Chapter contents

4 Disturbance

In the last chapter we saw that fertility controls the rate of production of biomass. Disturbance removes that biomass (Figure 4.1). Common examples of disturbance include fire, ice scour, and storms. The effects of herbivores are also classified as disturbance, although we will deal with herbivory in a later chapter. At the level of the plant, disturbance is any process that removes foliage, meristems, or other tissues. Disturbance is an all-pervasive process in nature (e.g. Sousa 1984; Pickett and White 1985; Botkin 1990). Recall that Figure 3.1 showed how fertility increased the biomass in a coastal marsh; Figure 4.2 shows the same experiment – but now four types of disturbance have been added. You can see that the amount of biomass in this marsh depends upon both fertility and disturbance.

But **disturbance** is a dangerous word. It is dangerous because many people assume they understand it when they do not. Let us define disturbance more precisely as *a short-lived event that removes biomass and thereby causes a measurable change in the properties of an ecological community.*[1] Hence, the word disturbance should be reserved for events that have three key elements: they are short-lived, they reduce biomass, and they cause a measurable change in properties of the system. If you are looking for a more general word that does not imply biomass removal, the word "perturbation" or even "event" is a good substitute. An event may not be a disturbance if it has no measurable effects.

FIGURE 4.1 Fire removes biomass from wetlands during droughts. It also alters fertility by volatilizing nitrogen and recycling phosphorus. If the fire is sufficiently intense to burn the organic soil, pools of water can form in the depressions. (Courtesy C. Rubec.) (See also color plate.)

This definition needs further clarification. What is short-lived? We use the life spans of the dominant organisms, as suggested by Southwood (1977). By short-lived, we mean an event with *duration much shorter than the lifespan of the dominant species in the community*. According to this definition, a fire or severe drought would generally be a disturbance. But not climate change and not eutrophication. By insisting upon measurable change we further require that you identify at least one property (e.g. biomass, diversity, species composition) and show that it has changed. No change, no disturbance (see Cairns 1980). This definition fits well with other work including Grime's (1977, 1979) work on plant communities, and Southwood's (1977, 1988) approach to measuring time relative to lifespans.

Although change in biomass is the predominant point, disturbances may change more than biomass.

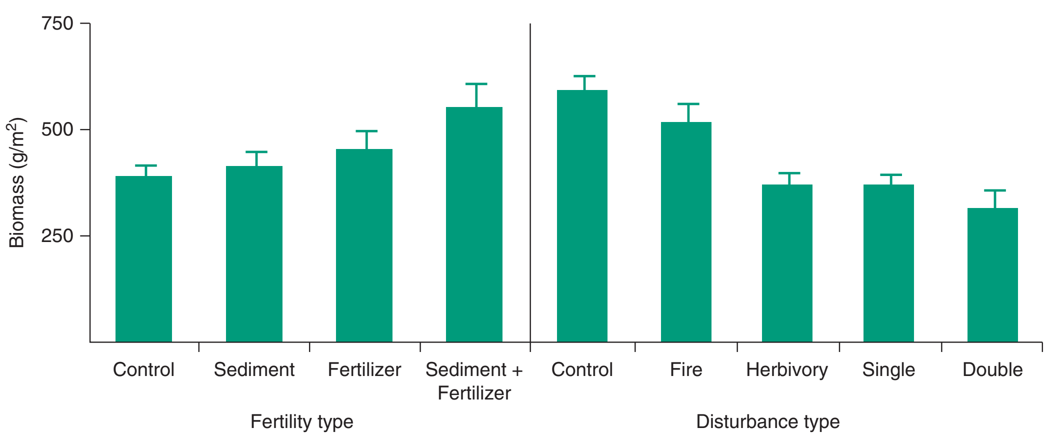

FIGURE 4.2 Biomass increases with fertility (left) and biomass decreases with disturbance (right). The disturbances are fire (annual burning), herbivory (mainly grazing by nutria), and a single or double application of herbicide. (From Keddy *et al.* 2007.)

[1] I have slightly narrowed usage of the term relative to the first edition.

Fire, for example, may also burn peat, creating new water-filled depressions. Waves may also remove silt and clay, producing coarse-textured infertile substrates. Ice can drag boulders to create furrows. Trees blown down by hurricanes can leave mounds of earth with an adjoining depression.

4.1 Disturbance has four properties

Having defined disturbance, it is important that we understand its four properties before we can move on to consider its effects.

4.1.1 Duration

Duration refers to how long an event lasts. A fire may last only a few minutes as the fire front passes. Burial by litter can kill salt marsh plants in as little as 8 weeks (Bertness and Ellison 1987). Flooding for 3 years may be required to kill most emergent wetland plants in freshwater marshes (Figure 4.3).

4.1.2 Intensity

Intensity refers to the severity of the effects of an event. A simple measure of intensity is the proportion of biomass at a site that is killed or removed. The more biomass removed, the more intense the disturbance. A grazing moose could remove 10% of the biomass at one site; a severe frost might kill half of the foliage; fire could remove all the above-ground biomass. Some events, such as ice scour and hurricanes, do more than remove biomass, and therefore have even higher intensity. A factor that disturbs one type of organism (say, plants) might not disturb another (say, wading birds), so the change in abundance of several groups might be measured simultaneously.

4.1.3 Frequency

Different types of events recur with different frequencies. Floods often happen on a yearly basis. Fires may occur once a decade, only after sufficient fuel has accumulated. Hurricanes may strike a section of coast a few times in a century. Water levels in the Great Lakes may reach extremes only once a century. In general, the greater the intensity of disturbance the lower the frequency.

4.1.4 Area

Different events affect different sized areas of landscape – a fallen tree may affect square meters, a fire may affect tens of hectares, while a hurricane may affect thousands of square kilometers.

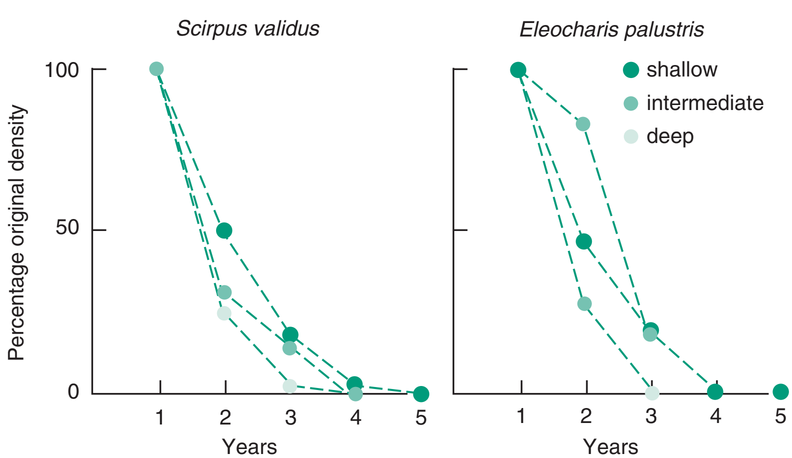

FIGURE 4.3 The effects of flooding to three different water depths on the survival of two emergent plant species. (From Keddy and Reznicek 1986, data from Harris and Marshall 1963.)

4.2 Disturbance triggers regeneration from buried propagules

When biomass is removed, resources such as light become more available. If the biomass is burned, the ashes will contain phosphorus. Buried reserves of viable seeds, often called **seed banks**, allow plants to rapidly recolonize disturbed patches and exploit the light and nutrients there. Seed densities in excess of 1000 seeds per square meter are common in both prairie marshes and freshwater coastal marshes, and densities in excess of 10 000/m^2 are common in wet meadows (Table 4.1). These high densities of buried seeds provide evidence of the importance of recurring disturbance and regeneration in wetlands. The importance of seed banks for regeneration is particularly well established in prairie wetlands (van der Valk and Davis 1976, 1978) and lakeshore wetlands (Keddy and Reznicek 1982, 1986).

For many marsh and wet meadow species, regeneration in gaps provides the only opportunity for establishment from seed. Buried seeds appear to detect these natural disturbances in three ways: increased fluctuations in soil temperature,

Table 4.1 **Densities of buried seeds found in a selection of wet meadows and marshes**

Wetland habitat	Seedlings/m^2	Reference
Prairie marshes		
Typha spp.	2682	1
Scirpus acutus	6536	1
S. maritimus	2194	1
Phragmites australis	2398	1
Distichlis spicata	850	1
Open water	70	1
Open water	3549	2
Scirpus validus	7246	2
Sparganium eurycarpum	2175	2
Typha × *glauca*	5447	2
Scirpus fluviatilis	2247	2
Carex spp.	3254	2
Open water	2900	3
Typha × *glauca*	3016	3
Wet meadow	826	3
Scirpus fluviatilis	319	3
Fresh or brackish coastal marshes		
Typha latifolia	14 768	4
Former hayfield	7232	4
Myrica gale	4496	4
Streambank	11 295	5
Mixed annuals	6405	5
Ambrosia spp.	9810	5
Typha spp.	13 670	5
Zizania spp.	12 955	5
Sagittaria lancifolia	2564	6
Spartina	32 826	6
Wet meadows in lakes or ponds		
Lakeshore, 75 cm water	38 259	7
Waterline of lake	1862	8
30 cm below waterline	7543	8
60 cm below waterline	19 798	8
90 cm below waterline	18 696	8
120 cm below waterline	7467	8
150 cm below waterline	5168	8
Small lake, shoreline	8511	9
Small pond, sandy	22 500	10
Small pond, organic	9200	10
Beaver pond, Canadian shield	2324	11

References: 1, Smith and Kadlec 1983 2, van der Valk and Davis 1978; 3, van der Valk and Davis 1976; 4, Moore and Wein 1985; 5, Leck and Graveline 1979; 6, Baldwin and Mendelssohn 1998a; 7, Nicholson and Keddy 1983; 8, Keddy and Reznicek 1982; 9, Wisheu and Keddy 1991; 10, Schneider 1994; 11, Le Page and Keddy 1998.

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increased quantity of light, and changes in the quality of light (Grime 1979). Thus, most plants adapted to exploit natural disturbances are stimulated to germinate by a combination of high light levels and fluctuating temperatures (Grime *et al.* 1981).

The intensity of the disturbance will determine the importance of buried seeds. If the disturbance does not kill below-ground biomass, the plants may rapidly regenerate from rhizomes. In one study of oligohaline coastal *Spartina* marshes, three levels of disturbance were created: controls, non-lethal disturbance, and lethal disturbance. The most intense disturbance resulted in vegetation with the largest number of species (Figure 4.4). In saline environments, seed densities are often lower: 50/m^2 (Hartman 1988) to 500/m^2 (Bertness and Ellison 1987) and a majority of the recolonization of the wetland results from expansion by neighboring plants. Periodic flooding with fresh water may, however, provide the opportunity for some salt marsh species to establish from buried seeds (Zedler and Beare 1986). Hence, a short period of rainfall or a freshwater pulse may have a long-term impact on species composition. We will return to this topic in Section 4.5.

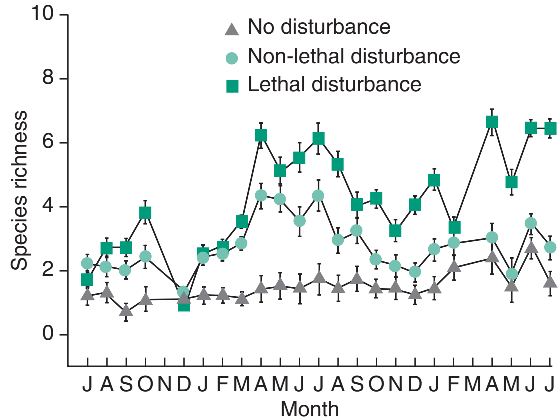

FIGURE 4.4 Effects of three levels of disturbance on the number of plant species in an oligohaline *Spartina* marsh in Louisiana (0.5 × 0.5 m quadrats, ±SE). (From Baldwin and Mendelssohn 1998a.)

