

5

Competition

Up to this point in the book we have largely focused on the physical factors that control the structure and function of wetland communities: flooding, fertility, and disturbance. It is now time to consider biological factors. We begin here with **competition**. We will define competition as *the negative effects that one organism has upon another by consuming, or controlling access to, a resource that is limited in availability*. That is, it is an interaction in which both organisms experience a negative effect. Competition is widespread and important, although its importance depends upon the species or the habitat being considered. As just one of many possible examples consider the effects of competition upon common marsh plants (Figure 5.1). The effects of competition were measured by moving six species of plants into two sets of conditions: clearings (no competition) and intact vegetation (competition). In every case, the plants in clearings grew significantly better than the plants with neighbors. The difference in the height of each pair of histograms gives one measure of how important competition was for that species – in this case, *Pontederia cordata* seemed to be the weakest competitor, since it showed the greatest reduction in vegetated plots.

The basis of competition is lack of resources. All living organisms require a rather limited number of elements to make up their bodies (Table 5.1).

Some organisms will accumulate these resources at the expense of others, thereby reducing growth, survival, or reproduction of their neighbors. An experiment like that in Figure 5.1 does not tell us which resource(s) were the cause of the competition, merely that it occurred. In plant communities, light is a particularly common source of competition; for animals, it is often food.

Competition is a biological force that relentlessly drives wetland communities toward dominance by a few kinds of species. In particular, wetland plant communities rapidly become dominated by a few species, usually those best able to exploit light. Consider a few examples. Marshes often become dominated by large leafy rhizomatous species in genera such as *Typha*, *Phragmites*, and *Schoenoplectus*. Wet meadows become dominated by tall rhizomatous grasses such as *Calamagrostis canadensis* or *Phalaris arundinacea*, or by shrubs. Aquatic communities become dominated by floating-leaved species in genera such as *Nymphaea* and *Nelumbo*. Even swamps are often dominated by a few tree species – *Acer saccharinum* or *Taxodium distichum*. And then there are the invasive species which often spread precisely because of their strong competitive abilities. Aquatic communities are at particular risk from free-floating exotics such as water hyacinth (*Eichhornia crassipes*), giant salvinia

Table 5.1 Major elements required by living organisms and their functions

Element	Function
C	Structure; energy storage in lipids and carbohydrates
H	Structure; energy storage in lipids and carbohydrates
N	Structure of proteins and nucleic acids
O	Structure; aerobic respiration for energy release
P	Structure of nucleic acids and skeletons; energy transfer within cells
S	Structure of proteins

Source: After Morowitz (1968).

(*Salvinia molesta*), or water lettuce (*Pistia stratiotes*); all other wetland types are at risk for invasives that produce dense canopies. The growing list of woody invasives such as melaleuca (*Melaleuca quinquenervia*) shows how canopy-forming species can rapidly transform habitats (Section 13.5) and tend to produce monocultures across a wide array of habitats.

The objective of this chapter is to provide some principles to understand how competition structures wetland communities, how natural forces tend to generate plant diversity, and how many human interventions decrease plant diversity.

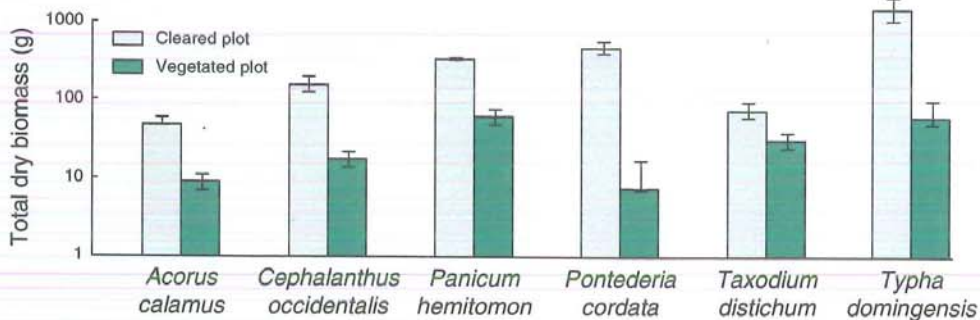


FIGURE 5.1 Competition has negative effects on plant growth, as illustrated by the difference in growth of six marsh plants when transplanted into cleared or vegetated plots in an coastal marsh. (Adapted from Gecho *et al.* 2007.)

5.1 Some examples of competition in wetlands

Before we delve into the details of the principles behind competition it will be helpful to consider a few specific examples and the experiments that have been used to study them.

5.1.1 Experiments are needed to detect competition

You cannot demonstrate that competition is occurring simply by making one-time observations of a wetland. Experiments are necessary. Hence, we have less evidence on the importance of competition than we do for physical factors. The design of experiments to detect competition and measure its impacts is a challenging topic that you will need to read about elsewhere (Underwood 1986; Keddy 2001). Here we will simply look at some examples that illustrate the types of experiments that have been done and what they tell us about the effects of competition in wetlands.

The basic approach to measuring competition is simple in principle – remove a species and measure whether any of the remaining species benefit – say with higher growth rates, higher survival rates, or more offspring. These kinds of experiments have been done. We will look at four groups that have been studied: plants, amphibians, fish, and birds.

5.1.2 Competition among plants

In Figure 5.1 you saw an experiment which looked at the effects of all neighboring plants combined. Often, experiments instead look at each pair of plants in isolation. Let us look at one such experiment conducted along the coast of southeastern North America. Selected plants were removed from wetlands, and then remaining species were monitored to see if any of them benefited from the removal. The study included both low marsh and high marsh. In the high marsh, *Spartina patens* was

removed, and in the low marsh, both *S. alterniflora* and *S. patens* were removed. The upper left panel in Figure 5.2 shows how to interpret such studies. Only one species, *Fimbristylis spadicifera*, showed a significant response to the removal of its neighbors! Apparently, competition was a weak force in this wetland.

The above study may have made a mistake by trying to look at too many species at once. Let us therefore look at a study involving fewer species, and more types of experimentation, but still in coastal marshes. In one part of this study, species were transplanted into situations with and without neighbors, and their performance was monitored. Performance was significantly lower when the plants had neighbors (Figure 5.3), showing that neighbors indeed had negative effects. The negative effects were much more dramatic than those in Figure 5.2. In general, competition severely reduced performance. Competition was important in both marsh zones (top *Juncus gerardi* zone, bottom *Spartina patens* zone). The one exception, *J. gerardi*, performed well even when transplanted into locations already occupied by other species, suggesting that *J. gerardi* is competitively dominant to both *S. patens* and *D. spicata*. This idea of competitive dominants and subordinates is one we to which we will return shortly.

Many invasive species are floating aquatics, including *Eichhornia crassipes* (water hyacinth), *Salvinia molesta* (giant salvinia), and *Pistia stratiotes* (water lettuce). The effects of floating-leaved aquatics are of particular interest because the competition has to be asymmetric – that is, a floating plants can shade a submersed one, but the reverse cannot occur (Keddy 1976). Consider the invasive *Hydrocharis morsus-ranae* (frog bit), which is spreading rapidly over ponds on my own property. To test for effects of competition from this species, Catling *et al.* (1988) anchored 70 circular 1-m² floating hoops in each of two study sites in eastern North America.

