Figure 1. Lush vegetation at Rumstick Cove on the coast of Rhode Island illustrates how productive a salt marsh can be. Yet salt-marsh plants and animals live in a harsh environment

The Ecology of a New England Salt Marsh

In the harsh environment of a salt marsh, plants and animals not only compete, but also cooperate to survive

Mark D. Bertness

The salt marshes of North America's coastal regions are home to some of the most productive biological communities in the world. In these broad expanses of mud and sand, covered by a lush carpet of grasses and rushes, life seems to thrive on the soothing rhythm of the tides. The thick growth hints that here is found fertile soil, washed by the sea—an environment where plants should thrive.

Yet a salt marsh is in fact a harsh environment, where survival is difficult for plants and animals alike. The receding tides leave the soil soaked with

in which the extent of tidal inundation defines distinct ecological zones. Close to the sea is the low marsh, the area covered each day by the high tide. Cordgrass *(tall grass bordering the water)* dominates this area. Beyond the mean high-tide line is the high marsh, which begins at a distinct line between cordgrass and salt-meadow hay *(lower left)*. The arrangement of plants and animals in the marsh is affected not only by environmental constraints such as the tides but also by competition and cooperation among species. (Except where noted, photographs courtesy of the author.)

salt; waves break violently over the plants during storms. At latitudes where winter wraps the marsh in ice, the plant carpet is easily uprooted by the movement of chunks of the ice sheet, pried loose by winter storms. The animals of the littoral zone—the shore between the high-tide and the low-tide lines—likewise endure environmental extremes, spending part of the day underwater and the rest of the day exposed to the air.

These physical constraints have a visible impact on the marsh. Plant life in a salt marsh is organized into zones, the grasses forming distinct strips between the tide marks. The most obvious explanation for the patterns that form across the intertidal landscape is a physical one: Organisms vary in their ability to tolerate conditions at different tide levels, and the competition for space in the marsh is won by species that do best at a given tide level. The clear patterning of life in salt marshes makes them a good field laboratory for the study of the forces shaping vascular-plant communities, but the simplicity of these patterns is deceptive. To survive under extreme conditions, plants and animals often cooperate. The ecology of a salt marsh is shaped not simply by adaptation and competition, but by a combination of physical forces and

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Figure 2. High marsh is partitioned by the extent of tidal flooding. Closer to the sea, salt-meadow hay *(right)* dominates the high marsh. The terrestrial border of the high marsh is covered by black rush *(left)*.

biological interactions, including cooperation. I have spent more than a decade studying the thriving salt marsh at Rumstick Cove, near my home in Barrington, Rhode Island. Along with others who have taken a close look at salt-marsh communities in New England and elsewhere, I have come to appreciate their underlying complexity.

Walking the Marsh

A walk from land to sea at Rumstick Cove begins at the edge of the high marsh, an area flooded only by monthly extreme tides. Black rush (*Juncus gerardi*) dominates this zone. This deep-green grass is a dense turf, and is tall enough to scrape your calves. Partway through the high marsh, however, there is a line: The black rush ends, and salt-meadow hay (*Spartina patens*) begins. This tidal line marks the mean highest tides of each month. Salt-meadow hay is a light-green grass, about as tall as your lawn would be without mowing. A few other grasses, such as spikegrass (*Distichlis spicata*), also grow here. And there are distinct grass-free patches, often filled with a succulent annual—slender glasswort (*Salicornia europaea*)—that adds color to the high marsh. Slender glasswort is green until fall; then it turns reddish. But in any season, glasswort is a very salty plant that can be pickled or taken as is and placed in a salad.

Just beyond the salt-meadow hay there is another line. This is the boundary between the high marsh and the low marsh—the mean high-water line of the tide. Below this line, there is no salt-meadow hay. It is replaced by the cordgrass (*Spartina alterniflora*) that dominates the low marsh, the area covered by each day's high tides.

Cordgrass, the tall, wispy grass that rolls back and forth in waves under a gentle breeze, is the plant that dominates the common image of a marsh.