4.3 Examples of disturbance controlling the composition of wetlands

Disturbance can be caused by a number of natural or man-made phenomena, from erosion and ice through to mowing and logging.

4.3.1 Erosion along rivers creates as well as destroys wetlands

In the lower reaches of watersheds, and in deltas, rivers flow though valleys filled with alluvial sediments (recall Figure 1.23). These alluvial sediments often have extensive floodplain forests (swamps) and to a lesser degree, marshes. The alluvial sediments are continually reworked by the river, and these cycles of erosion and deposition produce a wide array of wetland vegetation types.

One of the most dramatic examples comes from the Peruvian Amazon, where 26.6% of the modern lowland forest shows characteristics of recent erosion and deposition, and fully 12% of the Peruvian lowland forest is in successional stages along rivers (Figure 4.5). During one 13-year period the mean lateral erosion rate of meander bends was 12 m/yr. The total area of newly created land available for primary succession was 12 km^2, representing nearly 4% of the present floodplain area. The new substrates are first colonized by herbaceous plants (species of *Tessaria*, *Cyperus*, *Ipomoea*, and *Panicum*), then small trees (species of *Cecropia*, *Ficus*, and *Cedrela*) gradually form a closed canopy, and eventually these became mixed with later successional trees. Altogether there is a pioneer flora of 125 plant species (Kalliola *et al.* 1991). Salo *et al.* (1986) conclude:

(a)

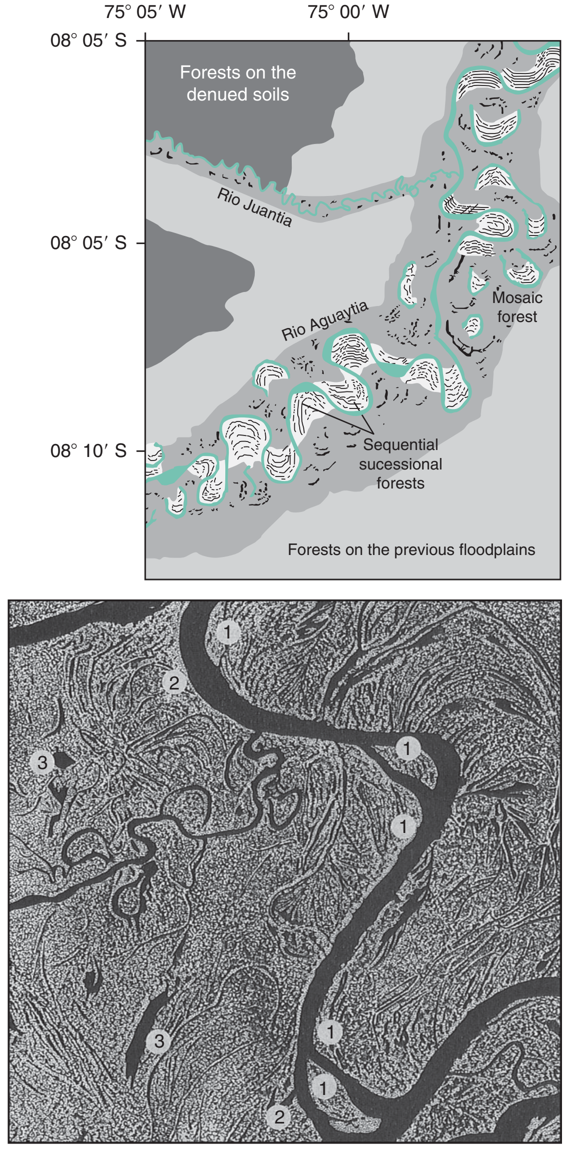

FIGURE 4.5 Disturbance from erosion continually creates new bands of vegetation in many floodplains. (*a*) Map of the meander system of the Ucayali R. at Pucallpa, Peru. (*b*) Landsat multispectral scanner image downstream from (*a*) showing 1–vegetation colonization, 2–eroding forests, 3–oxbow lakes. (From Salo *et al.* 1986.)

According to the repetitive nature of river dynamics, the migration of the river channel course creates a mosaic of successional forests within the present meander plain. The mosaic forest is composed of patches of differentially aged sequential successional forest and patches of forests originating from a succession on the sites of former oxbow lakes. The annual floods further modify the mosaic pattern.

Similar processes have been decribed in In New Zealand alluvial forests, where the presence of two conifers in the Podocarpaceae (*Dacrycarpus dacrydioides* and *D. cupressinum*) is the result of recurring disturbance on the floodplain. In northwestern North America *Populus balsamifera* establishes on newly deposited sediments (Nanson and Beach 1977) while in the Mississippi River delta it is *Salix nigra* (Johnson *et al.* 1985). Similar processes have been described in the Okavango delta of Africa (Ellery *et al.* 1993) and in floodplains along the River Murray in Australia (Roberts and Ludwig 1991).

Overall, there is good evidence that continual disturbance and reworking of alluvial sediments produce much of the plant and habitat diversity in floodplains, and partly account for the very high plant species diversity of tropical floodplain forests.

4.3.2 Fire creates a mosaic of vegetation types in the Everglades

It may be difficult to imagine a fire ripping through a stand of water lilies, but many kinds of wetlands do indeed burn during dry years. Fire in prairie potholes has already been mentioned. Fire frequency, along with hydrology, determines the kind of wetland found across much of the southeastern United States (Table 4.2). Fire is also regarded as a major control of plant diversity in boreal circumpolar peatlands (Wein 1983), pocosin peatlands (Christensen *et al.* 1981), and the Everglades (Loveless 1959).

Fire becomes important during prolonged periods of drought. Low-intensity fires can simply remove existing above-ground biomass, shift composition from woody to herbaceous wetlands, and increase plant diversity (Christensen *et al.* 1981;

Table 4.2 **Flooding and fire regimes in the many kinds of non-alluvial wetland communities found in the southeastern United States (Figure 3.3 shows one example); note how changing the soil, hydroperiod, or fire frequency produces a vast array of different types of wetlands**

Community	Canopy dominants	Soil organic matter	Hydroperiod/ water source	Fire frequency
Forested wetlands in basins				
pond cypress pond forest	*Taxodium ascendens*	mineral to organic	6–12 months rainfall	infrequent, 20–50 years
swamp tupelo pond forest	*Nyssa biflora*	organic to peat	6–12 months rainfall	rare, one fire per century
cypress dome	*Taxodium ascendens*	peat	6–9 months rainfall	20+ years
basin swamp forest	*Nyssa biflora*, *Acer rubrum*, *Liquidambar styraciflua*	organic	6–9 months groundwater	infrequent, 20–50 years
Wetland complexes (from forested to open water) in basins				
limestone pond complex (karst ponds)		mineral	deep groundwater	1–10 years/ yellow sand, 36–60 years/ white sand
coastal plain small depression pond		mineral	variable	dependent on surrounding forests
coastal plain lakeshore complex		mineral	variable	rare, one fire per century
Okefenokee swamp wetland mosaic		mineral–peat	variable	infrequent, 20–50 years
Woodlands and savannas on flat coastal terraces				
slash pine flatwoods	*Pinus serotina*	mineral	<3 months groundwater	3–10 years
wet longleaf pine flatwoods	*Pinus palustris*	mineral	<3 months groundwater	3–10 years
wet longleaf pine–slash pine flatwoods	*Pinus palustris*, *Pinus serotina*	mineral	<3 months groundwater	3–10 years
longleaf pine savanna	*Pinus palustris*	mineral	3–6 months groundwater	1–5 years
coastal plain pitcher plant flat	Many graminoid and herbaceous species and *Sarracenia* spp.	mineral	6 months groundwater	1–5 years
Woodlands and savannas in basins				
pond cypress savanna	*Taxodium ascendens*	mineral	6–9 months rainfall	20+ years
pond pine woodland	*Pinus serotina*, *Cyrilla racemiflora*	shallow organic and peat	6–9 months rainfall	10–20 years

Table 4.2 (*cont.*)

Community	Canopy dominants	Soil organic matter	Hydroperiod/ water source	Fire frequency
Evergreen shrub wetlands				
low pocosin	*Pinus serotina*, *Cyrilla racemiflora*, *Zenobia pulverulenta*	deep peat, >0.5 m	6–9 months rainfall	15–30 years
high pocosin	*Pinus serotina*, *Cyrilla racemiflora*, *Lyonia lucida*	shallow peat, <0.5 m	6–9 months rainfall	15–30 years
small depression pocosin	*Pinus serotina*, *Cyrilla racemiflora*, *Lyonia lucida*	shallow peat, <0.5 m	6–9 months rainfall	15–30 years

Source: After Sutter and Kral (1994).

Thompson and Shay 1988). More intense fires, however, can burn the organic soil of wetlands and create new openings with very different species composition, even open water (Loveless 1959; Vogl 1969). Since we have been told that "The importance of fire and its influence on the vegetation of the Everglades can hardly be over-emphasized" (Loveless 1959), let us begin with this example.

Although the landscape of south Florida is flat, the Everglades have many different vegetation types "from open water sloughs with sparse macrophytes to sedge and grass-dominated freshwater marshes, open pine stands and dense broad-leaved evergreen forest" (White 1994). This variation arises principally because of minor differences in elevation and hence water supply. Superimposed upon this are natural disturbances, principally fires, but also floods, droughts, storms, and freezing temperatures. These disturbances tend to be short-lived, but the communities recover from them slowly because the Everglades have very low nutrient levels. Hence, there is a basic asymmetry: disturbance is fast, recovery is slow. Occasional disturbances can generate a mosaic in which each patch of vegetation represents a different degree of recovery from the last disturbance. The rates of recovery will depend upon the amount of vegetation (if any) that persists through the disturbance, the influx of new propagules from adjoining areas, and the productivity of the site. As peat accumulates, there is a succession from open water sloughs to forested tree islands (Figure 4.6). Light fires will create patches in the vegetation; more severe fires consume peat, reduce the relative elevation, and return the site to an earlier successional stage.

During the past 20 years, approximately 25% of wet prairie and slough has been replaced by stands of saw grass, probably as a consequence of reduced flooding and decreased fire frequency. Wet prairies and sloughs have higher plant diversity, and are major sites of periphyton production and important habitats for crustaceans and fish. Drainage and fire control therefore have not only changed the vegetation, but the capacity of the area to produce and support other organisms. Restoration of the Everglades will require restoration of flooding and fire as natural disturbances, a topic to which we will return in Chapter 13.

