival of lower-ranked species varied with the initial arrangement of species, a set of parsimonious rules for survival in each grazing treatment can be deduced. Table 3.4 gives these rules in terms of the juxtaposition of species required for survival. The main features to note about the results are as follows.

Table 3.3 Results of a cellular automaton model on grasses. The results show initial banding arrangements of four species of grasses (R, L, A, P) and the species surviving after 500 iterations. See Figure 3.1 for species names. The model was based on an invasion experiment in a seminatural grassland described in Section 3.3. The most common result is given; the number of runs in which it occurred out of 10 is shown in parentheses. Surviving species are listed in the standard order RLAP, with each dash indicating an extinction. Grazing treatments are as follows: (1) summer grazing to mean sward height of 9 cm, no spring grazing; (2) summer grazing to mean sward height of 9 cm, spring grazing; (3) summer grazing to mean sward height of 3 cm, no spring grazing; (4) summer grazing to mean sward height of 3 cm, spring grazing.

Initial banding	Species surviving in each grazing treatment				
	Mean over whole experiment	(1)	(2)	(3)	(4)
RLAP	RLAP (10)	RLAP (10)	RLAP (9)	R - - P (10)	- LA - (7)
RLPA	RLA - (9)	RLA - (10)	RLA - (8)	R - AP (10)	- LA - (10)
RALP	RL - - (10)	RL - - (8)	RL - P (9)	R - - P (9)	RLA - (10)
RAPL	RL - - (10)	RLA - (5)	RL - - (8)	RL - P (10)	RLA - (10)
RPLA	RLA - (10)	RLA - (9)	RLAP (5)	RLAP (8)	- LA - (10)
RPAL	RL - - (10)	RL - - (6)	RL - - (7)	RL - P (9)	RLA - (10)
LRAP	RL - P (6)	RLAP (10)	RL - P (8)	R - - P (10)	- LA - (6)
LRPA	RL - - (7)	RLA - (8)	RLA - (6)	R - AP (8)	- LA - (8)
ARLP	RL - - (10)	RLA - (10)	RL - P (9)	R - - P (10)	- LA - (10)
ARPL	RL - - (10)	RLA - (10)	RL - - (6)	RL - P (10)	- LA - (6)
PRLA	RLA - (10)	RLA - (8)	RLAP (9)	R - - P (6)	- LA - (10)
PRAL	RL - - (10)	RL - - (9)	RL - P (10)	R - - P (6)	RLA - (10)
Random (unbanded)	- L - -	- L - -	R - - -	R - - -	- - A -
Competitive rank in transition matrix	L > R > A > P	L > R > A > P	R > L > A > P	R > P > L > A	A > L > R > P

Table 3.4 Results of a cellular automaton model on grasses. The results show initial banding arrangements needed for the survival of grass species after 500 iterations. See Figure 3.1 for species names. The term x denotes an allowable position for any species not identified by name. For example, xRxLxAx for target species A indicates that A will survive as long as the bands are ordered R, L, A, at the start; the fourth species P may be present anywhere (or absent altogether) without affecting the survival of A. In the column labeled “Ranks,” species are replaced with their competitive ranks in the underlying transition matrix. See Table 3.3 for explanation of grazing levels.

Target species		Initial banding patterns by species	
Rank	Identity	Identities	Ranks
Overall matrix			
1	L	xxxx	xxxx
2	R	xxxx	xxxx
3	A	xRxLxAx	x2x1x3x
4	P	xxAP*	xx34
(1) Grazing: Summer to 9 cm, no spring grazing			
1	L	xxxx	xxxx
2	R	xxxx	xxxx
3	A	xxxA or xxAP	xxx3 or xx34
4	P	xxAP	xx34
(2) Grazing: Summer to 9 cm, spring grazing			
1	R	xxxx	xxxx
2	L	xxxx	xxxx
3	A	xRxLxAx	x1x2x3x
4	P	xxxP	xxx4
(3) Grazing: Summer to 3 cm, no spring grazing			
1	R	xxxx	xxxx
2	P	Not xxRP*	Not xx12
3	L	xRxPxLx	x1x2x3x
4	A	xRxPxA*	x1x2x4
(4) Grazing: Summer to 3 cm, spring grazing			
1	A	xxxx	xxxx
2	L	xxxx	xxxx
3	R	xLxAxRx*	x2x1x3x
4	P	xxAP*	xx14

*Survival does not occur in every run with these conditions.