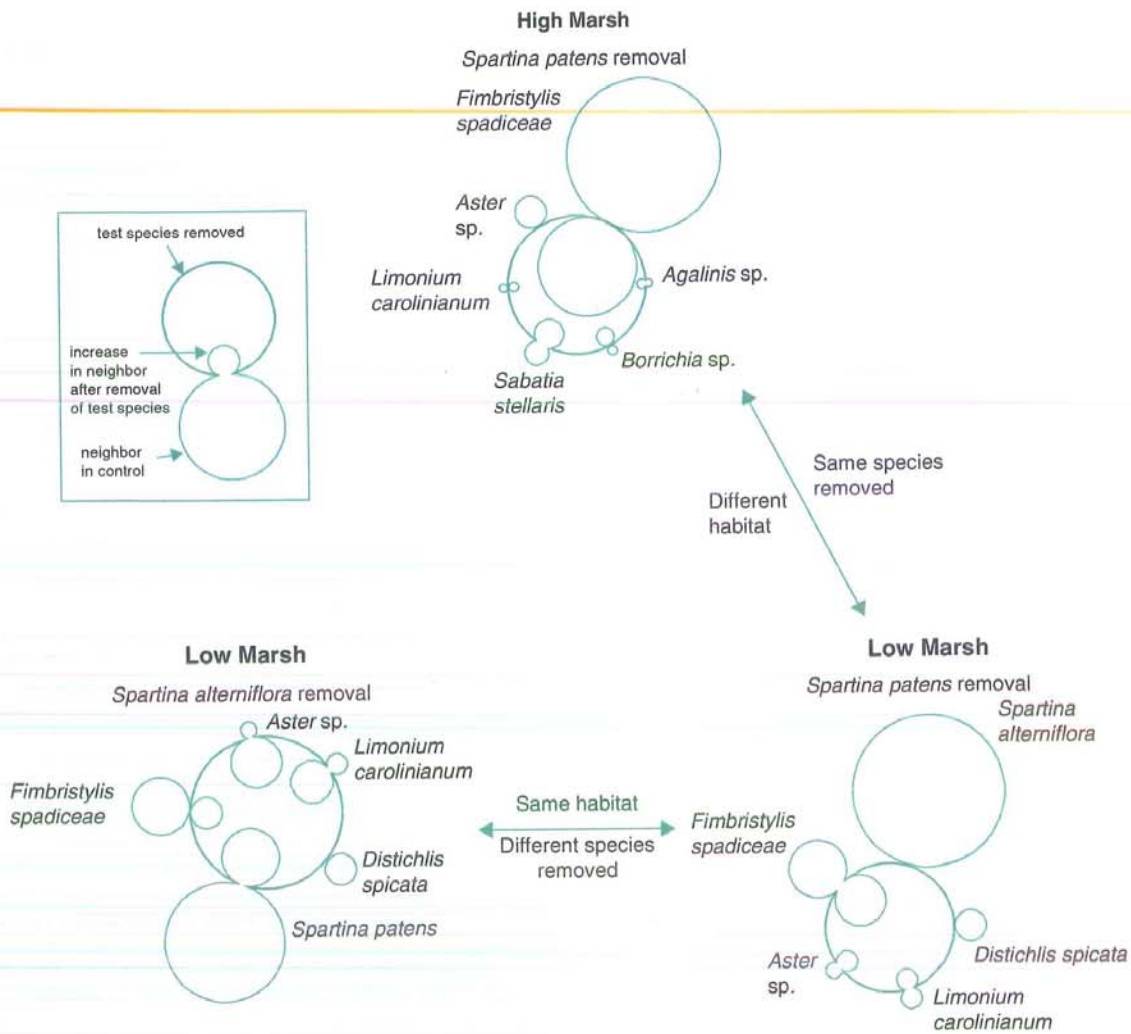


FIGURE 5.2 The results of a competitive release experiment among pairs of plants in a coastal wetland. Circle size is a measure of abundance either before or after the removals, as shown in the panel on the upper left. In this example, only the response of *Fimbristylis* was statistically significant. (From Keddy 1989 after Silander and Antonovics 1982.)

In half of the hoops, the frog bit was removed; in the other half it was added, to produce a cover of 65%. After just one growing season, the aquatic macrophytes in the removal plots had 72% cover, while those in the plots with frog bit had only 4% cover. The species that declined significantly included *Elodea canadensis*, *Myriophyllum heterophyllum*, *Potamogeton pusillus*, *P. nodosus*, *P. zosteriformis*, *Sparganium eurycarpum*, and *Utricularia vulgaris*.

5.1.3 Competition among larval amphibians

Many amphibians breed in temporary ponds in the spring. Do they compete with one another? There have been many studies, and the general answer is yes. In one study in North America, Wilbur (1972) examined pools containing three species of mole salamanders (*Ambystoma* spp.) along with a larger amphibian community including tiger salamanders,

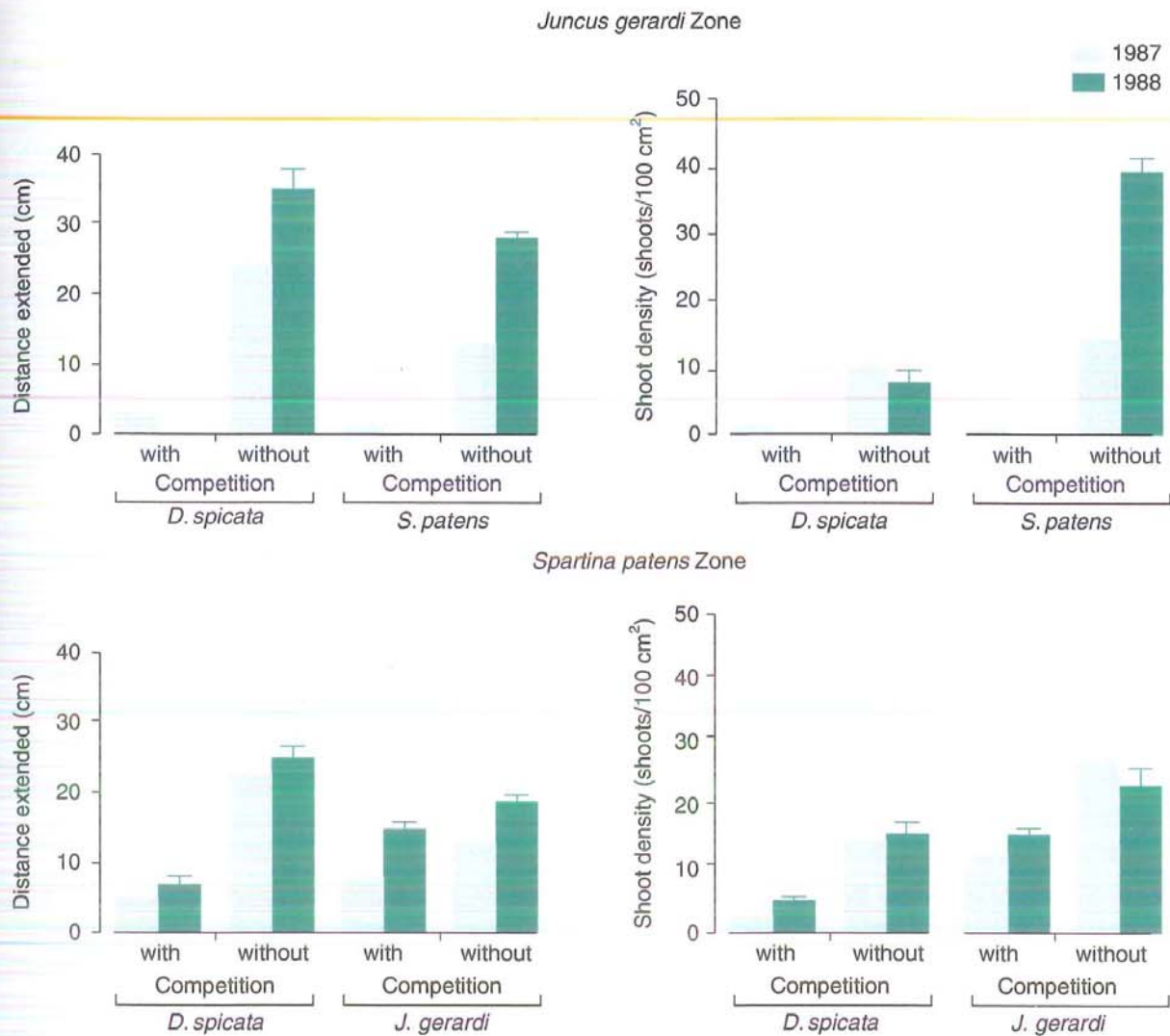


FIGURE 5.3 Effects of competition on three salt marsh plants, *Distichlis spicata*, *Spartina patens*, and *Juncus gerardi*, in two different vegetation zones. Plant growth was measured using distance extended (left) and shoot density (right) in plots with and without neighbors. (From Bertness 1991.)

American toads, gray tree frogs, and wood frogs. Cages were inoculated with different numbers and kinds of amphibian eggs. The cages had one, two, or three species. At the end of the summer, performance was measured three ways: survivorship, body weight, and length of time of the larval period for all survivors. There was intense interspecific competition (Figure 5.4). For example, *A. laterale* (left) had body weights reduced by nearly two-thirds when 32 neighbors were added. Further, there was asymmetry; *A. laterale* (left) was far more sensitive

to *A. tremblayi* than *A. tremblayi* (right) was to *A. laterale*.

5.1.4 Competition among fish in lakeshore marshes

Sunfishes are a group of spiny-rayed freshwater fishes that dominate the fish faunas of small lakes over much of central North America. In Michigan, for example, there are seven to ten species, five of which are in the genus *Lepomis*. There are three principal

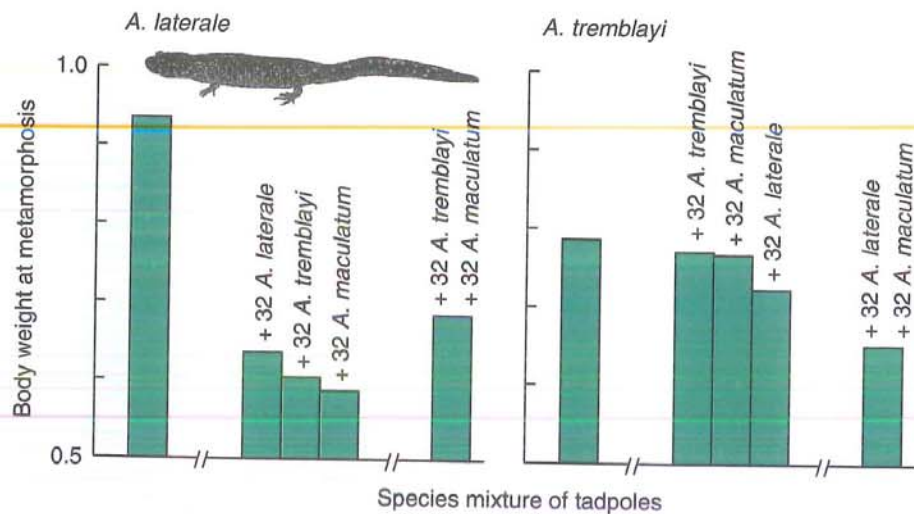


FIGURE 5.4 Effects of competition on salamanders *Ambystoma laterale* (blue-spotted salamander, 12 cm long, from Conant and Collins 1998), *A. maculatum*, and *A. tremblayi*, as measured by body weight at metamorphosis. The control animals lived in pens containing 32 individuals, while the others had experimental additions of either more of the same species, or more of two other salamander species. (Data and nomenclature from Wilbur 1972.)

habitat types: emergent vegetation, open water, and near the bottom. The pumpkinseed (*L. gibbosus*) feeds near the substrate whereas the bluegill (*L. macrochirus*) is found higher in the water column, with further separation among species based upon food size. The green sunfish (*L. cyanellus*) is restricted to the shallow and vegetated inshore habitats (Werner 1984; Wootton 1990). In one set of studies different mixtures of these three sunfish species were introduced into small experimental ponds (e.g. Werner and Hall 1976, 1979). When alone, each species occupied the emergent vegetation zone, where larger prey are found. When green sunfish were present, however, the bluegill and pumpkinseed were forced into the other habitats, to the open water or near the sediment.