Extensive deltas may be created largely by sediment from rivers, and shaped by flooding, but fire may also shape their composition. Jean and Bouchard (1991) believe that fires set by aboriginal inhabitants prevented woody plants such as alders

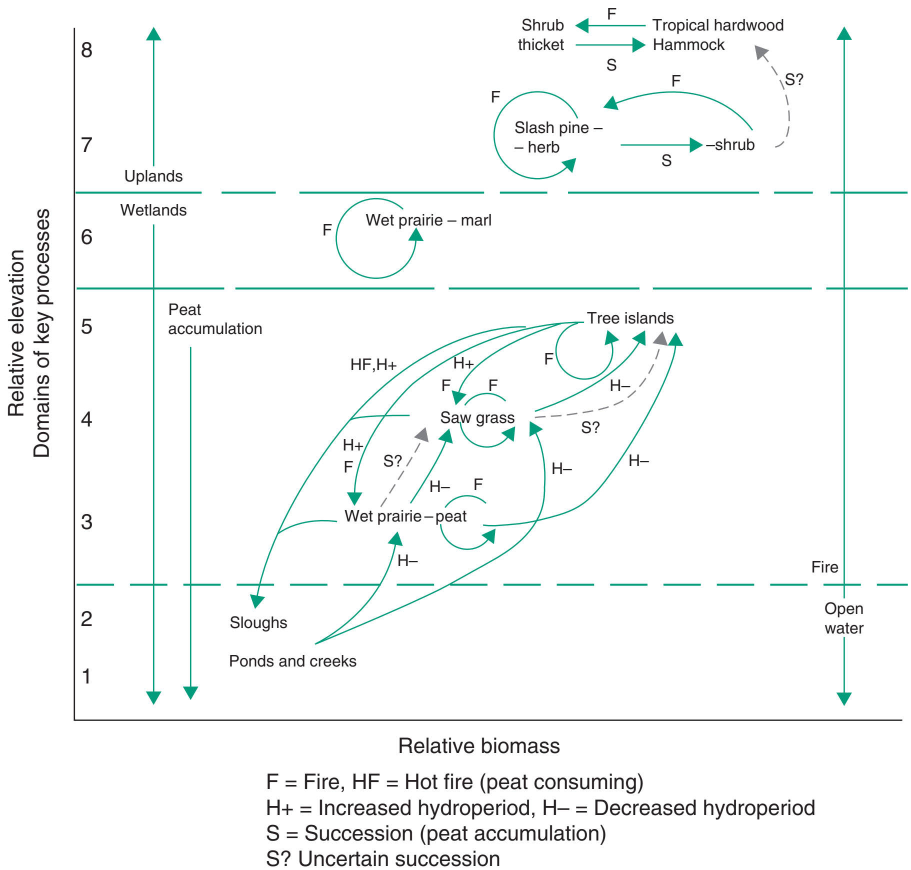

FIGURE 4.6 Plant communities of the central freshwater Everglades are strongly affected by fire. In the absence of fire, wooded tree islands can form. Light fires change plant composition, while more severe fires consume peat and can create new shallow water sloughs. (From White 1994.)

from invading wet meadows along the St. Lawrence River in eastern North America. Fire also appears to control litter accumulation and plant diversity in *Carex*-dominated wetlands along the St. Lawrence River (Figure 4.7). Farther north, in the Peace–Athabasca delta, fire reduced the density of the dominant species, and increased the number of dicotyledons that germinated (Figure 4.8).

Peatlands are particularly useful for the study of fire because, under certain circumstances, charcoal layers and macrofossils record both the fire history and the vegetation responses to the fire. *Sphagnum*-dominated peatlands are probably the most abundant peatland type in western boreal North America. Many have charcoal layers as a consequence of past fires (Kuhry 1994). The study of cores taken from the peat indicates that there has been a fire approximately every 1150 years. While this may be a surprisingly high rate of fire frequency for a wetland, it is still an order of magnitude less frequent than estimates of fire frequency in coniferous forests in western boreal Canada (e.g. Ritchie 1987).

Of course, fire frequency depends in part upon climate. During the hypsithermal, a period of warmer and drier climate about 7000 years ago, fire frequencies in peatlands appear to have been twice a high as in the past 2500 years. These fires not only burned the vegetation, but they also burned

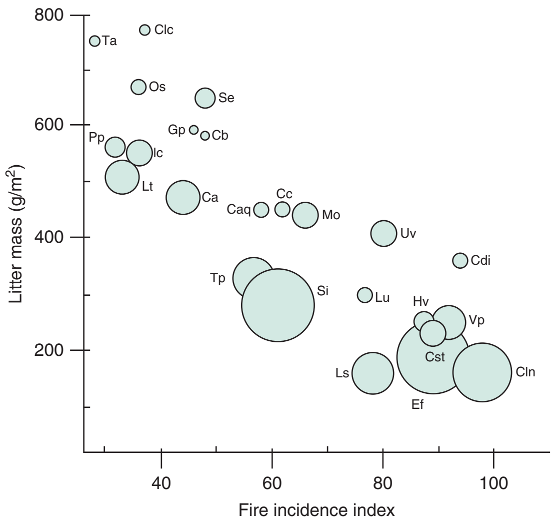

FIGURE 4.7 The amount of litter (litter mass) and plant species diversity are related to fire incidence index in a riverine wetland (letters refer to species, circle diameter indicates the diversity of the vegetation in which each occurs). (After Auclair *et al.* 1976b.)

the superficial peat deposits. In spite of this, the cores suggest that the effect of peat surface fires on vegetation was short-lived. This is apparently also the case in contemporary reports of peat fires. An interesting natural history story complements these findings; *Sphagnum* can apparently regenerate from stems at depths 30 cm into the peat deposit (estimated to be 25–60 years old) (Clymo and Duckett 1986).

What might the relationship between fire and peat accumulation be? Kuhry (1994) estimated fire frequency as the number of macroscopic charcoal layers per 1000 years, and peat accumulation rates were determined from radiocarbon dating. There was a negative relationship between peat accumulation rates and fire frequency (Figure 4.9). It appears, then, that the flush of nutrient-rich ash released by burning (and the presumed higher plant growth rates) does not compensate for the loss of peat consumed by the fire. Thus, fires retard the growth of peatlands. This has consequences for the study of global warming because peatlands are an important

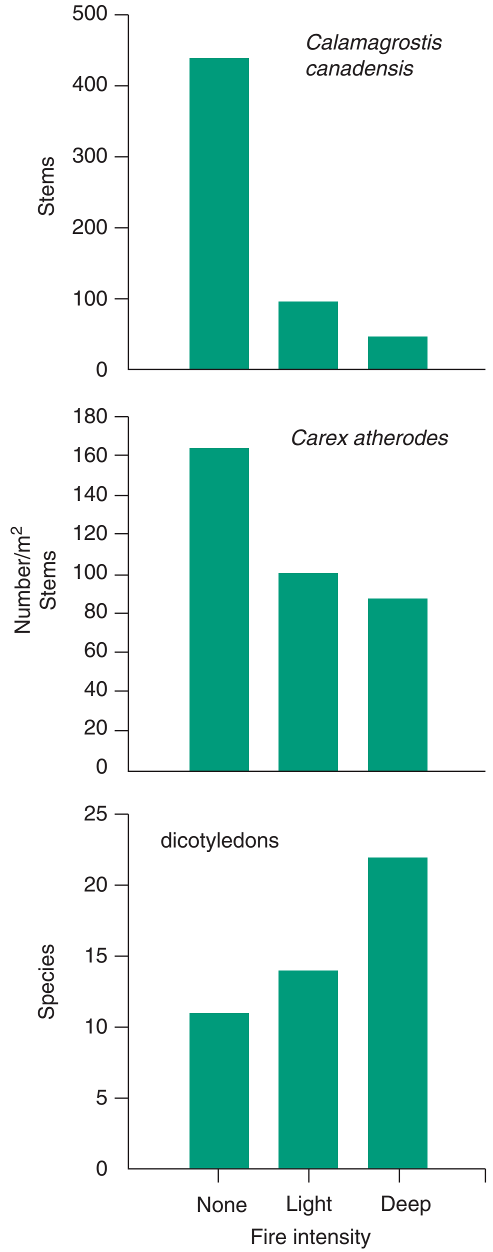

FIGURE 4.8 Some effects of fire intensity upon wetland plants in the Peace–Athabasca delta. (From data in Hogenbirk and Wein 1991.)

reservoir for carbon storage. An increase in temperature would presumably lead to higher frequencies of burning, which, in turn, would lead to further releases of stored carbon in the peatlands (Gorham 1991; Hogg *et al.* 1992) and lower rates of formation of peatlands.

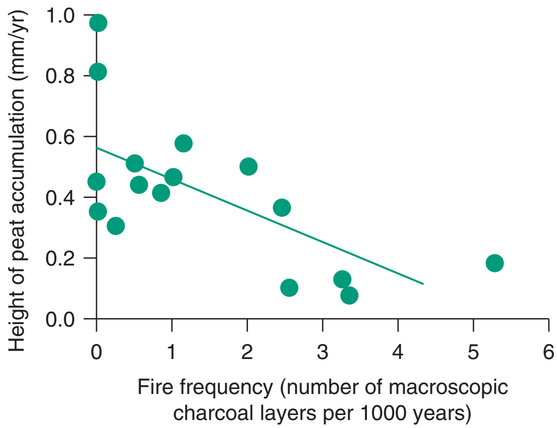

FIGURE 4.9 Peat accumulation is related to fire frequency in peatlands of western boreal Canada. (From Kuhry 1994.)

The effects of severe fires in British peatlands were observed in 1976. The period between May 1975 and August 1976 was the driest in England since at least 1727. In the North York Moors National Park 62 uncontrolled fires burned in the summer of 1976 (Maltby *et al.* 1990). Some of the most severe fires affected 11 km^2 where fire burned deeply into blanket peats and largely removed the areas of thinner peat. Further disturbance was caused by wind and rain erosion, and freeze–thaw processes. The post-fire vegetation was dominated by bryophytes, at first with *Ceratodon purpureus* and after a decade with *Polytrichum* spp. Perhaps, they suggest, bryophyte-dominated patches reflect past fires.

As fire changes the vegetation, it also affects the animals found in wetlands. One study found more birds on a burned shoreline than on an adjacent unburned area (Table 4.3). In another study of fire, experimental 0.10-ha plots were burned in water fowl impoundments (Laubhan 1995). The type of vegetation depended upon when the site was burned. Sites burned in the spring had greater cover of

Table 4.3 **Resident birds on unburned and burned portions of a shoreline wetland near the Florida/Georgia border. The numbers represent totals obtained from 63 sampling trips in 1971**

Species	Control	Burned
Common egret (*Casmerodius albus*)	5	22[a]
Bobwhite (*Colinus virginianus*)	14	1
Cardinal (*Richmondena cardinalis*)	2	14[a]
Common crow (*Corvus brachyrhynchos*)	0	10[a]
Common gallinule (*Gallinula chloropus*)	8	25[a]
Great blue heron (*Ardea herodias*)	0	8*
Little blue heron (*Florida caerulea*)	7	32[a]
Mockingbird (*Mimus polyglottos*)	0	6
Common grackle (*Quiscalus quiscula*)	0	15[a]
Red-winged blackbird (*Agelaius phoeniceus*)	66	150
Snowy egret (*Leucophyx thula*)	0	7
Total	102	290

[a] Paired *t*-tests for repeated samples, but no replication of treatments.
Source: From Vogl (1973).

annual plants and produced many seeds whereas sites burned in summer were more than three-fourths bare ground. Hence, spring burns can create favorable conditions for waterfowl by stimulating seed production, whereas summer burns produce mud flats favorable to migrating shorebirds. Burning is also used to enhance marsh vegetation for muskrats (Smith and Kadlec 1985a). Since much of the effort to manipulate marshes for wildlife is by creating patches, we will return to this topic below (Section 4.4)

4.3.3 Ice causes intense disturbance at many scales

Anyone who has seen enormous great cakes of ice grind against the shoreline during spring flooding will be impressed by the power of ice scour to modify vegetation. In salt marshes or large lakes, one can often find meter-square pieces of marsh, with 20 or more centimeters of substrate, chopped out of the ground and moved aside. In floodplains, trees may have scars near eye level that mark where ice cakes hit them during the spring.