First, the aggregation of conspecifics into bands clearly increases the length of time to extinction. Even though the competitive relationships were transitive, aggregation provided a spatial refuge for weaker competitors and permitted their survival in the medium term (Silvertown *et al.* 1992). Although ultimately weaker species were excluded, survival for an estimated 500 years suggests a delay that could be of considerable ecological significance. Few communities remain unperturbed by disturbance

or environmental change for 500 years. In a community where species are finely mixed, and indeed overlapping (e.g., Roxburgh *et al.* 1993), indirect effects such as apparent mutualism may further delay the elimination of weak competitors (Lawlor 1979; Stone and Roberts 1991).

Second, because different grazing treatments alter the relative invasiveness and invasibility of species and hence their competitive ranks, they produced different outcomes from the same initial conditions. This is as one might expect from the differences in competitive hierarchy already noted in Figure 3.1, but the effects are made considerably more complicated by the initial spatial configuration of the lattice.

Third, a species' rank in the competitive hierarchy is not a sufficient basis for predicting how the initial spatial configuration of neighbors will affect its survival. This can be seen by replacing the species names with their ranks in the five grazing treatments. One can then ask whether the rules are constant for a species ranked, say, third, regardless of which species actually occupied that position. Survival rules translated into ranks are shown in Table 3.4; if anything, they are less consistent than the rules based on the identity of species. However, our results do not totally escape generalization on the basis of ranks. As might be expected, species 1 (i.e., that with the highest competitive ability) survived any arrangement of its competitors. In four of the five matrices, species 2 also survived any arrangement of its competitors. For species 3, the identity rather than rank of the first and second species was important; location at an edge was not essential to survival. For species 4, location at an edge was always required if the species was to survive, often with a particular immediate neighbor but not necessarily species 3.

3.6 Concluding Comments

Here we briefly revisit the four main issues of this chapter. First, plant ecologists have developed various ways of manipulating local densities of individuals to investigate competition in the field. Second, these field experiments tell us that interspecific competition is widespread; positive interactions also occur, but have been little studied. Even more poorly understood are +/- relationships. Such interactions might seem unlikely between plants, but Schwinning and Parsons (1996a, 1996b) recently examined the interaction between the grass *Lolium perenne* and white clover (*Trifolium repens*) and concluded that the spatial and temporal dynamics are similar to those seen between predator (in this case, the grass) and prey (the clover). Evidently there are more kinds of interactions between grassland plants than might at first be imagined.

Third, the few studies that have looked at several species in a community allow one to make some preliminary comments about competition matrices. The matrices tend to be transitive, but species' ranks alter with treatments such as grazing and nutrient addition. This is true of studies measuring invasion as well as those simply measuring short-term performance, and it is a property that is important for modeling grassland communities as spatio-temporal processes. Even though a species' competitive rank is contingent upon a range of environmental factors, it seems possible that relative competitive abilities might be predicted from traits, given a sufficient knowledge of both the trade-offs between traits and the fitness consequences of different trait values in different environments. In grasses, tiller size seems to be a promising trait for use in predictions.

Finally, our exploration of the spatial dynamic consequences of different transitive competition matrices leads us to suggest that the spatial configuration of competing species imposes an extra level of complexity on the system so that knowledge of species' competitive ranks is not sufficient to predict the outcome, at least over the medium term.

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