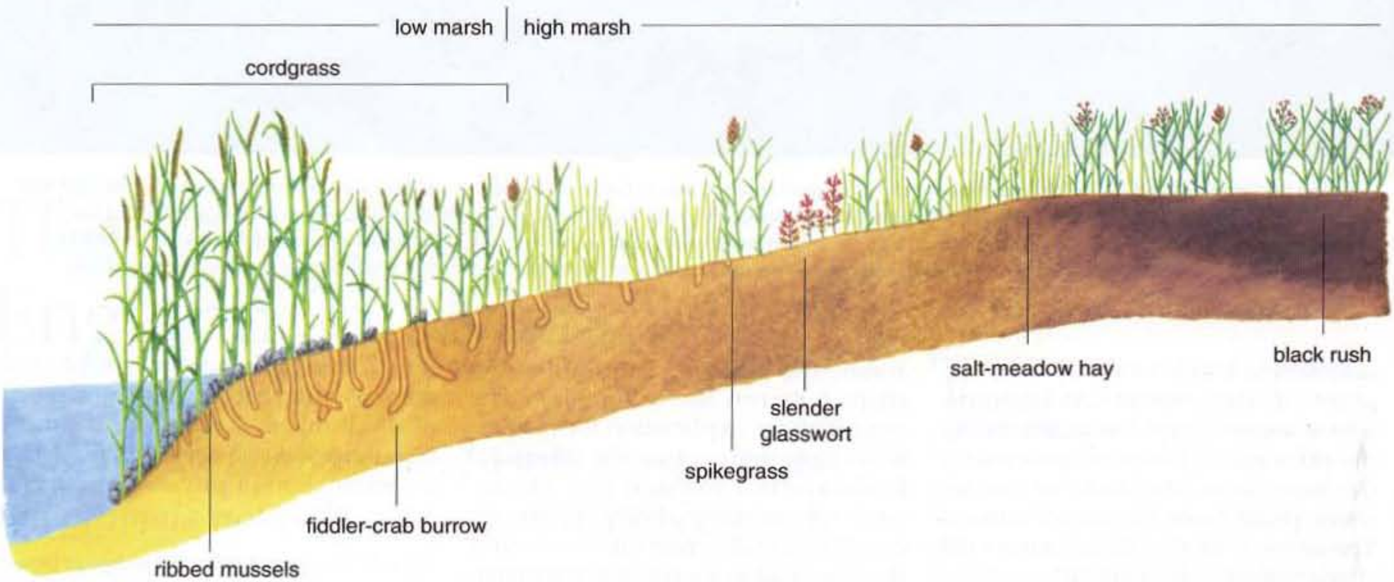

Figure 3. Distinct zones characterize a New England salt marsh, for animals as well as plants. On the coastal side of the low marsh, shown in cross section, thick beds of ribbed mussels are attached to the roots of cordgrass. The mussels decrease in abundance as one moves inland, and the marsh soil becomes dotted with small holes, the burrows of fiddler crabs. These too, however, are largely limited to the low marsh. Even the cordgrass of the low marsh is divided into two zones: The cordgrass closer to the sea is tall and the cordgrass farther from the sea is short because soil there is composed of compacted peat produced by the decay of the grass. The high-marsh zones of salt-meadow hay and black rush are primarily monocultures, but disturbed areas support small populations of spikegrass and slender glasswort.

At the edge of the border marked by the high-tide line, the cordgrass is short, less than 30 centimeters tall. But as you move closer to the sea the cordgrass becomes taller, sometimes reaching nearly two meters in height. As you bend down to look at the muddy soil around the roots of the tall cordgrass, small holes are evident in the ground, perhaps as many as 175 in a square meter of soil. These are openings to the burrows of fiddler crabs. The fiddler crab is small, less than three centimeters across, and the male has one very large claw that he holds the way a violinist carries his instrument—hence the name.

If you push through the last stems of cordgrass during low tide, you come to a muddy beach. Densely packed beds of ribbed mussels cover the transition from the cordgrass to the sea. Sometimes as many as 1,500 mussels can be found in a single square meter, attached near the roots of the cordgrass.