The effects of ice begin with freezing along the shoreline forming an “ice foot” (Geiss 1985). Sediment can become incorporated into this ice foot. There is also the constant grinding as ice freezes to the shore and shifts as water levels rise and fall. Movement of spring ice can create ridges and a distinctive undulating topography along shorelines (e.g. Bliss and Gold 1994). The power of ice to create such ridges is vividly illustrated by a single ice push occurrence in Lake Ontario in March 1986, which piled ice to a height of 2.5 m and moved boulders greater than 200 kg (Gilbert and Glew 1986). Entire sections of shoreline can be torn out of place when ice is lifted by rising water levels (Figure 4.10). Many northern rivers have a conspicuous trim line where ice has cut a sharp lower boundary to the riparian forest, allowing herbaceous wetland to expand (Gill 1973); you can see this in Figures 2.13 and 2.14. Ice can also create dams and change local flood regimes and water flow patterns (Prowse and Culp 2003).

One way to measure how ice damage varies with elevation is to put wooden pegs into a wetland in the autumn, and measure the amount of damage accumulated over different periods of time. Figure 4.11 shows a typical vertical profile of ice damage on shores, with and without exposure to waves. Organic content and silt/clay content are also negatively correlated with ice damage (Table 4.4). Frequently, woody plants grow closer to the water on shores protected from ice damage (Keddy 1983). A substitute for such direct measurements is to determine the water levels during the period when a shoreline is frozen (Rørslett 1985).

Given the importance of ice scour on shorelines, it seems that there is much more that could be done with such simple techniques. For example, entire beds of pegs of different sizes could be used to map both the intensity and area of winter disturbance. These could be compared to known water levels during the winter. Both could be tested for their ability to predict vegetation patterns.

4.3.4 Waves create disturbance gradients

Waves are events of very short duration and high frequency. But the cumulative effects of chronic exposure to waves are complex. In his study of British lakeshores, Pearsall (1920) summarizes both direct effects (e.g. biomass removal from plants, uprooting, seed dispersal) and indirect effects (e.g. erosion of nutrients, sorting of substrates, litter transport). Exposure to different amounts of wave energy can create very different types of wetland communities.

Information on wave effects goes back at least as long as people have sailed. Storms destroyed much of the Spanish Armada, thereby changing European history. They also badly damaged artificial channel ports constructed for the Normandy landings in the Second World War, almost changing European

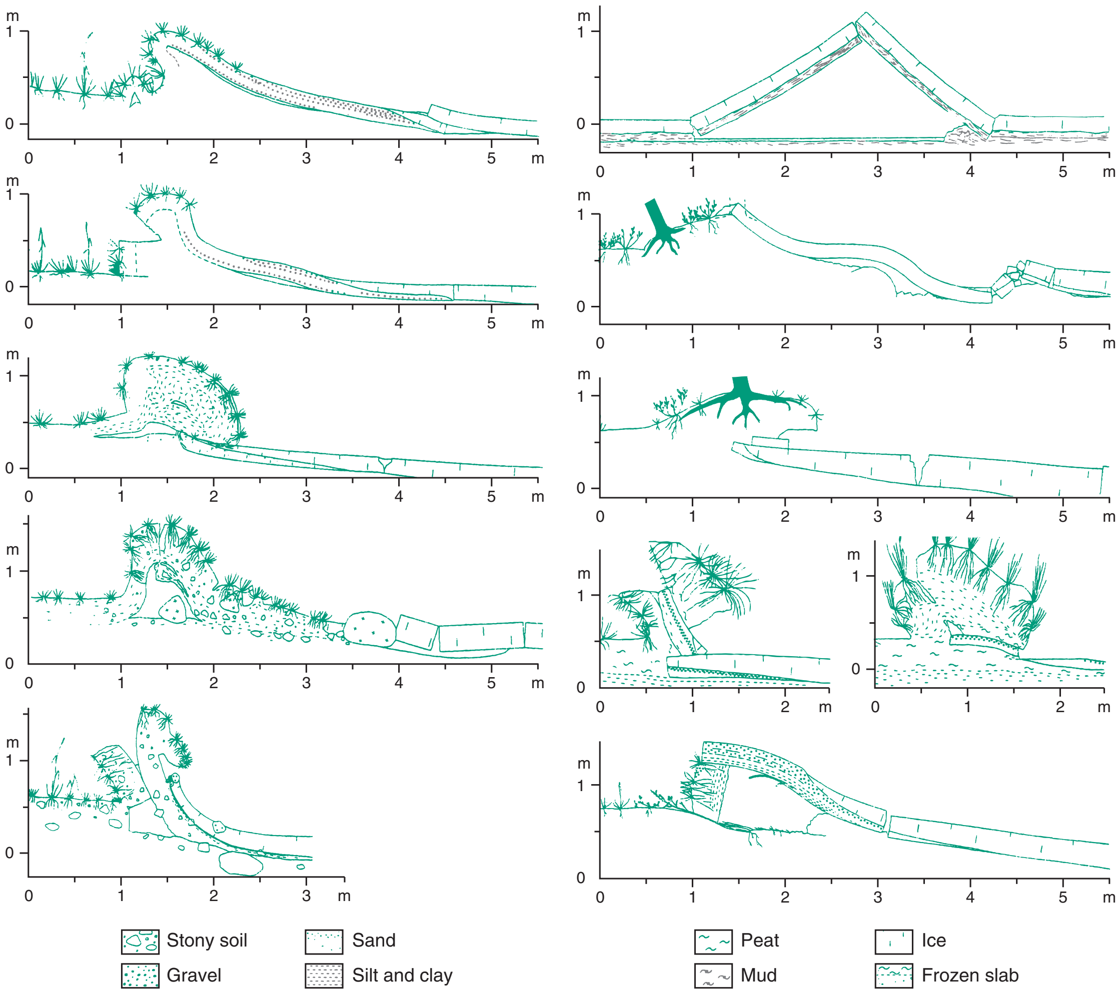

FIGURE 4.10 Ice can have a major impact upon shoreline wetlands and shoreline topography. (From Alestalio and Haikio 1979.)

history again (Blizard 1993). It is therefore natural that much of the work on waves can be found in manuals published by military agencies including the U.S. Army Corps of Engineers (e.g. U.S. Army Coastal Engineering Research Center 1977). Their equations have been recently adapted for use by aquatic ecologists (e.g. Keddy 1982, 1983; Weisner 1990). Overall the principle is simple: the amount of wave energy arriving at a shoreline increases with distance to the opposite shore (fetch) and with the number of directions from which waves can arrive. Using data on fetch and wind directions, one can rank areas of shoreline in terms of relative degrees of wave energy that they experience. Such exposure gradients change the proportion of silt and clay in sediments, and, in turn, the zonation patterns of shoreline species. Moderate exposure to waves seems to expand the areas of wet meadows and marshes, while high levels of exposure produce open sand or gravel shorelines.

Chronic wave exposure removes fine particles and leaves coarser substrates. Soil texture is known to have major effects upon germination (Harper *et al.*

Table 4.4 **Scouring by ice can reduce the silt and clay content of the soil (an indirect measure of fertility), reduce the organic content of the soil, and increase the area of habitat without shrubs, as shown by these data from a temperate zone lakeshore. Ice scour was measured by over-winter damage to wooden pegs in $n = 121$ quadrats**

	Silt and clay	Organic content	Shrub-free area
Ice scour	−0.37[a]	−0.47	0.31

[a] Correlation coefficients, $p < 0.001$.
Source: After Wisheu and Keddy (1989b).

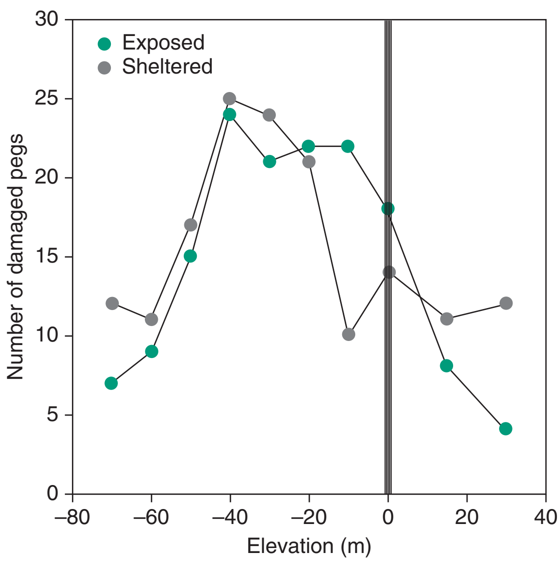

FIGURE 4.11 Ice damage (measured by the number of ice-damaged pegs) as a function of elevation on two contrasting shorelines. The vertical line shows typical late summer water levels. (Unpublished data in which 25 1.25-cm diameter wooden pegs, each 20 cm long, were pounded 10 cm into the ground in the summer of 1980 and damage was assessed the following spring. The study site is described in Keddy 1981.)

1965; Oomes and Elberse 1976; Vivian-Smith 1997). Given the conspicuous gradients in soil texture on shorelines, and the importance of regeneration from buried seeds (Salisbury 1970; Leck *et al.* 1989), we might anticipate that germination of marsh plants will be significantly affected by exposure. When seeds of ten shoreline plants were sown along a soil texture gradient, germination was generally highest in the fine susbstrate (Keddy and Constabel 1986).

Waves can also amplify the effects of ice and kill plants directly. When we planted 840 wetland plants on seven sections of lakeshore (Wilson and Keddy 1988), fewer than one-third (265) were still alive the following year. Some species were particularly sensitive; *Viola lanceolata* and *Drosera intermedia* were both nearly all dead. The remaining species had rates of mortality from 32% to 91% depending upon the exposure of the site to waves. Since the effects of waves and ice may vary from year to year, depending, say, upon the timing of ice breakup and the direction of winds at that time, these factors together can impose a great deal of disturbance that, while predictable in the long run, is local and patchy on a year-to-year basis.

4.3.5 Animals create many types of disturbance in wetlands

Animals eat plants and thereby remove biomass. An entire chapter on grazing follows this one in Chapter 6. The general conclusion from that chapter is that grazing can have major effects on wetlands, but the area of habitat affected is often rather small. There are exceptions – extreme damage can occur over large areas occasionally, when large populations of muskrats feed in prairie marshes, or large populations of geese feed in coastal marshes.

Animals have other effects beyond grazing, however. We have already noted the effects of beavers on wetlands (Section 2.3.3). Another animal that makes ponds, albeit much smaller ponds, is the alligator (Figure 4.12). During winter dry periods, gator holes may be the only ponds remaining in a wetland (Loveless 1959; Craighead 1968). The alligator maintains ponds by pulling loose plants and dragging them out of the pool. Thicker muck is either pushed or carried to the edges of the pond.