5.1.5 Competition among birds in marshes

Birds are a very obvious form of life in most wetlands. It seems natural to ask whether the kinds of birds you see, and where you see them, is influenced by competition. Let us be clear that the focus here is on competition between species. We know, of course, that *within* a species, male birds compete with one another for access to females; indeed Darwin addressed this issue more than 100 years ago.

Here, however, we want you to know whether competition between species can influence the kinds of birds that you might see in a particular wetland.

The yellow-headed blackbird and red-winged blackbird are easy to identify by their yellow heads, or red wing patches, respectively. They conveniently perch in clear sight. Both species prefer to build nests in deeper water where cattails are emergent. Perhaps the deeper water offers some protection against nest predators, ranging from snakes to feral cats. The yellow-heads seize the deep-water sites, even chasing out red-wings that have already arrived. The red-winged blackbirds are then displaced into shallower water or even upland sites around the pond (Miller 1968). Hence, we have a clear case of competition, with the yellow-headed blackbird dominant over the red-winged blackbird.

Of course these are just two species, and as Rigler (1982) reminds us (Section 12.3) if there are 100 species of birds in a wetland, there will be nearly 5000 possible competitive interactions between pairs of bird species. (Actually 4950, if you ignore the interaction of each species with itself.) Although you will frequently see the above two species of blackbirds included in ecology books, they may be misleading – are they typical of the other 4949 interactions that might be occurring? To answer this question, we have to consider more species.

Looking for other birds that nest in or near cattail marshes, grackles, another kind of blackbird, have little effect on red-winged blackbirds, and red-wings in turn have only minor effects on grackles (Wiens 1965). Marsh wrens, however, are fierce competitors, breaking eggs and killing the nestlings of blackbirds (Bump 1986; Leonard and Picman 1986). What about other waterbirds, like herons and ducks? Experimental evidence is harder to obtain. Some biologists suggest that the present differences in their diets or leg lengths or nest locations shows that there was strong competition in the past. This argument, known as “the ghost of competition past” is speculative (Connell 1980; Jackson 1981).

Overall, then, the kind of birds we see in particular wetlands seems likely to be largely the result of the available habitats and food sources (Weller 1999). True, there are a few remarkable exceptions – such as the yellow-headed blackbirds displacing the red-winged blackbirds, and marsh wrens smashing the eggs of both blackbirds. But these examples may be noteworthy precisely because they are so atypical. The surprising truth may be that since birds are so dependent upon habitat, it is competition among plants that has the biggest effects on birds, since it is competition among plants that does indeed influence habitat.

5.2 Competition is often one-sided

Many textbooks leave the impression that competition occurs between pairs of species that are nearly equal in competitive ability. Anyone who watches sports will realize that the occurrence of nearly equal competitive abilities between two teams is infrequent – how many tied games do you see? More often, there is a clear winner and a clear loser. The greater the difference between the winner and the loser, the more one-sided the competition. Of course, if the interaction is one-sided enough, the loser may not even be there any longer. One-sided competition is usually called **asymmetric competition**. The greater the difference between the performance of the two species, the greater the asymmetry (Keddy 2001). We generally refer to the loser as the **subordinate species**, and the winner as the **dominant species**.

Consider the fish study above. It illustrates asymmetric competition, with the green sunfish winning. There is an important and often overlooked consequence of asymmetric competition – species are not always found in their preferred habitat. The green sunfish remained in the preferred habitat because it was the dominant species. The other two species were forced by the green sunfish to occupy suboptimal habitat. To put it in other words, these fish all shared

a preference for emergent vegetation. The fact that they occupied different habitats was actually the result of competitive displacement of subordinate species by the dominant species. This is nearly identical to the situation with the blackbirds.

Now consider some plant examples. Both Bertness (1991) and Catling *et al.* (1988) found strong asymmetric interactions. *Juncus gerardi* was dominant over the other salt marsh species. The floating plant *Hydrocharis morsus-ranae* could shade submersed plants until few were left.

To what extent might such asymmetry be a general property of plant competitive interactions? In order to determine if something is common, you need lots of examples. In this case, we need many experiments that have measured competition. Think again about a sports example. What is the average degree of asymmetry in a particular sport? If all the teams were nearly equal, the average asymmetry would be small, nearing zero except for random events like dropped balls or dishonest referees. In real ecosystems we almost never have enough studies to judge just how asymmetric competition tends to be. Not nearly enough studies have been made on asymmetry in large numbers of species interactions. There is one exception, an experiment in which seedlings of

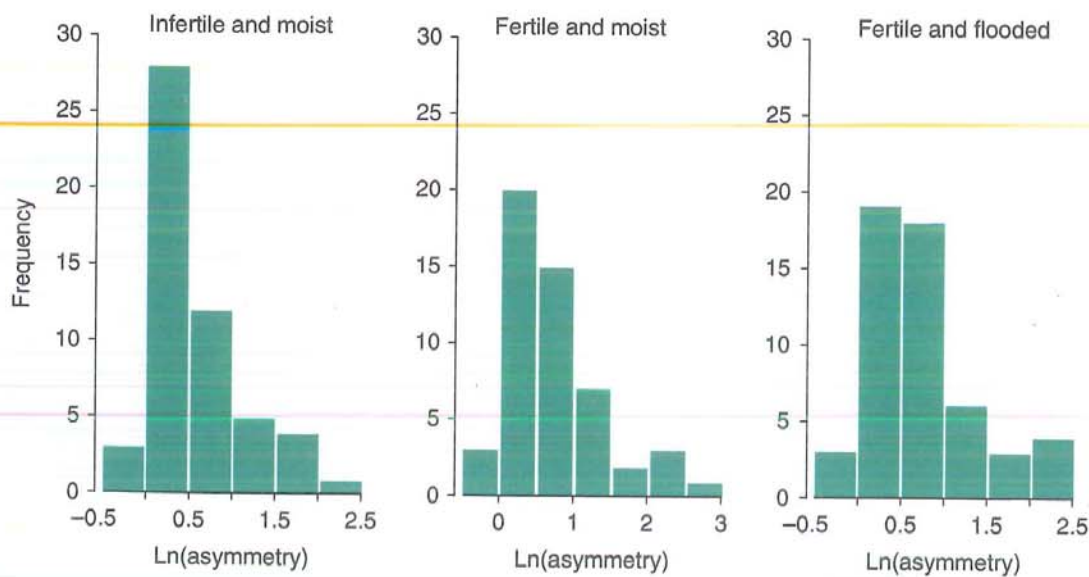


FIGURE 5.5 Asymmetry of competitive interactions among 20 wetland plant species in three different wetland environments. (Courtesy B. Shipley, after data in Keddy *et al.* 1994.)

17 freshwater marsh and wet meadow plants were grown in pairs with three other species, yielding 51 competitive interactions. A measure of asymmetry was calculated for each of these pairs plus pairs (3) of the other species. The interactions were strongly

asymmetric (Figure 5.5). Moreover, the degree of asymmetry changed with environment, being greatest under fertile and flooded conditions resulted in greater asymmetry than did the unfertilized, moist condition.

5.3 Competition for light produces competitive hierarchies

If competition among plants is asymmetric – and most examples show it is – then strong competitors will tend to dominate landscapes. Weak competitors will be less common, and may indeed be absent entirely if they have already been displaced by the dominant competitor. But by looking at the landscape, we would never guess that these species were absent solely because of their weak competitive abilities. In fact, if competition is generally asymmetric, a most interesting question emerges: why are there so many species in wetlands? Why do we not find just the same few strong competitors in nearly every situation?

This question also has management and conservation implications. Is it possible that rare species are often weak competitors? How do weak competitors survive at all? What if humans make interactions more asymmetric by fertilizing

wetlands? What types of conditions might provide refuge for weak competitors? We will return to these themes later in the chapter, and later in the book. Let us continue with this topic by looking at the tendency of a few species to indeed dominate marshes. As noted in Chapter 1, large areas of the world's wetlands are dominated by large leafy species with deeply buried rhizomes: think of *Phragmites australis*, *Typha latifolia*, *Calamagrostis canadensis*, or *Cyperus papyrus*. And then there are genera like *Schoenoplectus*, *Carex*, *Rhynchospora*, *Phalaris*, *Vossia* . . . All have species with dense canopies that can produce nearly solid single species stands (also called monospecific stands). Think of the number of problems produced by invasion of wetlands by *Phragmites* and *Typha* alone. Is there a general principle we can find?