By the end of your journey, it is clear that the zonation of a salt marsh is precise, a distribution dictated by the limits of the tides. There is no cordgrass on the terrestrial side of the high marsh. There is no black rush near the boundary between the high marsh and the low marsh. Specific constraints must impose this arrangement.

Border Disputes

Early investigators believed that environmental variation caused the distri-

Figure 4. Plant morphology affects competitive ability. Spikegrass stems are separated by lengths of belowground runners *(left)*. This makes for a less densely growing plant, but one well adapted for colonizing new areas. Black rush *(right)* has turf morphology—dense groups of stems arising from a belowground mat of roots and rhizomes. Turf grasses do not rapidly invade new areas, but turf morphology is competitively superior to runner morphology over time.

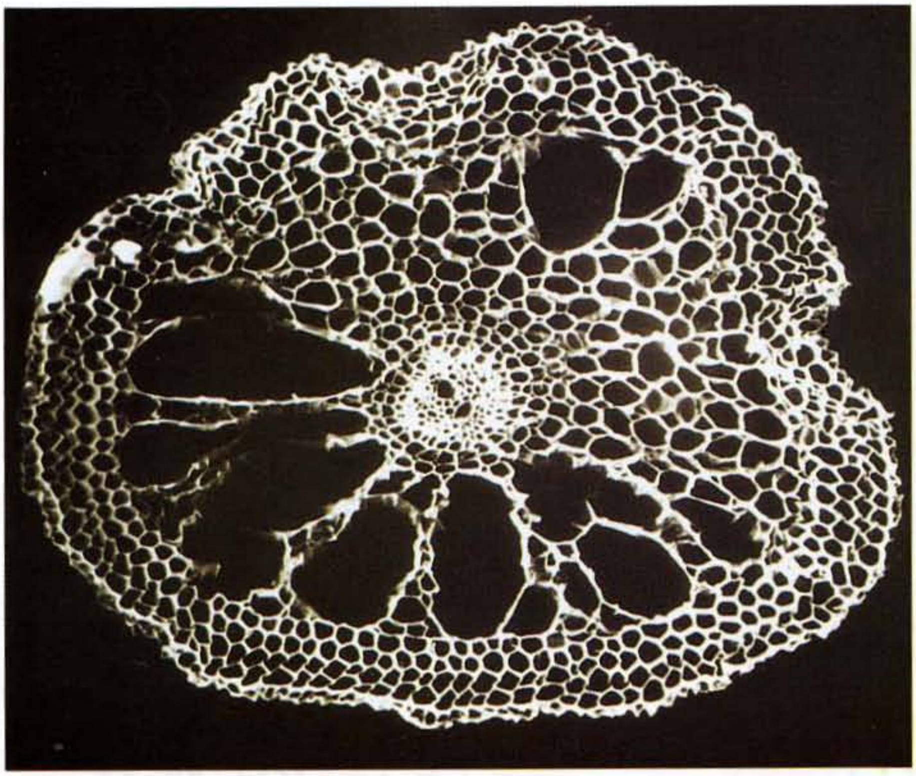

Figure 5. Aerenchymal tissue provides oxygen to the roots of cordgrass by creating a passageway through the plant. In this photomicrograph showing a cross section of a stem, the tissue is visible as a series of circular structures along the perimeter. Repeated flooding by the tide keeps the low-marsh soil waterlogged and thereby deficient in oxygen. Without oxygen in the soil, plants have difficulty using the available nutrients. Cordgrass partially solves this problem by transporting oxygen from its leaves, through the aerenchymal tissue to the roots to oxygenate the soil. (Photograph courtesy of Irv Mendelssohn, Louisiana State University.)

Figure 6. Fiddler crabs enhance the productivity of cordgrass by digging burrows in the low marsh for protection from predators during high tide. The crabs' burrowing aerates the soil, increases the soil's drainage and helps decompose belowground debris.

bution of plants across marshes. The distinct borders between patches of salt-marsh vegetation were seen as clear examples of the varying ability of species to adapt to tidal conditions. Experiments on rocky beaches, however, had suggested that other biological factors—specifically predation and competition among species—significantly affect the zonation of plants and animals in littoral habitats. Could the same forces create zones of plants in a salt marsh? Because herbivores had been shown to have little influence on the survival of marsh plants, I suggested that marsh-plant zonation might arise from a combination of environmental variation and competitive interactions.