Gator holes were once a predominant feature of southern wetlands, and are still evident in the

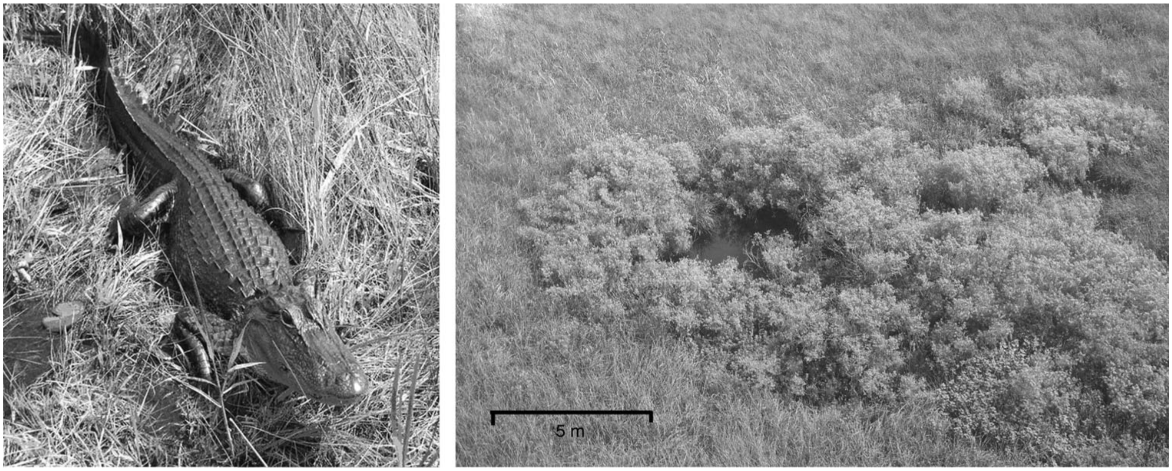

FIGURE 4.12 A gator hole in the Everglades along with its creator and occupant (not to scale). The alligator excavates a hole, which supports aquatic plants and animals, and the earth mound around the edge of the hole develops its own characteristic plant community. Large expanses of wetland can be dotted by such holes and mounds. (See also color plate.)

Everglades. Craighead reminds us that alligators were once much more common, that "in the first two decades of this century every inland pond, lake and river held its quota of alligators." He suggests a density approaching one alligator per acre in some regions. The naturalist William Bartram, who traveled the St. John's River in 1774–6, described alligators massed around his boat. He reported (Bartram 1791) that, when camping on beaches, it was necessary to keep a large fire burning all night for protection.

Gator holes are "reservoirs for an amazing biological assemblage." Within them live "diatoms, algae, ferns, flowering plants, protozoans, crustaceans, amphibians, reptiles and fish" (Craighead 1968). The productivity of these ponds is enhanced by uneaten food. Larger animals, such as hogs and deer, are killed by drowning but may be left for several days for ripening. The aquatic flora includes widespread genera such as *Myriophyllum*, *Utricularia*, *Potamogeton*, *Nymphoides*, and *Najas*. The shallow water near the banks has marsh genera such as *Peltandra*, *Pontederia*, and *Sagittaria*. Connecting the gator holes are well-developed trail systems. These trails may be eroded by heavy gators into troughs that are 15 cm deep and 60 cm wide. Up to this point, we have considered alligators to be a cause of disturbance; alligators may also simultaneously reduce the rates of disturbance by other animals like nutria (Keddy *et al.* 2009).

Animals and physical factors may both have impacts on wetlands. Prairie potholes (Section 2.3.4) are affected by four major kinds of disturbance, all of which can shift the type of wetland vegetation that occurs (van der Valk and Davis 1976, 1978). First, water may act as a disturbance. If there is too little water, the pond becomes a mud flat and many of the marsh plants die (Figure 4.13, upper left). If there is too much standing water, and they are submerged for several years, many marsh plants will also die (Figure 4.13, lower right). In either case, the return of more typical water levels allows regeneration of the plants from buried seeds, the "marsh seed bank" in the center of the figure. Muskrats also feed on wetland plants, and since they will dig up plants to eat the rhizomes too, their effects can be severe. If muskrat populations become dense enough, they can strip the vegetation from a wetland, producing what is known as an "eat out." Fire can also burn through potholes during periods of drought. Hence, the

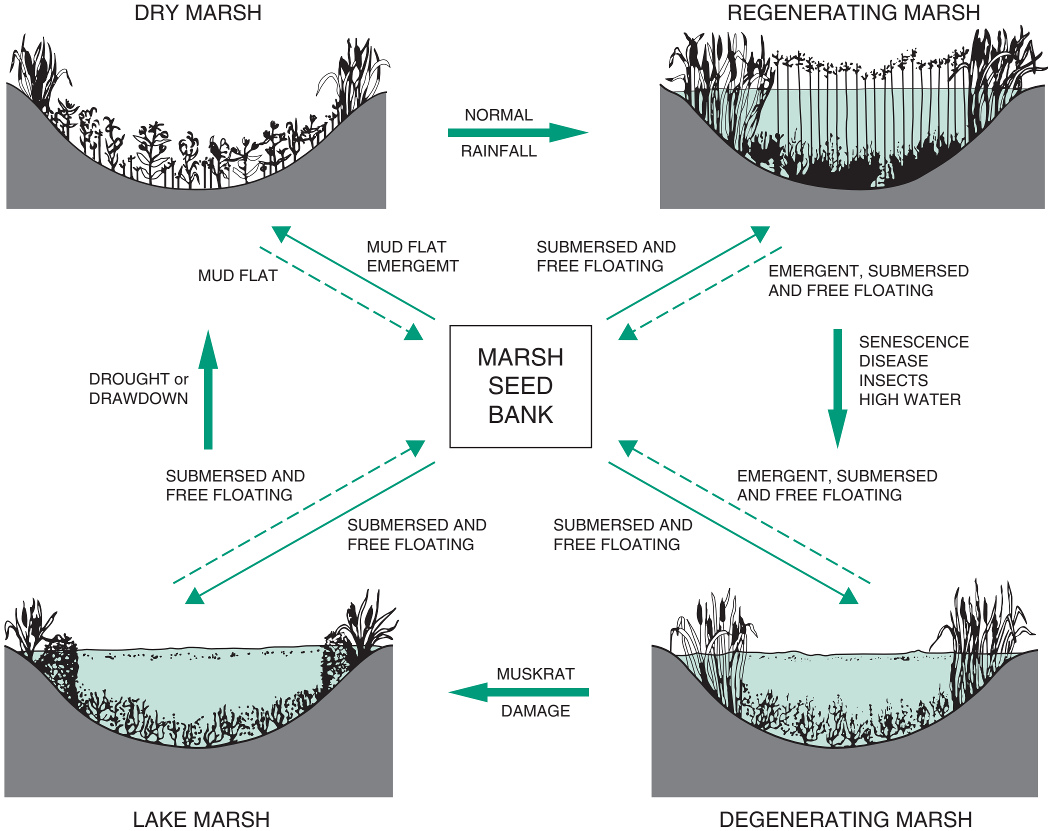

FIGURE 4.13 Disturbance by muskrats and drought can shift prairie potholes from one ecological state to another. (After van der Valk and Davis 1978.)

vegetation in a prairie pothole depends upon how long ago a disturbance occurred, whether the disturbance destroyed only the shoots or the rhizomes as well, and how long the vegetation has had to recover.

4.3.6 Traditional disturbances include mowing and peat-cutting

In Europe there is a long cultural history of mowing wetlands (Elveland 1978, 1979; Elveland and Sjoberg 1982; Müller *et al.* 1992). At some sites with a long history of mowing or grazing, distinctive plants and animals occur as a consequence of the continual removal of biomass. Mowing is common elsewhere, too. In China, reeds are collected for paper-making. In Iraq reeds are used for making homes. Many small farms in North America used to depend upon collection of "marsh hay" for feeding animals. When mowing ceases, stands of a few large marsh plants such as *Phragmites* or *Typha* may replace meadows that have high plant diversity.

Peat-cutting (Figure 4.14) could be considered a more extreme kind of mowing, in that the substrate is removed to be burned as a fuel. Disturbance by past peat-cutting is thought to be an important factor generating plant diversity in European peatlands. For example, there were nineteenth-century peat cuttings in the Norfolk Broadland where 50–70 cm of peat had been removed, down to the underlying

FIGURE 4.14 Peat is a traditional source of fuel in many northern regions, and peat-cutting is a source of disturbance in peatlands. This stereograph shows cutting and carting turf at a bog near Kiltoom, County Roscommon, Ireland. (Courtesy Library of Congress, P&P.)

clay (Giller and Wheeler 1986). These became ponds ("turf ponds") which now have unusual vegetation types including species-rich fens. To maintain such rich fen communities, continued peat-cutting may be a necessary management tool. This is consistent with the suggestion that peat-cutting will be necessary in much of western Europe in order to remove nutrients accumulating from atmospheric deposition (Sansen and Koedam 1996). Modern peat-cutting for the horticultural industry creates much larger disturbances, with the result that restoration becomes more complicated (Campbell and Rochefort 2003; Cobbaert *et al.* 2004).

Prairie potholes are also affected by mowing. Walker and Wehrhahn (1971) studied the environmental factors controlling prairie wetlands in Saskatchewan, Canada, and concluded that the most important environmental factor was disturbance ("grazing, mowing and natural disturbance"). This result occurred in spite of their original intention to avoid disturbed sites. Species such as *Eleocharis palustris, Glyceria grandis, Alopecurus aequalis*, and *Beckmannia syzigachne* occurred in disturbed areas.

4.3.7 Logging is a widespread disturbance in forested wetlands

Logging certainly removes biomass from a forest and is therefore a disturbance. The removal of trees from wetlands continues around the world, from people hand-harvesting mangrove firewood in the Ganges delta, to enormous skidders hauling second-growth cypress logs out of the Mississippi River delta. Some wetlands are protected to varying degrees by legislation requiring sustainable logging. Others are not. The removal of the biomass itself may have relatively small effects, compared to secondary effects, which include ruts from skidders and the construction of roads and canals to transport logs or logging equipment. There is no space here to discuss properly the status of the world's wetland forests, and the degree to which they are, or are not, being logged in a sustainable manner. There is

FIGURE 4.15 A two-drum pull boat working in a canal that was cut into a cypress swamp in Louisiana (date unknown). (From Williams 1989.)

enormous variation in types of logging and degrees of sustainability. Canada allows logging of peatlands in the boreal forest. The alluvial forests of the Congo remain at great risk. The military dictatorship in Burma is depleting that country's forests rapidly. Overall, we can say that the ultimate criterion for evaluating logging disturbance has to be sustainability – that is, whether the forest will regenerate. Since the seedlings of wetland trees are sensitive to flooding, minor changes in hydrology can have a big impact on whether seedlings can re-establish.

Let us look at one historical example – cypress swamps (Norgress 1947; Mancil 1980; Williams 1989; Conner and Buford 1998; Keddy *et al.* 2007) – which typifies the logging history of wetlands, and which illustrates how the negative effects can linger and interfere with regrowth. Large areas of the American south were once covered in cypress forest, or cypress mixed with species of tupelo (recall Figure 2.10). The Timber Act of 1876 allowed the sale of large tracts of swamp for 25 to 50 cents per acre. Huge tracts were purchased by wealthy timber barons. Teams of loggers felled the enormous trees and steam-powered pull boats used cables and winches to drag the fallen trees to the open water. Canals for pull boats were excavated at 3048 m intervals, allowing entire forests to be stripped systematically (Figure 4.15). The repeated skidding of logs along a track scoured a mud- and water-filled ditch 1.8–2.4 m deep. In some places, logs were winched into canals from one point, in which case the pull boat runs radiate outward like spokes of a wheel. Logging activity peaked in the early 1900s, and a few decades later the forests were exhausted and the mills began to close. In summarizing the impact of the industry on the local economy, J. H. Foster of the U.S. Forest Service said the lumber industry:

> . . . obtained their lands at low prices and have made fortunes from the increase in the value of the timber. The industry does not develop the country permanently and the earnings are seldom invested where they are of any benefit to the community. (Norgress 1947, p. 1051).