Let us begin with an observation by Sculthorpe, who is of historic significance because he wrote an important monograph on aquatic plants (1967). When he talks about reed swamps, he says:

Although ... compositional changes may occur, it is apparent that numerous ... plants tend to form extensive pure stands. These species assert their status early and attain a seasonal or permanent predominance. Of the numerous factors responsible, rates of vegetative reproduction and antagonism between species of similar or different life form are perhaps the most important. Vigorous vegetative spread, by means of rhizomes, stolons, and tubers, is a typical attribute of several reed-swamp dominants, notably species of *Carex*, *Glyceria*, *Phalaris*, *Phragmites*, *Schoenoplectus* [*Scirpus*], and *Vossia*. In a favourable site one species may gain an early initiative and increase much faster than any competitor ... most mature reed-swamps are so dense that they resist infiltration by larger free-floating rosettes and severely reduce the amount of light reaching the water, thus indirectly inhibiting the growth of invading submerged species. (pp. 426–7)

Note the two processes Sculthorpe emphasizes (1) rates of vegetative reproduction and (2) antagonism, by which he means competition. We could rephrase this as a hypothesis: that many wetlands are occupied by competitive dominants with rapid rates of vegetative spread and dense canopies. The presence of dense canopies suggests that competition is for light, and the dominant species is the one best able to shade its competitors.

One way to assess this would be to grow plants underneath such canopies to measure how much their growth is reduced by shading. This experiment has been done, although in pots rather than under field conditions. The experiment involved first creating artificial wetlands dominated by a single species. Seven species were used to create such conditions. The experiment included species that form dense canopies (e.g. *Typha angustifolia*), species that occupy gaps in wetlands (e.g. *Penthorum sedoides*), and an invasive species that is spreading in wetlands (*Lythrum salicaria*). After 3 years, 48 other

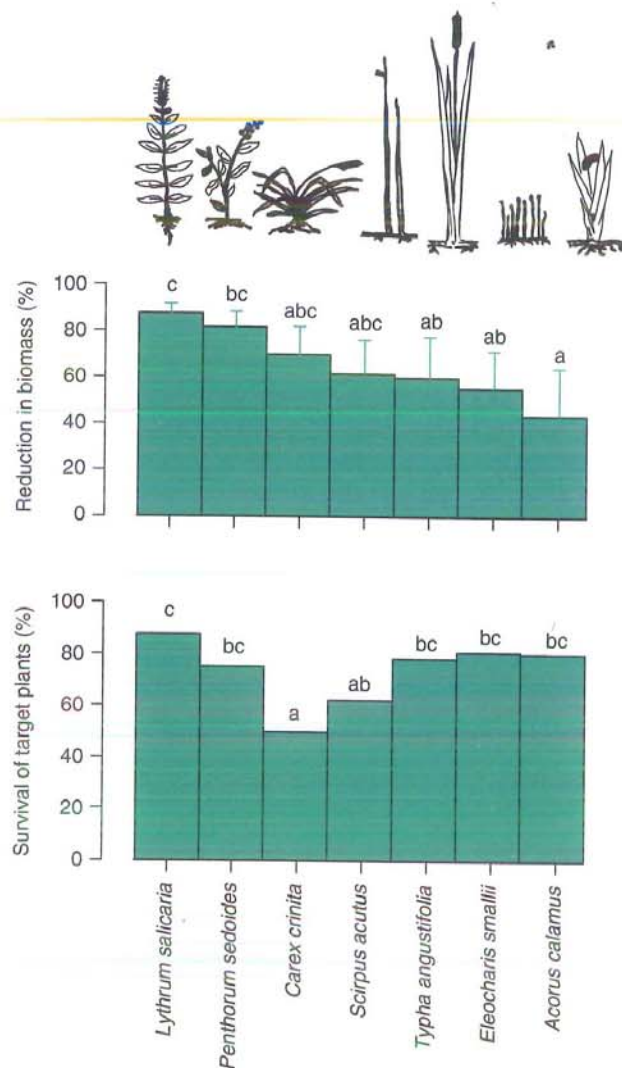


FIGURE 5.6 Effect of seven different perennial marsh plants (illustrated at top, named at bottom) upon the growth (biomass) and survival of 48 other (target) wetland plant species. Note that they are ordered by their ability to suppress other wetland species. The relatively small effects of *Typha angustifolia* likely result from the small size of the pots, which may have limited above-ground competition. (From Keddy *et al.* 1998.)

species of wetland plants were introduced to these monocultures and allowed to grow for 4 months. The effects on the performance of these 48 species was calculated as the standardized difference between their weight when grown alone, and their weight when grown under a canopy. Overall, the monocultures reduced growth and survival by more than one-half

(Figure 5.6). This indicates for a broad array of wetland plants (48 species in this case) that the presence of a canopy has significant negative effects on their growth.

Pot experiments do have their limitations.

A better, although more difficult experiment, would involve transplanting native species into an actual marsh, putting some in clearings (that is, without competition) and putting others into intact vegetation. That, of course, is what was done to produce Figure 5.1. The intact vegetation was not a monoculture, but it was dominated by two clonal species with dense canopies (*Schoenoplectus americanus* 28% cover and *S. robustus* 10% cover, along with *Sagittaria lancifolia* 8% cover). Now for more background: this was part of a larger study in which 16 species were introduced

to cleared and vegetated plots. There were other factors studied in this experiment, including the effects of added sediment and the effects of herbivores (Geho *et al.* 2007). The data used to illustrate effects of competition came from plots that were protected from herbivores. *Taxodium distichum* and *Typha domingensis* are shown for comparison, because of their ecological importance in these habitats; both were most affected by grazing, which obscured the effects of competition shown in the figure. This is a reminder that although competition may be an important factor in wetlands, it is rarely the only factor. The effects of competition must always be interpreted knowing that other factors – in this case grazing – are also present.

5.4 Dominant plants are often larger than subordinate plants

Are there some general ways to recognize plants that are competitive dominants in wetlands? We have Sculthorpe's opinion, while other plant ecologists (Grime 1979; Givnish 1982; Keddy 2001) agree that height is one of the important characteristics of dominant plants. One way to assess this is to measure the competitive ability of a large number of species, and measure some of their life history traits such as height, and ask if the two are related. Gaudet and Keddy (1988) did exactly this – they measured relative competitive performance of 44 freshwater wetland plants from a wide array of habitats. They estimated relative competitive performance by measuring the relative ability of each of these

44 species to suppress a common indicator species, the invasive *Lythrum salicaria*. The more the test plants were able to reduce the growth of *L. salicaria*, the better competitors they were judged to be. Gaudet and Keddy then looked for plant traits that could predict this ability. Both height and above-ground biomass were good predictors of competitive performance (Figure 5.7). In this experiment, species including *Typha latifolia* and *Phalaris arundinacea* both had high competitive ability. We may thus conclude that competition may be very important in wetlands, that species often tend to have unequal competitive abilities, and that many wetlands are dominated by species with dense canopies.

5.5 Escape in space: competition in patches

Perhaps some weak competitors indeed survive by finding patches where the dominant plant does not occur, like the clearings created in the experiment shown in Figure 5.1. Others have already thought about this. More than 50 years ago Skellam (1951) showed that weak competitors can indeed survive – as long as they can disperse better than strong

competitors. The argument goes like this (Pielou 1975). Imagine two competing species that reproduce once a year. Let A be the stronger competitor and B the weaker competitor. Wherever they coexist, A invariably wins. Therefore, the only habitat in which B can reproduce includes those sites in which it occurs alone (Figure 5.8). Assume that the landscape