I tested my ideas at Rumstick Cove. After describing the plant-zonation pattern in detail, my students and I experimentally examined the distribution of plants across the marsh; we transplanted salt-marsh plants from one zone to another, both with and without neighboring competitors. Through this work, we began to understand what controls the salt-marsh borders.

In one respect, cordgrass controls itself. Beneath tall cordgrass, near the water, the soil has little peat. But the growing cordgrass continuously produces more belowground debris, and the burrowing crabs hasten its decomposition. As this material compacts, it becomes peat. Peat decreases substrate drainage, and the consequently waterlogged soil is low in oxygen. These factors combine to limit the productivity of cordgrass. As a stand of cordgrass matures, it effectively destroys its own habitat. This process creates the variation in the productivity of cordgrass that is seen as you move down the shore. Higher on shore, cordgrass is short; its soil is rich in peat, and thus its growth is stunted. Cordgrass grows better near the water—uninhibited by deposits of peat—and pushes ever farther into the sea.

Other interactions in a salt marsh involve competition between species. In fact, cordgrass is limited to the low marsh more by competition than by its production of peat. If cordgrass is transplanted to an area free of neighboring plants, it grows rather well in the high marsh. But if cordgrass is transplanted near salt-meadow hay or black rush, these plants quickly eliminate the cordgrass.

Likewise, salt-meadow hay and spikegrass both grow best in the terrestrial portion of the high marsh, the black-rush zone; but black rush eliminates its competitors.

Aaron Ellison of Mount Hollyoke College and I showed that competitive relationships among salt-marsh plants are primarily determined by two factors: morphology and the timing of spring emergence. Both black rush and salt-meadow hay have dense mats of roots, rhizomes and aboveground tillers (shoots). Cordgrass and spikegrass tillers, however, are separated by relatively long lengths of belowground runners. In most competitive interactions, turf morphology—the mats of roots, rhizomes and tillers—defeats runner morphology. As a consequence, salt-meadow hay and black rush exclude cordgrass from the high marsh, and spikegrass is limited to disturbed areas within the high marsh. On the other hand, runner morphologies are more mobile than turf morphologies; therefore, cordgrass and spikegrass can rapidly colonize an area. That increases the success of cordgrass in the ever-changing low marsh. These bits of information explain most zones, but leave one question: How does black rush exclude salt-meadow hay from the terrestrial portion of the high marsh? Black rush wins this battle through timing. It emerges in March, nearly two months ahead of any other perennial grass in the marsh, and thereby defeats salt-meadow hay, even though the two plants have similar morphologies.

Environmental variation alone does explain some patterns in the marsh. In some cases, a plant simply cannot tolerate a specific environment. For example, black rush, salt-meadow hay and spikegrass all die within a single season if transplanted to the low marsh, even if they are planted in an area with no competition with cordgrass.

Cooperation and Cordgrass

The low marsh is the most difficult marsh environment for plants. The soil is extremely salty and lacks oxygen. Irv Mendelssohn of Louisiana State University showed that anoxic soil can prevent plants from using the nutrients in the soil. Moreover, the low marsh is continually battered by physical disturbances, especially erosion and ice damage. The lapping of waves throughout the year eats away the shoreline. In the

Figure 7. Sheets of ice cover the low marsh during winter. During high tide, the sheets of ice can uproot large patches of cordgrass that are attached to them, disturbing the edge of the low marsh. For the marsh to survive, each year's production of cordgrass must exceed the amount of cordgrass lost to winter ice damage.

Figure 8. Ribbed mussels protect cordgrass from erosion. The mussels attach themselves to the roots of the cordgrass by strong filaments called byssal threads. In this way, mussels join a series of plants into a common and thereby stronger structure. Moreover, the attachment of the mussels stimulates the cordgrass to produce more belowground roots, further strengthening the plants that protect the marsh from the constant battering of the tides.