More than 100 years later you can still see both parallel and wheel-shaped markings in the wetlands north of New Orleans (Figure 4.16). As a result, not only were the trees removed, but the hydrology was permanently changed, which may have made these swamps more susceptible to saltwater pulses from

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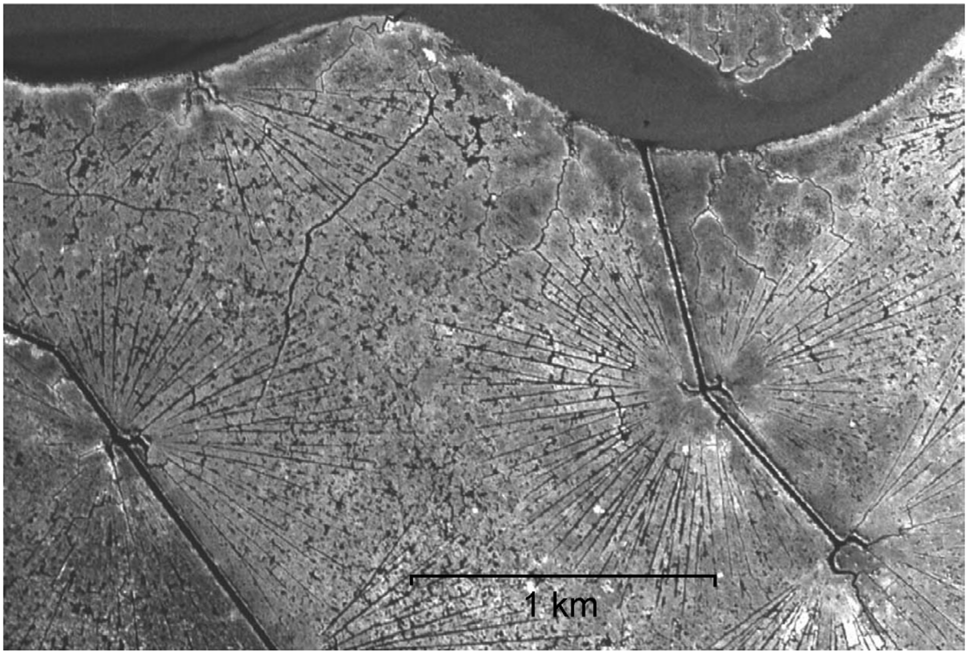


FIGURE 4.16 Aerial view of the wetlands between Lake Maurepas and Lake Pontchartrain in Louisiana. These marshes were once cypress swamps. The parallel and wheel-shaped markings are mud- and water-filled ditches made by pull boats dragging trees through the swamp during logging operations in the early twentieth century.

hurricanes, and less able to respond to rising sea levels. Large areas with failed regeneration have become anthropogenic marshes. The degree to which coastal swamps can be re-established requires that we consider not only past logging history, but the effects of levees, of sediment deposition, and of rising sea levels.

4.3.8 Hurricanes impose a predicable series of events

Humans tend to view hurricanes and other major storms as catastrophes. From the point of view of a wetland, however, a hurricane is simply a major but infrequent disturbance. Storm tracks show that major storms produced by warm ocean water are a regular occurrence in coastal areas (Figure 4.17). Humans have short memories, and often do not see the recurring element of hurricanes, even when warned that they are inevitable. Wetlands, and the species in them, have, however, been affected by hurricanes for tens of thousands if not millions of years. The main effects of a hurricane are predictable (e.g. Conner *et al.* 1989; Loope *et al.* 1994; Turner *et al.* 2006):

- felling of trees (wind)
- saltwater pulses (storm surge)
- freshwater pulses (rain)
- sediment redistribution (waves).

This sequence of events is more or less predictable.

Felling of trees When the storm comes on shore, the strong winds fell trees, creating tree-fall mounds and gaps for regeneration. There is good evidence that trees native to gulf coast forests such as longleaf pine and bald cypress are less damaged by strong winds than species that have been

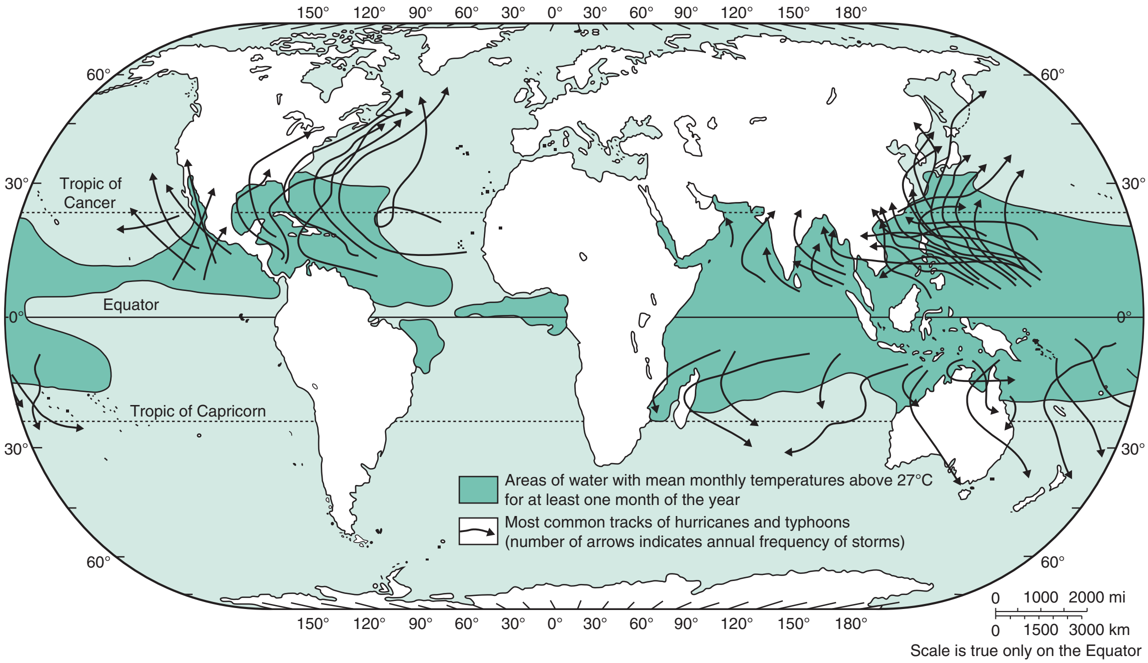


FIGURE 4.17 Hurricanes and typhoons are a natural and recurring source of disturbance in wetlands. (From *Encyclopedia Britannica* 1991.)

produced by human modification of these landscapes. It is possible that the dead trees stimulate increased fire in the wake of hurricanes (Myers and van Lear 1998).

Saltwater pulses Strong winds push a wall of seawater inland. This causes flooding, and it raises the salinity of the wetlands that are inundated. This wall of seawater carries seeds and woody debris across different kinds of wetlands. When it recedes, salinity levels are elevated and salt-sensitive species like bald cypress may die as a consequence.

Freshwater pulses Heavy rainfall also accompanies hurricanes, raising local river levels, and diluting the salt water. Hence, it is by no means obvious that the combination of a saltwater pulse followed by heavy rain will necessarily change local salinity levels.

Sediment redistribution The waves generated by the winds can churn up sections of marsh, releasing sediment, and then redistribute the sediment (Liu and Fearn 2000; Turner *et al.* 2006). At larger timescales, hurricanes are implicated in both destroying and building coastal wetlands. River deltas normally go through cycles of building aggradation and degradation over some thousands of years (Boyd and Penland 1988, Coleman *et al.* 1998) (Figure 4.18). Often, the last trace of an ancient delta is a chain of offshore sand islands. The process may not be smooth. Major floods may build sections of new delta; major hurricanes may destroy sections of degrading deltas. The process may therefore be more like a series of steps.

The effects of hurricanes can be compared to those of fire. Both are natural processes that have affected wetlands for millennia. Both are viewed by humans as catastrophes. Both, however, are essential for

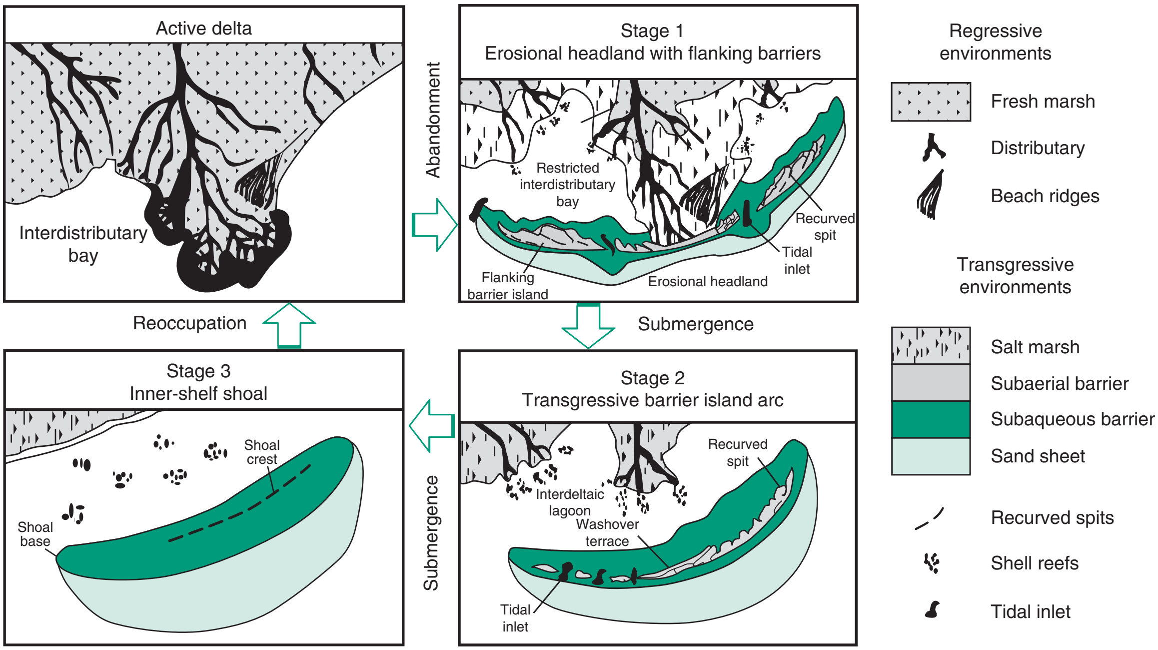


FIGURE 4.18 Deltas grow as sediment accumulates at the mouth of a river, but once the river changes course, the delta gradually deteriorates into islands and offshore shoals. Storms and hurricanes play a significant role in reshaping the sediment. (From Penland *et al.* 1988.)

producing the natural array of wetland types and natural distribution of plants and animal species. Perhaps the best advice we can give humans is not to build their homes in areas that flood regularly or burn regularly.

4.3.9 Frosts can convert mangrove swamp to salt marshes

Cold can also kill plant tissues and change wetlands. One important transition point in coastal wetlands is the temperature threshold at which mangroves can, or cannot, survive. At this threshold, herbaceous wetlands become wooded wetlands. This transition point occurs at about 32° North latitude and 40° South latitude (Stuart *et al.* 2007). Pulses of cold weather kill mangroves. For example, in the 1980s, cold winter weather killed mangrove forests (*Avicennia germinans*) in Florida, and it is estimated that 30 years will be required for recovery (Stevens *et al.* 2006). Similar events occurred in Louisiana. Hence, frost sets the latitudinal limits of mangal (Figure 4.19).