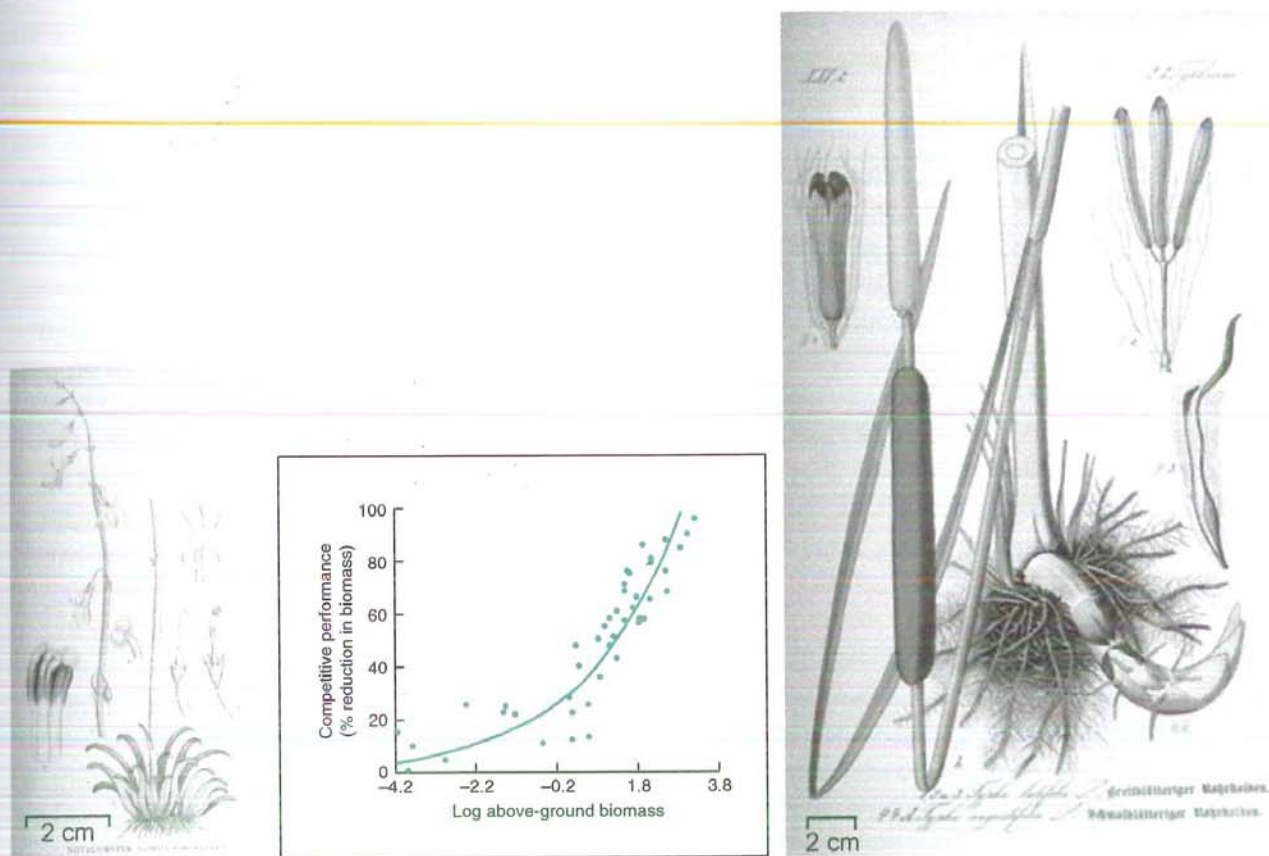


FIGURE 5.7 Competitive performance increased with plant size across an array of 44 wetland species. Small rosette species (e.g. *Lobelia dortmanna*) occur on the left side of the figure, while large leafy species (e.g. *Typha latifolia*) occur on the right. Competitive performance was measured as the percent reduction in biomass of a common test species. (After Gaudet and Keddy 1988.) [See also color plate.]

has N sites, or patches of habitat, and that at equilibrium the expected proportion of sites with a single A individual at the end of the growing season is Q . This means that NQ of the sites are dominated by species A. Therefore, only $N(1 - Q)$ remain for B to occupy. If we call this remaining portion of sites (those that allow B to survive) q , then q must be greater than zero for the competitive subordinate to survive in that landscape. We want to know how much better dispersal of B must be for this to occur.

Therefore, let F and f be the number of seeds produced by species A and B, respectively. For species B to persist, ffF must be great enough to ensure that $q > 0$. It can be shown that, for this to occur, ffF must exceed $-Q/(1 - Q) \ln(1 - Q)$. Provided this condition is met, species B will continue to occur in the landscape in spite of its weak competitive ability. There may be many cases where the types of disturbance we saw in Chapter 4 provide circumstances for this kind of process to operate.

5.6 Escape in time: competition and disturbance

There is another alternative to dispersing to a disturbed patch. The alternative is to wait for a disturbance to make a patch where the plant already

occurs. If disturbances occur often enough, which we have seen is often the case, it may indeed be best to sit and wait for the competitive dominant to be

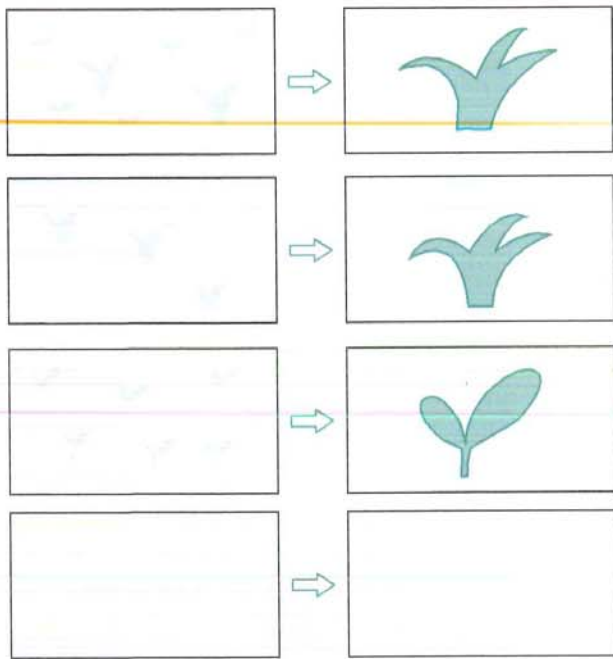


FIGURE 5.8 Weak competitors can survive by escaping to habitat patches that are not occupied by stronger species. Four possible combinations of seedlings are shown on the left, and the outcome of adults is given on the right. (From Pielou 1975 after Skellam 1951.)

killed. Many species seem to have adopted this strategy. We saw in Table 4.1 that many marsh plants have enormous numbers of buried seeds. Since these seeds can remain dormant for many years, if not decades, they need only wait – and soon a fire, flood, or grazer will create the conditions for them to germinate. If you look closely at many seed bank species, they have small seeds that seem to lack any dispersal agent. They simply fall in place and wait

for disturbance to create a clear patch. Some species may also wait for disturbance as adults – small fragments of rhizome may persist under a competitive dominant, and quickly produce new shoots after a disturbance. Indeed, plants may persist for years as small fragments of rhizome. When the competitive dominants die, they rapidly produce vigorous shoots and flowers.

There is an important exception. Most species of trees do not have seed banks. They appear to depend almost exclusively upon dispersal in space. It is not clear why this should be the case, but it seems to be true for a broad array of tree species around the world. Many trees produce wind-dispersed seeds; the cottonwood trees that establish along river banks are a good example. Other wetland trees produce seeds that float and are carried by floods to new sites; cypress and tupelo are two examples. Some trees in the Amazon produce hard fruits that are dispersed by fish.

The lack of tree seeds in soil is important for managing many wetland types. It means that when managers lower water levels or burn wetlands to stimulate germination from buried seeds, it is largely herbaceous plants that establish. Invasion by woody plants takes longer, and requires living woody plants nearby as a seed source. This delays their establishment. Of course, given the importance of competition for light, woody plants will usually eventually dominate wetlands – unless another fire or flood or drought kills the woody plants and allows marshes to re-establish.

5.7 Gradients provide another way of escaping in space

So far we have established that wetlands have intense competition, at least among the plants. Hence, many species found in wetlands have to avoid competition by finding temporary gaps in the vegetation. This may involve dispersal to a newly created gap, but can also involve dispersal forward in time to a future disturbance. Disturbance is such an all pervasive

force in wetlands that there is always likely to be a patch somewhere that is not yet occupied by dominant competitors. It is less clear to what extent these generalizations apply to animals, partly because there is an insufficient number of experiments. However, the little evidence available suggests that animals are often affected by

competition, and may be displaced by competition to habitats that are suboptimal. Examples of this include both fish (Werner and Hall 1976, 1979) and blackbirds (Miller 1968).

There is one other possible escape from competition. It is possible that certain habitats have inherently low levels of competition, and that these habitats provide refuges from competitive dominants. Perhaps there are certain conditions that continually kill competitive dominants, allowing weaker competitors to survive. Since competitive dominants often have large leafy canopies, we may propose that habitats that make it difficult to produce or maintain such canopies are prime candidates. Since producing large shoots requires rapid growth and available nutrients, habitats that are chronically low in nutrients may be less likely to support such species. At very least, the rate at which competitive dominants cover the landscape should be reduced. Similarly, chronic disturbance may continually remove shoots, and once the below-ground organs die from lack of energy from shoots, it may take a very long time indeed for the dominants to re-establish. Candidate factors include waves (which break off shoots), ice (which grinds off meristems or uproots rhizomes), and fire (which removes shoots). A combination of low nutrients and recurring disturbance might be expected to be the worst of both worlds for dominant plants: not only are the shoots continually disrupted, but the resources to replace them are in short supply.

A series of experiments has been carried out to test whether competition does change in the predicted way along such gradients. Before showing the results, we need to note that plants present experiments with a particular problem: they grow and compete in two entirely different habitats, above and below ground. There is little reason to believe that competition among roots for nitrogen and phosphorus will obey the same rules as competition among shoots for light. Hence, we have to deal with above- and below-ground competition as separate factors. There are two possible extremes: above- and below-ground competition show the

same patterns along gradients, or above- and below-ground competition show the opposite patterns along gradients. There are theoretical grounds for thinking that each might be the case (Grime 1979; Tilman 1982), but rather than indulge in theoretical arguments, the task is to design an experiment.

Experiments that test for gradients of competition must by their very nature be large, because the same experiment has to be repeated at multiple locations. If you don't include a large number of possible habitats, you can't test for a competition gradient. Hence, there are many fewer examples. Most come from work done along shorelines, where wetlands are spread out along a gradient running from infertile sandy shores to fertile densely vegetated bays. What might the patterns in competition be along such a gradient? To answer this question, one can transplant one or more species into a series of habitats along this gradient, each habitat having both cleared and uncleared plots. After a period of time, all the plants are harvested. We will call these plants grown in test plots "phytometers" (*sensu* Clements 1935) since we are using them to measure the level of competition at each site in a standard manner. If there is no difference between the growth of the phytometer in the cleared plot and the vegetated plot, there is no competition at that location. Think for example of Figure 5.1 again – if there was no difference between the cleared plots and vegetated plots, there would be no evidence for competition. The greater the difference between the two, the more intense the competition. The results of several experiments arranged along gradients indicated that the effects of competition increased with fertility and biomass (Wilson and Keddy 1986a, b). Moreover, it appeared that the plants were sorted along the gradient according to their relative competitive ability.