Figure 9. Mats of dead cordgrass disturb growth in the high marsh. During the winter, the action of the tides and floating sheets of ice mow down thousands of stems of cordgrass. By spring, the intertidal basin is covered by a layer of floating cordgrass stems. Then, high tides can carry the mats—sometimes larger than a football field—onto the high marsh, leaving them stranded there. Sometimes a mat of cordgrass is stranded in the high marsh for months before another tide washes the mat away or it decays. The mat of cordgrass can kill all underlying vegetation, leaving a bare substrate.

winter, sheets of ice cover the low marsh in wave-protected areas. In Rhode Island I have found these sheets of ice to be 10 to 30 centimeters thick and frozen to the underlying cordgrass. During severe high tides, large chunks of ice, up to 10 meters across, and the incorporated substrate of the marsh can be torn away and rafted offshore. For the marsh to survive, the growth of cordgrass must exceed the destructive effects of erosion and ice damage.

Cordgrass survives in the low-oxygen soil of the low marsh largely because of a morphological specialization. Cordgrass contains aerenchymal tissue—an internal pathway that allows air to move from the tips of the leaves to the ends of the roots, oxygenating the soil. And dense stands of cordgrass move disproportionately more oxygen into the soil. In other words, cordgrass plants thrive by cooperation; dense stands do better than sparse plantings because the increased oxygen makes the soil more hospitable for the plants.

Nevertheless, cordgrass has other help in dealing with the low-oxygen soil. As I said earlier, fiddler crabs are prolific in the low marsh, and dig many burrows. A burrow is usually 10 to 30

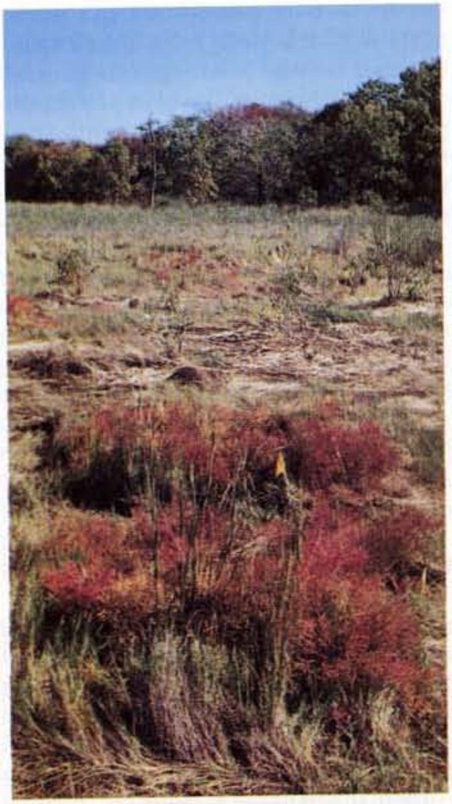

Figure 10. Slender glasswort *(left)*, the most salt-tolerant of the high-marsh plants, invades bare spots *(right)* that are created when stranded mats of cordgrass kill vegetation. In areas with no vegetative cover, the sun evaporates water from the soil, leaving a layer of salt on the surface. Slender glasswort, which can germinate and develop in hypersaline conditions, is the first plant to colonize bare spots.

centimeters deep and provides shelter from predators during high tides. These burrows, however, are in a constant state of flux. Some are abandoned; others collapse. Old burrows are often modified or enlarged. Through this process, the crabs work over much of the top 10 centimeters of soil during each season. This increases the drainage of the soil, the decomposition of belowground debris and the oxygen content of the soil. The fiddler crab is the earthworm of the low marsh, and can be largely responsible for the high productivity of the tall cordgrass.

Likewise, ribbed mussels contribute to the survival of cordgrass. Tom Jordan of the Smithsonian Environmental Research Center and Ivan Valiela of Boston University calculated that a mussel can filter as much as five liters of seawater per hour in search of plankton. This results in the deposition of nitrogen-rich feces that can increase the growth of cordgrass by 50 percent in a single season. Moreover, mussels buffer cordgrass against physical disturbance. A special gland in mussels secretes strong, proteinaceous filaments called byssal threads. Mussels use a series of these threads to attach to the roots of cordgrass, binding marsh soil from erosion. The cordgrass, in response, grows more belowground roots. This, indeed, is a team effort.