A warmer climate with rising sea levels might allow mangroves to expand northward into what are now cypress marshes, as well as possibly changing cypress swamps into mangrove swamps. However, this scenario requires several cautions. If an increase in mean temperature is accompanied by an increase in variation in temperature, it is possible that cold pulses flowing from the north will remain sufficiently frequent to kill mangroves. Other factors associated with warmer climates include rising sea levels, increased hurricane frequency, and increased salinity from evapotranspiration. Overall, however, models suggest that if global temperatures rise, the area of mangroves in areas like Florida is likely to increase with time, probably at the expense of freshwater wetlands (Doyle *et al.* 2003).

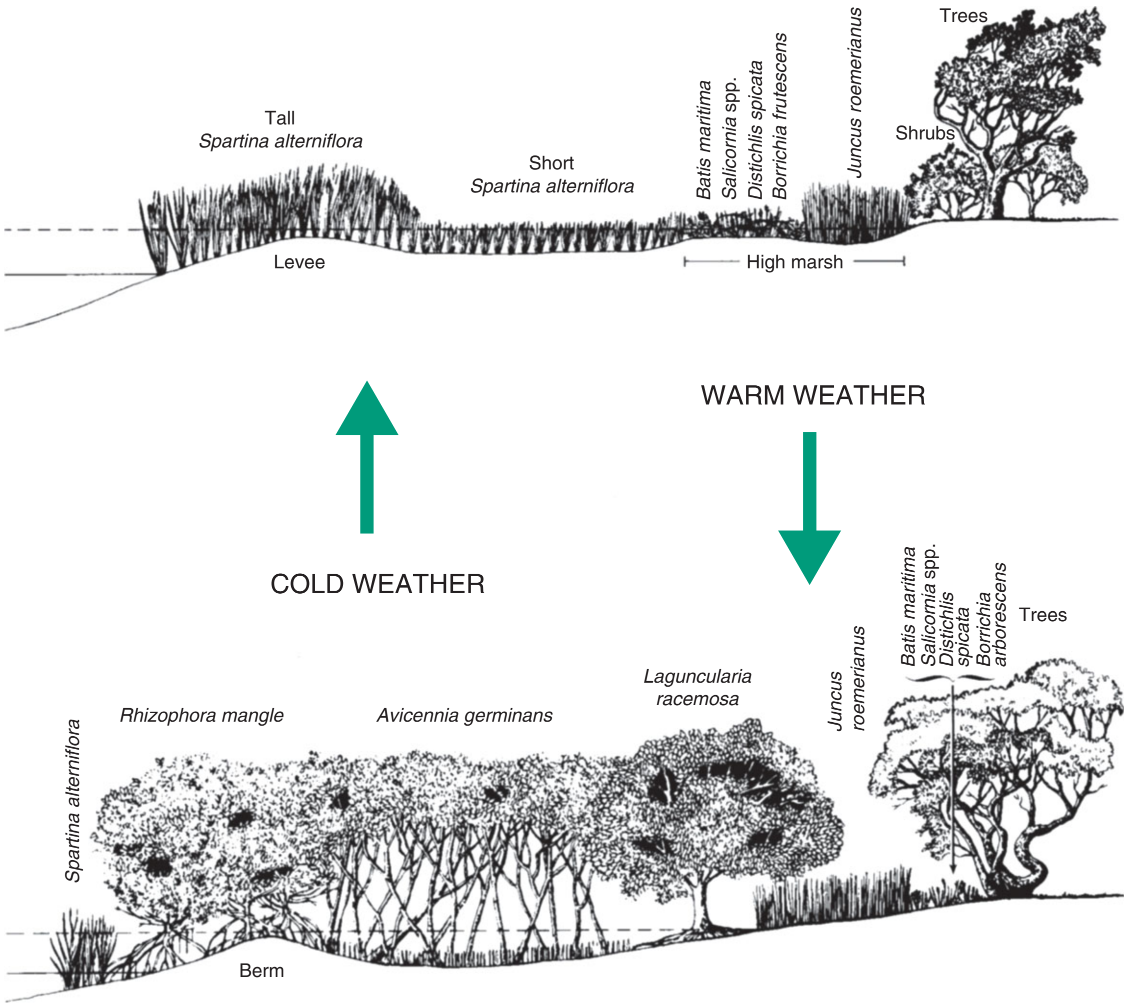
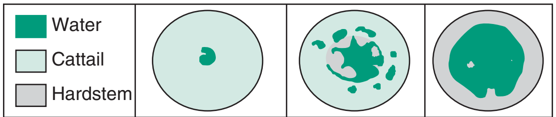


FIGURE 4.19 The threshold between herbaceous salt marsh and mangrove swamp is set by the frequency of periods of freezing weather. The top panel shows northern Florida and the bottom panel shows southern Florida. (Adapted from Montague and Wiegert 1990.)

4.4 Disturbances can create gap dynamics

In some situations, disturbance occurs as discrete patches (Sousa 1984; Pickett and White 1985). In such circumstances, one can measure the rate at which new patches are formed, and the rate at which they are colonized. Much of the research on patch dynamics focuses on forests, where storms can create patches ranging from the size of a single fallen tree to entire stands blown down (Urban and Shugart 1992). There are fewer studies of patch dynamics in wetlands, yet we might reasonably expect this



Water depth	Shallow	Medium	Deep
Vegetation	Dense	Moderate	Sparse
Size of bird populations	Medium	Large	Small
Bird species richness	Low	High	Low
Number of muskrats	Few	Many	Few

FIGURE 4.20 Gaps in the vegetation create habitat interspersion in freshwater marshes and control the suitability of the marsh for ducks, muskrats, and other species. (After Weller 1994a.)

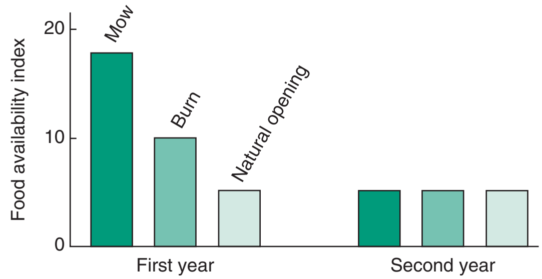


FIGURE 4.21 Burning and mowing can change the abundance of invertebrates in marshes. (From Ball and Nudds 1989.)

process to be important. Examples might include patches burned by fire, eaten by muskrats, cut out by ice cakes, killed by floating mats of litter, or buried by alluvial deposits. We will look at examples from fresh and salt marshes.

4.4.1 Patch creation and management of freshwater marshes

Waterfowl prefer patches in marshes. Patches can be formed by flooding, fire, or herbivores (e.g. Weller 1978, 1994a; van der Valk 1981; Ball and Nudds 1989). Figure 4.3 showed that as little as 3 years of flooding can kill stands of emergent plants and create a new patch type. Recurring disturbances can create a mosaic of different vegetation types; the simplest example may be dense stands of cattails interspersed with patches of open water (Figure 4.20). Experimental studies have shown that breeding ducks select a 1 : 1 ratio of these two patch types (e.g. Kaminski and Prince 1981).

Since many shallow-water marshes are slowly dominated by cattails, mosaics can often require deliberate human manipulation (Verry 1989). A variety of mowing implements from machetes to 50-hp tractors have been used to cut cattail stands (Kaminski *et al.* 1985). While cutting temporarily reduces shoot density, the main factor limiting regrowth is the duration of flooding after the mowing. A depth of 40 cm of water in the spring can prevent regrowth (Kaminski *et al.* 1985). In another mowing study, circular patches of 0.02, 0.09, and 0.15 ha were either cut or burned into cattail stands along Lake St Clair in Canada (Ball and Nudds 1989). Food availability for waterfowl was estimated by sampling the aquatic invertebrates. Mowed patches had higher invertebrate availability than burned patches (Figure 4.21), but there was no detectable effect of patch size. They conclude that, if the objective is to increase food supplies for ducks, mowing is superior to burning; not only does it produce more invertebrates, but the clearings last longer.

Fire and mowing were also manipulated in a 3500-ha brackish marsh in California, where over 100 000 dabbling ducks may over-winter (Szalay and Resh 1997). The dominant plant here is the grass *Distichlis spicata*; stands of this plant were either subjected to hand mowing or burning in late summer, and then flooded. Since flooding immediately after burning or mowing can eliminate *Distichlis* (Smith and Kadlec 1985b), the experimental flooding was delayed until some weeks after mowing. During the following winter, invertebrate biomass was sampled. The dominant macroinvertebrates were a *Chironomus* larva (Diptera) and a water boatman, *Trichocorixa* (Hemiptera). Copepods were the dominant microinvertebrate. Burning increased the abundance of *Chironomus* and *Trichocorixa* by roughly a factor of ten relative to controls, but mowing did not have significant effects. Invertebrate populations are thus sensitive to perturbations such as fire and mowing, and the timing, area, and intensity of disturbance can affect their relative abundance.

4.4.2 Salt marshes: recolonization of bare patches is mainly by rhizomes

In the typical zonation of salt marshes in eastern North America two species are dominant, *Juncus gerardi* higher on the shore and *Spartina patens* lower on the shore. Bare space is often generated when dense mats of litter are deposited by tides. The litter is mainly leaves of *S. alterniflora*. If covered for more than 8 weeks, marsh plants are generally killed (Bertness and Ellison 1987). The resulting bare patches are recolonized in several ways. Some species arrive as seeds (e.g. *Salicornia europea*). Some species arrive as runners from adjoining plants (e.g. *Distichlis spicata*). Eventually the patches are reinvaded by *J. gerardi* and *S. patens*. There is thus a continual process of patch creation and patch recolonization (Bertness 1991). Unlike in freshwater marshes, seed banks appear to play only a minor role in the re-establishment of vegetation; instead, vegetative expansion from adjoining plants predominates (Bertness and Ellison 1987; Hartman 1988; Allison 1995).

To explore these dynamics, Bertness made artificial bare patches of three sizes ranging from 0.06 to 1 m^2. He then transplanted seedlings and tillers of four species into these patches and recorded their survival (Figure 4.22). He reports that larger patches (left) had higher salinity than the surrounding vegetation, and that survivorship therefore increased as patch size/salinity decreased. Transplants into existing vegetation (as shown by the column C for controls) also had very low survival in spite of low salinity in the surrounding vegetation, showing that competition from existing vegetation also prevents the establishment of transplants (see Chapter 5). Apparently competition is temporarily reduced in gaps and the important factors then become relative colonization rates and relative tolerances to salinity. The relative amounts of *Salicornia europea*, *Distichlis spicata*, and *Juncus gerardi* or *Spartina patens* therefore depend upon the frequency of disturbance in these marshes.

In more southern areas, particularly those with Mediterranean-type rainfall patterns (wet winters, dry summers), salinity may play an important role in creating large patches of new marsh. During dry years, hypersaline conditions develop; marsh species such as *Spartina foliosa* and *Typha domingensis* cannot tolerate these conditions and are slowly replaced by salt-tolerant species such as *Salicornia virginica*. This process is reversed during abnormally wet years, when higher stream flows and longer rainfalls flush accumulated salt from the soil. This creates a low-salinity gap in which seedlings can germinate and establish. If the gap is short (3–6 weeks), only halophytic species such as *S. foliosa* can establish, but if it is extended, brackish and freshwater marsh species can establish as well. The duration and intensity of the next hypersaline period will then determine which of these species survive. There is thus a constant cycling through different vegetation types driven by changes in moisture supply (Figure 4.23).

On the topic of saline wetlands, you could think about the effects of frost on mangroves as generating a similar type of patch dynamics. Rather than there being a single point that defines the northern limit of mangroves, we may think of the zone receiving frost as a region in which mangroves suffer recurring death and recolonization, thereby driving changes in the composition of other shoreline species.