There is at least one complication to the above pattern – plants have to compete with one another in two different environments at the same time: above ground and below ground. That is, there can be shoot competition, or root competition,

or some combination of the two. How might these two kinds of competition change along such a gradient? Since there has been only one large experiment to date, I will describe it in more detail. Two species were used as phytometers, *Carex crinita* and *Lythrum salicaria*. The habitat was a gradient of biomass found in a sand shoreline system along the Ottawa River. At one end were open sand shorelines with small numbers of stress-tolerant plants. And the other end of the gradient there was a sheltered bay that was densely vegetated with canopy-forming species. At 60 different locations, competition intensity was measured and separated into above-ground and below-ground competition. Total competition intensity increased with increasing biomass (Figure 5.9, top), and this was solely the result of an increase in above-ground competition intensity (Figure 5.9, middle). Below-ground competition intensity was constant along the gradient (Figure 5.9, bottom).

If biomass gradients indicate the presence of competition gradients, we can make a prediction: the competitive ability of a species will predict where it is found in a wetland. If so, where are the weak competitors found in nature? To answer this question, Gaudet and Keddy (1995) first measured the relative competitive ability of 44 wetland plant species (recall Figure 5.7), and, independently, measured their position along several different gradients. Sites with higher biomass had stronger competitors (Figure 5.10a). Stronger competitors were more common in sites with more organic soils (Figure 5.10b). Stronger competitors also occurred in sites having higher levels of nitrogen or phosphorous (Figure 5.10c, d). Stronger competitors were also positively associated with levels of the lesser nutrients, magnesium and potassium (Figure 5.10e, f). In general, then, habitats with low biomass and small plants – sandy shores, wet meadows, shoreline fens, pannes, some kinds of wet prairies – have species with relatively low competitive ability.

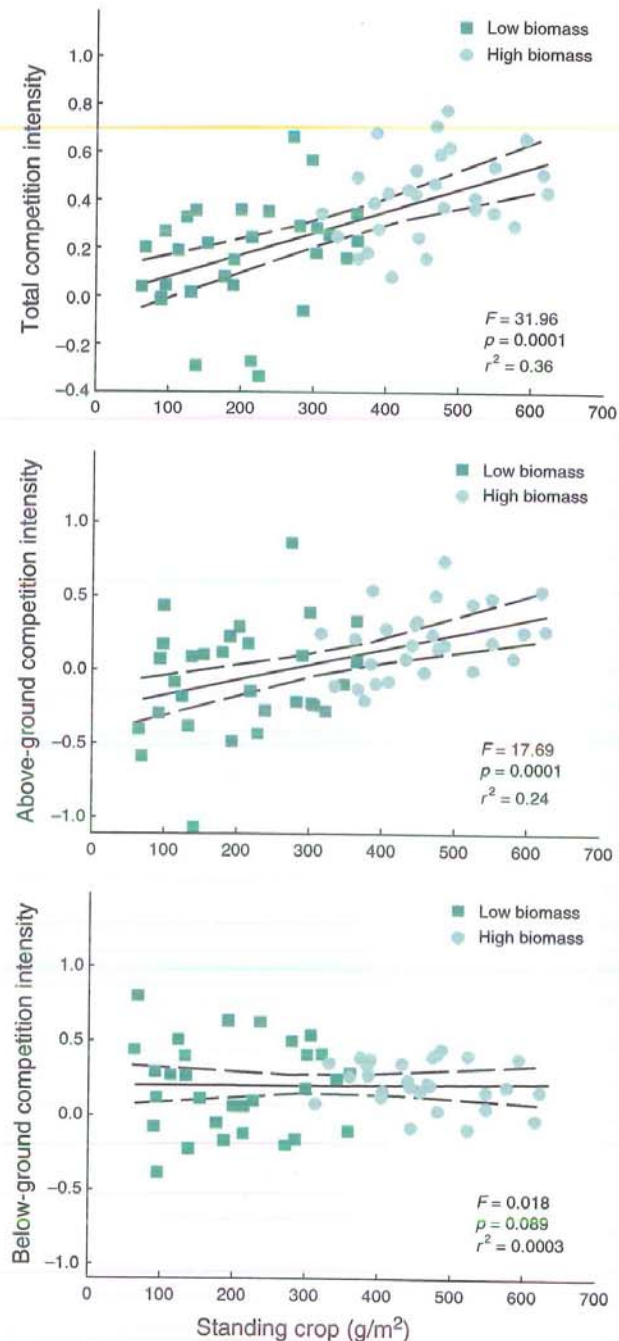


FIGURE 5.9 Competition intensity increased with standing crop in a set of 60 experimental plots representing a gradient from open sandy shoreline to densely vegetated marsh. Most of this was the result of changes in above-ground competition (middle panel). Below-ground competition (bottom) did not change along this gradient. (From Twolan-Strutt and Keddy 1996.)

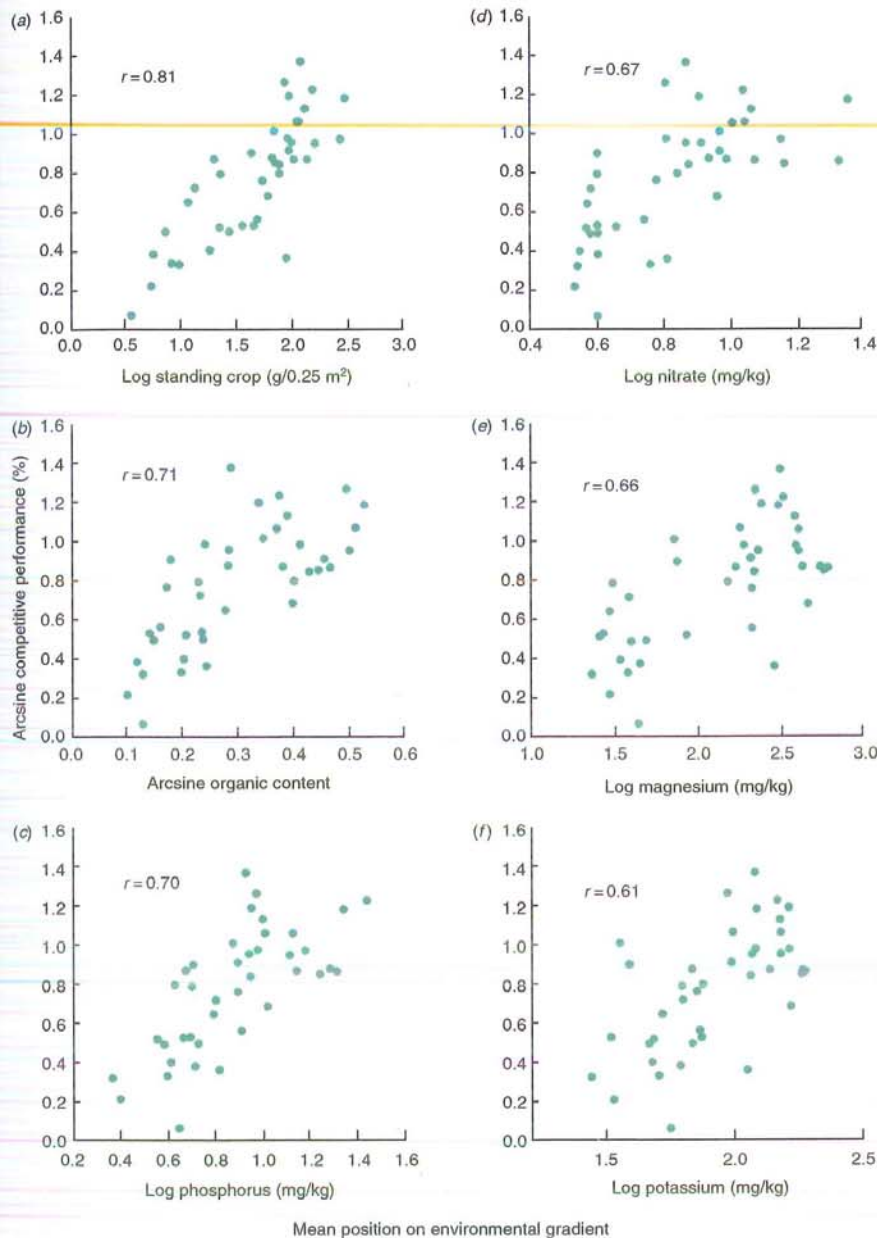


FIGURE 5.10 Competitive performance of 40 wetland plants was correlated with their field distributions along six different field gradients. (From Gaudet and Keddy 1995.)