Figure 11. Spikegrass colonizes bare soil by sending out runners belowground. In the high marsh, spikegrass is largely limited to bare spots because of the superior competitive abilities of salt-meadow hay and black rush. Like slender glasswort, spikegrass can survive in hypersaline conditions; but spikegrass does so by receiving water, through its runners, from plants in less saline areas. Once established, spikegrass shades the soil, reducing evaporation and soil salinity.

Dealing with Disturbance

When you are standing on the seaward edge, the low marsh seems a more difficult environment than the high marsh because its soil is waterlogged and constantly eroded by the tide. Nevertheless, walking through the high marsh you find bare patches in the midst of the stout green grasses. And particularly in the spring, large mats of entangled, dead cordgrass stems are scattered throughout the high marsh, where they can kill the underlying vegetation. Some of these mats are bigger than a football field and more than 10 centimeters thick. The high marsh, too, is a demanding habitat.

Floating plant debris creates chronic physical disturbances in the high marsh. During the winter, sheets of ice driven back and forth by the tides clip cordgrass stems. By early spring, floating mats of tangled cordgrass skeletons cover the intertidal low marsh. Extreme high tides in the spring raft these mats of dead cordgrass onto the high marsh and leave them stranded when the tide ebbs. The mats may clutter the high marsh for months before decaying or being washed away. Plants trapped under the stranded mat often die, leaving bare soil.

Although at first a bare patch is a competition-free environment, it rapidly becomes a challenging habitat. The sun heats the exposed surface. As the water in the soil evaporates, salinity increases, particularly near the surface. How high the salinity goes depends on the size and location of the bare patch. Larger bare patches have more surface exposed; more water evaporates, and the soil becomes more saline. The highest salinity is found in large bare patches near the border between the salt-meadow hay and the black rush. Here the salinity of the soil can be 30 times the soil salinity under the dense perennial vegetation in the high marsh. Closer to the sea, frequent flooding limits the accumulation of surface salt. And farther into the black rush, rainwater dilutes any salty soil.

The hypersaline soil in bare spots creates water-balance problems for most plants. Scott Shumway of Wheaton College demonstrated that a hypersaline environment prevents germination of the seeds of most marsh plants. Even a healthy seedling often dies if transplanted to hypersaline soil, because the salty soil pulls water from the plant.

Glasswort, however, thrives in hypersaline bare patches. This plant readily germinates in extremely salty soil. Ellison and I found that seeds or seed-bearing skeletons of slender glasswort are often conveniently carried to the bare spots by the cordgrass mats. Because of these two factors, slender glasswort typically dominates bare spots during the first year of regrowth.