5.8 Competition gradients produce centrifugal organization

We have therefore established that competition occurs in wetlands. Some wetlands are dominated by large leafy competitive dominants that produce high biomass communities – cattail or papyrus marshes being obvious examples. Other sites that are infertile and disturbed have low biomass, which

is associated with lower competition intensity, and provide a refuge for species that are weaker competitors. We can combine these observations into a centrifugal model (Figure 5.11). This model combines many biomass gradients, and therefore many kinds of wetland gradients, into

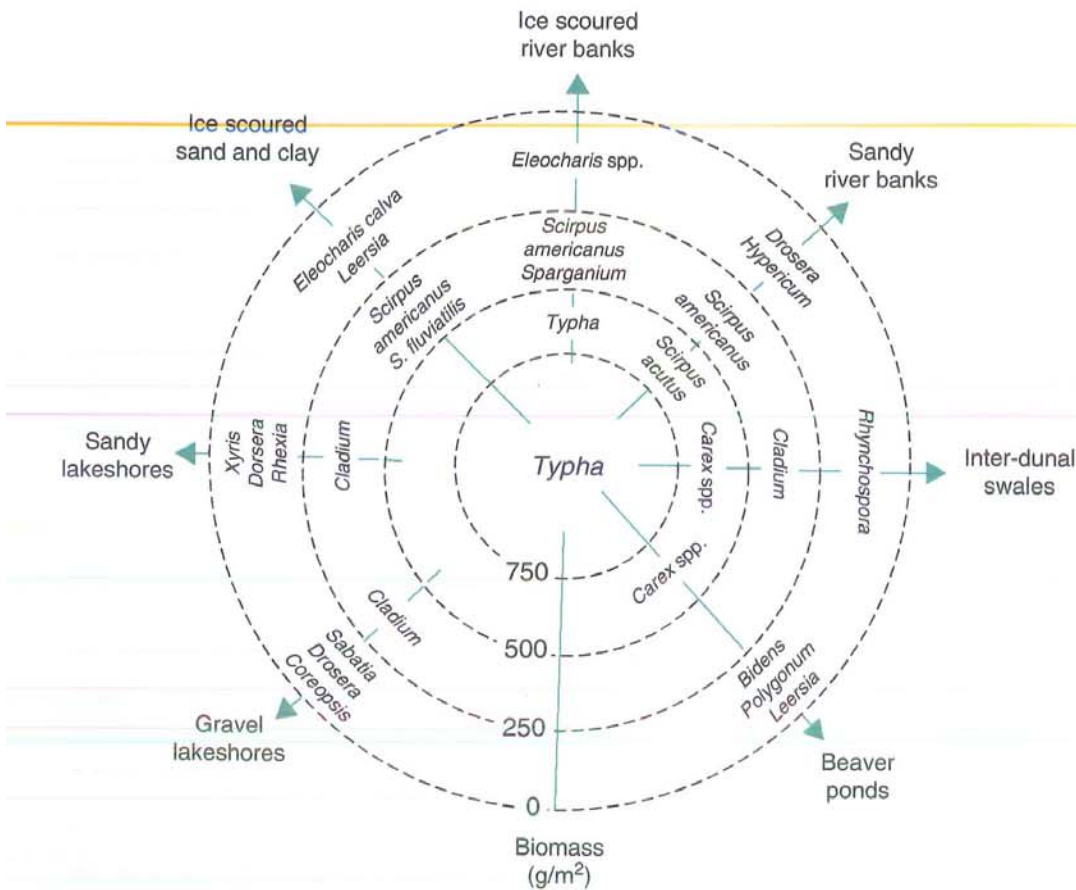


FIGURE 5.11 Centrifugal organization in herbaceous wetlands. The core habitat (fertile, undisturbed) has high biomass (ca. 1000 g/m^2) and is dominated by large canopy-forming species such as *Typha*. The low-biomass peripheral sites have many different kinds of environmental constraints and kinds of species. (After Moore *et al.* 1989.)

one diagram. Let's take a closer look at some of its implications.

5.8.1 The centrifugal model links high competition with low diversity

From the perspective of the centrifugal model, there are a few types of core habitats and a very large number of peripheral habitats. The core habitat is typically dominated by one of a few largely leafy rhizomatous species – Figure 5.11 shows *Typha*, but other genera such as *Phragmites*, *Phalaris*, *Scirpus*, *Calamagrostis*, and *Papyrus* are typical core species.

Arrayed around the core habitat are many different kinds of low-biomass communities. Low-biomass

sites can be produced by many different kinds of environmental factors. Some peripheral sites may have low phosphorus levels. Some peripheral sites may have low nitrogen levels. Some may have low nitrogen and phosphorus levels combined. All three of the foregoing situations could occur with high or low soil calcium. And all these nutrient combinations could occur in sites that are burned, or washed by waves, or scoured by ice. Some unusual low-biomass habitats may even be the result of forces that no longer occur, such as continental glaciers, post-glacial rivers, or ancient lakes. There are so many kinds of peripheral habitats that it is hard to generalize about them. We can say that they have low biomass and unusual species. Beyond that, one

needs to look closely to discover the cause of the low biomass and the particular kind of species that occur.

5.8.2 Rare species are most often found in peripheral habitats

An important prediction of the centrifugal organization model is that rare species will be restricted to peripheral habitats. Since the number of rare and endangered species in the world continues to grow, we may need to place a particular emphasis upon management for peripheral habitats.

Peripheral habitats often have distinctive, and unusual, plant species. The particular species depend upon where you happen to live or travel. Here are a few examples that are included in this book. An infertile wet meadow near Georgian Bay (Figure 3.3c) may have *Rhexia virginica* and *Drosera intermedia*. An infertile low-biomass habitat in the Everglades (Figure 3.3b) may have *Cladium jamaicense* and *Utricularia vulgaris*. An eroded shoreline along a river may have *Pedicularis furbishii* (Figure 2.5e). An infertile wet meadow in Nova Scotia may have *Coreopsis rosea* and *Sabatia kennedyana* (Figure 1.7b). An infertile low-biomass panne on the edge of Lake Ontario (Figures 1.6b, 1.7a) may have *Parnassia glauca*, *Lobelia kalmii*, or *Physostegia virginiana*. An infertile wet prairie may have *Platanthera leucophaea* (Figure 3.4b). An infertile depression along the Gulf Coast of North America (Figure 3.3d) may have several species of *Sarracenia* and *Pinguicula*. Infertile coastal bogs in the Carolinas may have *Dionaea muscipula* (Figure 3.4a). These are only a few examples, and you could find many more. The point is that there are many kinds of peripheral habitats and many kinds of unusual species that can occur where conditions limit the accumulation of biomass and prevent the invasion by clonal canopy-forming species.

We can draw a few general conclusions:

- Any landscape will have far more peripheral habitats than core habitats.
- The peripheral habitats in a landscape contain most of the biological diversity.

- The core habitats will tend to be dominated by a few species.
- Any factor that increases fertility, or decreases disturbance, will tend to force more habitats into the core type of habitat.

5.8.3 Peripheral habitats are at risk

We saw in Chapter 3 that fertility has an important role in controlling the habitats and species in wetlands. Humans are increasing the nutrient levels in wetlands, a process known as eutrophication. We saw that eutrophication produces changes in individual plant communities, as documented in early work on the fertilization of interdunal communities (Section 3.1.5) and in experimental communities (Section 3.5.4). Modern humans have many ways to increase the fertility of wetlands: human sewage, sewage from all the animals being raised to feed people, drift and runoff from fertilized fields, mining phosphorus rocks, removing nitrogen from the atmosphere, and even burning coal and oil. We have already seen that increased levels of nutrients in rainfall are threatening rare plants and their habitats in Europe (recall Section 3.5.6). From the perspective of the centrifugal model, these are processes that push peripheral habitats toward the core, increasing plant biomass, and decreasing plant diversity. Overall, peripheral habitats as a group are at risk from eutrophication.

We saw in Chapter 4 that disturbance is a natural process in landscapes. Humans are reducing the natural disturbance regimes that used to create wild places. Natural fires are largely suppressed, although they are usually replaced by much hotter conflagrations that have far more severe consequences. We have seen this repeatedly in western North America, particularly California. Roads and cities are natural fire breaks that prevent fires from naturally spreading across landscapes. Large herds of wild grazing animals are increasingly rare; and some types of herbivores are now extinct. No longer are large wet prairies in central North

America grazed by millions of bison, or burned by lightning-caused fires. Increasingly, wet meadows exist as small fragments surrounded by human-dominated landscapes.

There is growing evidence from North American wetlands that wet meadows are being replaced by competitive dominants such as *Typha × glauca*. Once established, *Typha × glauca*, like other dominants (Grime 1979) produces a dense canopy and thick deposits of litter. The causes of this change are unclear – hypotheses include changes in hydrology (more stable water levels), changes in fertility (higher nutrient levels), changes in herbivory (lower grazing intensity), changes in disturbance (fire suppression), and genetic changes (hybridization with *T. angustifolia*) (e.g. Newman *et al.* 1998; Boers *et al.* 2007; Wilcox *et al.* 2008). Note that almost every category of causal factors – hydrology, fertility, disturbance, herbivory, and competition – is implicated. It may well be that all these factors together are producing the change, causing a continent wide shift to one vegetation type.

While we will return to this issue in Chapter 9, the principle is clear. Increased fertility, or decreased natural disturbance, leads to higher biomass. Small plants are replaced by large canopy-forming species, and diverse communities are replaced by simpler ones. Overall, peripheral habitats slowly become more like core habitats, leading to an overall decrease in the diversity of wetland vegetation types (Figure 5.12). Small plants from orchids and carnivorous plants (Figure 3.4) to evergreen rosette

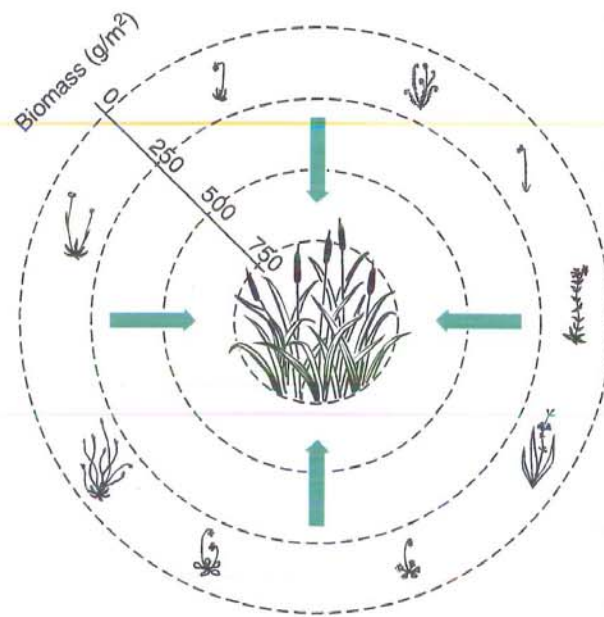


FIGURE 5.12 By increasing fertility and reducing natural disturbance, humans push wetlands from species-rich peripheral habitats to densely vegetated core habitats (dark arrows). In this figure, the core species is in the genus *Typha*. The peripheral species (from top, clockwise) are in the genera *Drosera*, *Utricularia*, *Rhexia*, *Sagittaria*, *Drosera*, *Parnassia*, *Eleocharis*, *Sabatia*, and *Pinguicula*. Many species in peripheral habitats are at increasing risk from human changes to the landscape.

species (Figure 1.17d) are increasingly at risk. Without careful management of wetlands, the future will belong to large clonal plants, and most wetlands will have core habitats with dense shade and large accumulations of litter.

5.9 Rare animals are found in peripheral habitats: the case history of the bog turtle

Thus far we have discussed plants, since they make it relatively easy to do large experiments, and because they provide the habitat for animals. We have moved from the basic principles of competition along gradients to the concept of peripheral habitats with many kinds of weak competitors.

It is a bit of a leap, but let us conclude with looking at how competition among plants can affect a vertebrate species. If there are animals that are restricted to peripheral habitats, then the invasion of these habitats by large leafy competitors may indeed illustrate how plant competition can affect animal

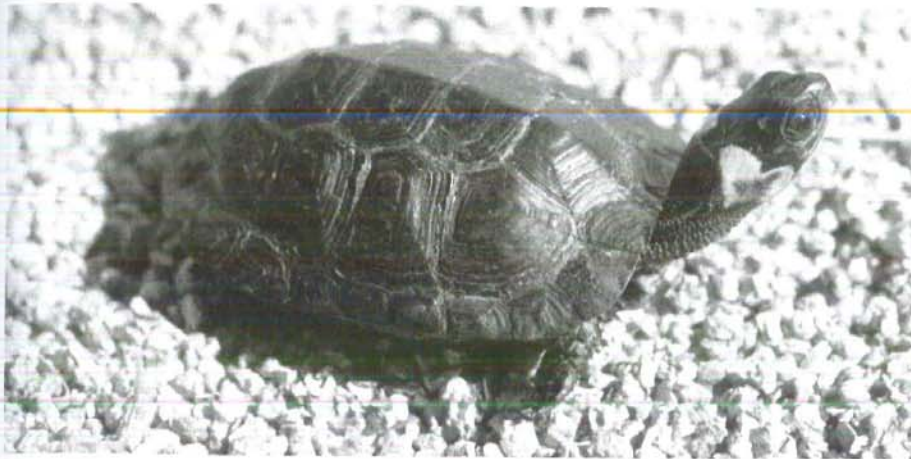


FIGURE 5.13 Animals may also depend upon peripheral habitats. The bog turtle (*Clemmys muhlenbergii*), North America's smallest turtle (9 cm, 115 g), occurs in wet meadows. (Photo courtesy R. G. Tucker, Jr., U.S. Fish and Wildlife Service; map, U.S. Fish and Wildlife Service.) (See also color plate.)

populations. Here is one possible example. Let me be clear that it is just one example. There are likely many more such species around the world. Our example will be the diminutive bog turtle, which most of you have probably never seen. Yet this turtle is being put at risk by plant competition. Here is the story.

The bog turtle is the smallest turtle in North America, with adults generally less than 10 cm long (Figure 5.13). It ranges from New York in the north to Georgia in the south, and has protected status in many states because its population is declining. Since it lays only a few eggs a year, populations can only grow slowly. This turtle lives in wet meadows and fens. Here is how the New York Natural Heritage Program (2008) describes its habitat:

In New York, bog turtles occur in open-canopy wet meadows, sedge meadows, and calcareous fens. The known habitat in the Lake Plain region of the state includes large fens that may include various species of sedges, such as slender sedge (*Carex lasiocarpa*), bog buckbean (*Menyanthes trifoliata*), mosses (*Sphagnum* spp.), pitcher plants (*Sarracenia* sp.), scattered trees, and scattered shrubs. In the Hudson River Valley, bog turtle habitats may be isolated from other wetlands or they may exist as part of larger wetland complexes. These wetlands are often fed by groundwater and the vegetation always includes various species of sedges. Other vegetation that is frequently found in southern New York bog turtle sites includes shrubby cinquefoil (*Potentilla fruticosa*), grass-of-parnassus (*Parnassia glauca*),

mosses (*Sphagnum* spp.), horsetail (*Equisetum* sp.), scattered trees such as red maple (*Acer rubrum*), red cedar (*Juniperus virginianus*), and tamarack (*Larix laricina*), and scattered shrubs such as willows (*Salix* spp.), dogwood (*Cornus* spp.), and alder (*Alnus* spp.).

Another habitat description (McMillan 2006) says:

... bog turtles are most likely to occupy sunny meadows with soft, wet soils and low-growing vegetation ... For nesting, they seek the sunlight of an open canopy and hummocks, where *Carex stricta* or other sedge species and sphagnum moss offer slightly raised, drier habitat. These higher areas are critical because bog turtles nest within their core habitat, rather than travelling upland like most other turtle species ... Restored habitat must also include soggy soils. Here the turtles spend most of their time, half-buried in muck. The same near-steady water temperatures that cool turtles on hot days keep them warm on colder days ... And when it's time to hibernate in late September, a bog turtle moves to the base of a shrub or other sheltered area, where seeping groundwater ensures a constant temperature until it emerges into the warmth of May.

In 1997 the Endangered Species Act designated the bog turtle's status as "threatened." Although this turtle is also harmed by factors like the pet trade and by roadkill, a key problem is the loss of habitat. Wet meadows, as we have seen in Chapters 1–4, depend upon natural disturbances, such as water level fluctuations of large lakes. In the absence of disturbance, they become dominated by shrubs and trees. Note that the first habitat description even mentions *Parnassia glauca*, which is the wet meadow species in Figure 1.7a. As we have seen above, wet meadows are being invaded by large clonal plants such as *Phalaris arundinacea*, *Lythrum salicaria*, and *Phragmites australis*. Hence, the long-term survival of bog turtles means maintaining natural disturbance regimes, and possibly using fire or grazing to prevent dominance by competitively dominant plant species (McMillan 2006; Smith 2006).

Many other wet meadow species are likely to benefit from such management, including box turtles, spotted turtles, wood turtles, Baltimore checkerspot butterflies, bog buckmoths, sedge wrens, and several rare sedges and orchids (McMillan 2006).

CONCLUSION

Competition for resources is an important biological process in wetlands and can be measured only with experiments. It is known to be important for many kinds of plants, and controls their distribution in time and space. Its importance for animals is less well understood, although there are occasional cases where it seems to be very important, including certain salamanders and certain birds.

It may be that many kinds of animals are affected indirectly by competition among plants rather than directly by competition with other animals. There are two important examples. First, animals that are restricted to peripheral habitats are negatively affected when those habitats are turned into core habitats with dense vegetation and closed canopies. Second, animals that require wet meadows and marshes are negatively affected when these habitats become wooded. Although we have not looked in depth at competition from woody plants in this chapter, it is apparent from many of the examples in Chapters 2 and 4 that in the absence of recurring flooding or disturbance,

many kinds of herbaceous wetlands will become forested wetlands, with consequent changes in the plants and animals.

Competition is often one-sided, or asymmetric, where competing species have different competitive abilities. Strong plant competitors with rapid rates of vegetative spread and dense canopies will tend to dominate in habitats with ideal conditions. Weak, subordinate species may survive by dispersing to or growing into patches unoccupied by the dominant species as a result of the disturbance processes described in Chapter 4. They also may be displaced to less desirable locations (peripheral habitats) where the dominant species is unable to establish. Such gradients in competition are the basis for the centrifugal model of plant community organization in which the central core habitat is occupied by large leafy competitive dominants. As one moves away from these conditions and resource limitations increasingly affect growth, biomass declines as does competition. Peripheral habitats at the gradient ends, where competition is lowest, typically support distinctive and rare plant and animal species and protection of these habitats is critical for maintaining species diversity.

The ultimate challenge of wetland management is to maintain examples of all the different types of wetlands that occur in nature, and to ensure that they retain their natural biological diversity. Hence, it is important to understand how fertility, disturbance, and competition interact to produce different kinds of wetland habitats. Some types of wetlands are easy to create – small impoundments with cattails and painted turtles and red-winged blackbirds. Other types of wetlands are hard to maintain and even harder to create. As a consequence, entire suites of species are disappearing from our landscape. Gopher frogs. Bog turtles. Wood storks. Snail kites. Although there are often other issues like hunting or road mortality, too often there is one single cause: insufficient habitat. The task of the wetland manager is to retain this diversity, and to re-create the habitats that these species need. In order to maintain the full range of wetland types, and their full diversity of species, we need to appreciate how competition organizes wetlands.