Glasswort's reign, however, is tem-

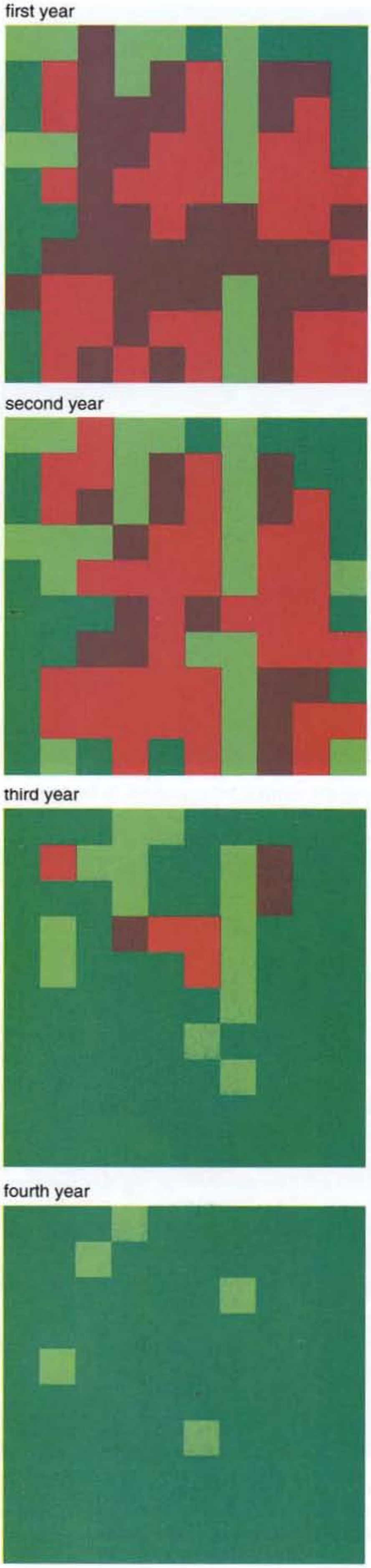

Figure 12. Succession of species in a bare spot in the black-rush zone of the high marsh results from cooperation and competition among plants. New bare spots in the black-rush zone become extremely hypersaline because of direct exposure to sunlight. By the end of the first year, more than one-third of a disturbed spot remains bare *(brown)*. Slender glasswort *(red)* and spikegrass *(light green)*, however, are relatively salt-tolerant and cover more than half of the ground, providing shade that makes the soil more habitable for black rush *(dark green)*, which cannot tolerate the hypersaline soil. In the second and third years, after the physical conditions are improved by the initial invades, black rush invades the area. The results of competition become clear by the third year. Black rush covers approximately three-fourths of the area and competitively displaces the initial invaders. After four years, no bare soil remains, slender glasswort is completely excluded and spikegrass covers only a few percent of the zone. The once-bare spot is dominated by black rush.

porary. Spikegrass moves in shortly, invading bare spots through asexual means. This salt-tolerant New England marsh perennial produces long rhizomes, just a few centimeters below the surface, that invade the bare spots. Shumway showed that these invading rhizomes survive the saline soil and produce young shoots because, through the rhizomal connection, they receive water from surrounding plants growing in less saline soil. The spikegrass prospers and shades the soil, reducing evaporation and thereby reducing soil salinity. As the salinity of the soil decreases, the habitat becomes more hospitable to other high-marsh perennials, particularly those with turf morphologies. Within two to four years, either salt-meadow hay or black rush displaces both slender glasswort and spikegrass.

Much as the crabs, mussels and cordgrass cooperate to occupy the seaward edge of the low marsh, high-marsh perennials work together to reclaim hypersaline bare spots. Salt tolerance and competitive ability are inversely related in plants of the high marsh in New England. The less competitive but more salt-tolerant plants first invade bare spots. This facilitates succession, making the habitat livable for the more competitive but less salt-tolerant perennials. Here again, a cooperative effort among the plants emerges only if the bare spot is hypersaline, and thereby stressful. If a bare spot has a low level of salt, the spot is filled through strictly competitive interactions among the high-marsh plants. So local conditions determine whether a patch is invaded cooperatively or competitively.

Cooperation Is Important

Ecologists have overestimated the universal role of competition in nature. Phrases such as "survival of the fittest" certainly evoke and perpetuate this misconception. Over the past 20 years, many ecologists have examined natural communities in search of competition, and have found it to be particularly pervasive in physically mild habitats. Early in this century, ecologists accepted, uncritically, that species can cooperate to reclaim disturbed habitats. Because of this *untested* acceptance, contemporary ecologists largely reject this idea. Nonetheless, many recent experiments show that positive interactions among organisms often play a large role in natural communities.

Physically harsh environments generate, as a matter of course, cooperation among organisms. David Wood of California State University at Chico and Roger Del Moral of the University of Washington found facilitation among plants during early succession in subalpine habitats on Mount St. Helens. Other reports show that interactions among the same organisms can be competitive in benign environments and cooperative in harsh environments. For example, Mark Hay of the University of North Carolina's Marine Science Center showed this in turf-forming seaweed. Examples such as these reveal that a New England salt marsh is one habitat among many in which biotic interactions are competitive under mild physical conditions and cooperative under harsh physical conditions. Both competitive and cooperative forces likely play major roles in the organization of most natural communities.

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