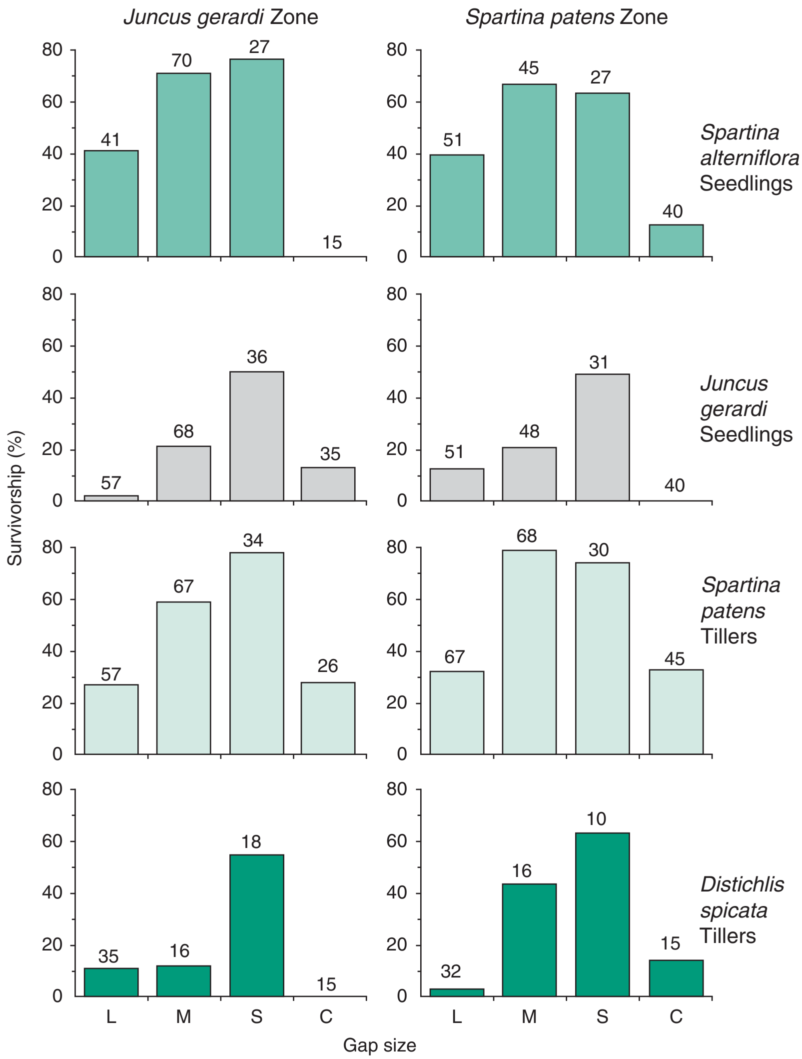


FIGURE 4.22 The effects of the size of gaps upon the survival of four transplanted marsh plants (L = large, 1 m^2; M = medium, 0.5 m^2; S = small, 0.25 m^2; C = control, dense vegetation). (From Bertness 1991.)

4.5 Measuring the effects of disturbance in future studies

It is often difficult to compare studies of disturbance because there are so many kinds of disturbance. If we are going to understand better the effects of disturbance on plant communities as a whole and wetlands in particular, we must more precisely define, and then measure, the relative effects of disturbance upon community properties. One way disturbance could be measured consistently is to measure relative change in species composition. There is a wide range of measures of similarity between samples (Legendre and Legendre 1983). Using a standard measure of ecological similarity, one could define a range of disturbance intensities from 0 (the community is the same before and after

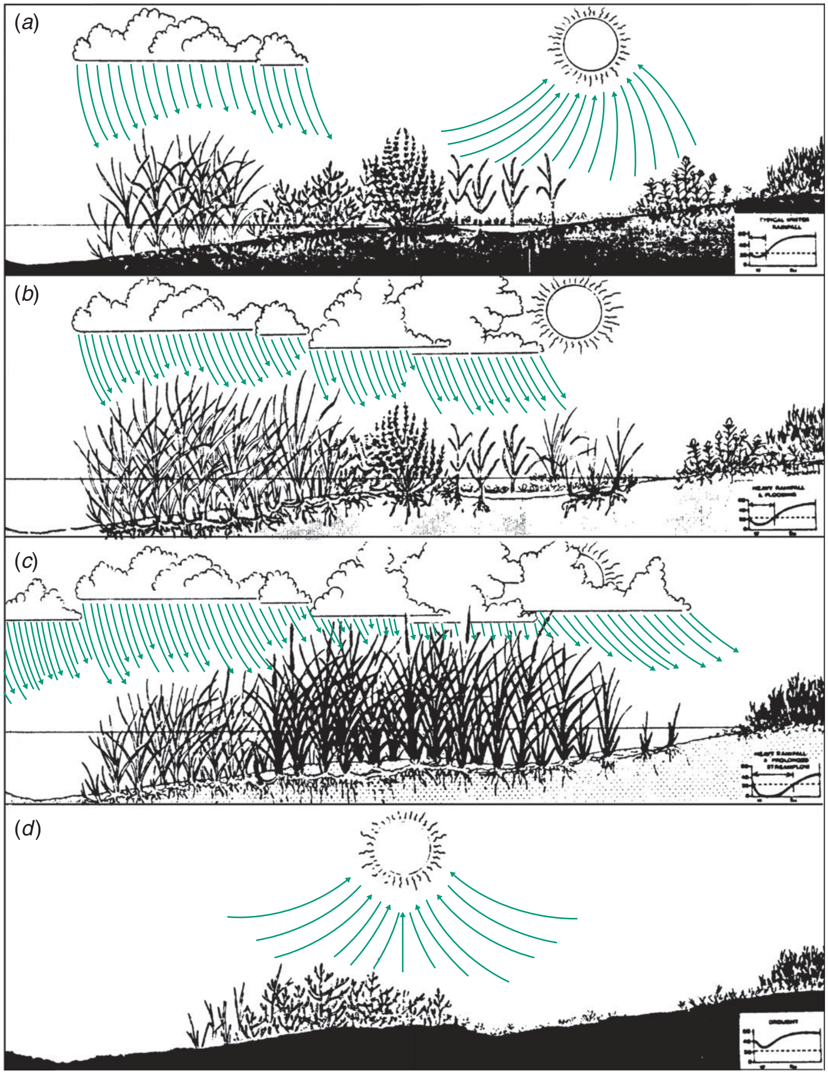


FIGURE 4.23 Cyclical changes of salt marsh vegetation in arid climates. (*a*) Typical situation where brief periods of low salinity allow salt marsh species to germinate and establish. (*b*) Floods reduce salinity and allow expansion of *Spartina foliosa*. (*c*) Prolonged flooding illuminates salt marsh vegetation and allows brackish marsh species to establish. (*d*) Periods without rainfall or flooding create hypersaline conditions which kill all but a few highly salt-tolerant species such as *Salicornia virginica*. (From Zedler and Beare 1986.)

the event) to 1 (the community is completely different after the event). Figure 4.3 showed that the deeper the flooding of a wetland, the more rapid the decline in abundance of two emergent plants. If we were measuring the degree of similarity each year, it is obvious that the dissimilarity through time increases most rapidly with the deepest flooding (that is, most intense disturbance). We would observe similar effects if, instead of using composition, we used biomass of these plant species as our measure.

In addition to measuring disturbance consistently, it would also be useful to determine how the effects of disturbance vary among different types of habitats or among different groups of species. Here is an example that did both. Moore (1998) artificially created bare patches in five different riverine wetland habitats ranging from exposed sandy shorelines to sheltered organic bays. At each of the five sites, 1-m^2 bare plots were created and the vegetation in them repeatedly compared with undisturbed controls over two growing seasons. There were two questions: (i) did the effects of disturbance change among the five wetland types and (ii) did the effects of disturbance vary with the way in which the plants were assessed: species, guilds, and communities? Suprisingly, a single growing season was sufficient for community-level properties such as biomass, richness, and evenness to return to control levels. The dominants removed at each site tended to remain depressed for the first growing season, although by the second year effects were negligible. At the guild level, recovery was also rapid, although there were minor changes, such as a modest increase in facultative annuals. The species level of organization tended to be the most sensitive to disturbance. Overall, it appeared that removing above-ground biomass had a marginal effect on this vegetation type; this may not be a great surprise, given the dynamic nature of riverine wetlands.

The measurement of disturbance effects is often complicated by changes in wetlands that occur while the study is ongoing. Moore tested whether removal effects varied among five wetland vegetation types by measuring the magnitude of removal effects for each ecological property and for each wetland site standardized to account for initial differences and changes with time. Returning to the beginning of this chapter, recall that for an event to qualify as a disturbance, there has to be some change in properties. Hence, we need to ask: (1) what is the effect of an event like drought or biomass removal, (2) is it significantly different from zero, and (3) how does it vary among sites or species? Moore's measure of removal effects for each variable was

$$Z = (x_0 \times y_t)/(x_t \times y_0)$$

where x_0 is the mean value for the property in the control sites during the pre-treatment survey, x_t is the mean value in the control sites during the post-treatment survey, y_0 is the mean value measured in the disturbance treatment during the pre-treatment survey, and y_t is the mean value measured in the disturbance treatment during the post-treatment survey (see Ravera 1989). The value is thus independent of initial levels of the properties, and is independent of ongoing temporal trends in the community. A Z value of 1.0 indicates no treatment effects, while values above or below 1 indicate

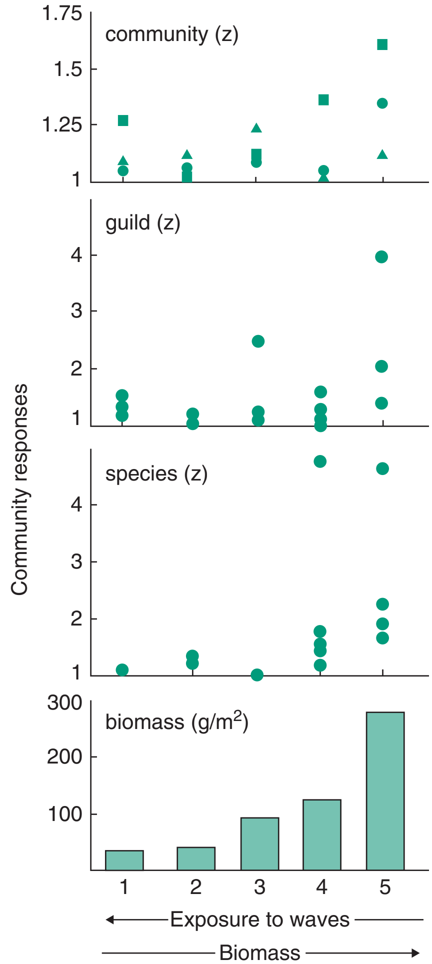


FIGURE 4.24 Effects of experimental disturbance (the removal of all biomass) upon several properties of five different wetland communities. The community gradient is arranged from exposed sites (left) to sheltered bays (right), which produces the biomass gradient shown in the bottom panel. Z is used to measure the amount of change from controls 1 year after the disturbance; the greater Z, the greater the departure from control values. The top panel combines three response variables: cover ▲, richness ■, and evenness ●. After 1 year (shown) the effects were significant at the species and guild level, but not at the community level; after 2 years, the effects were non-significant. (After Moore 1998.)

increase or decrease. Hence, it should be possible to compare effects of disturbance quantitatively for a wide array of properties of wetlands and types of species. In the case of Moore's study, the experimental disturbance had the greatest effects in sheltered bays (Figure 4.24). Perhaps this is because these are the wetland communities where disturbance was normally most infrequent.

CONCLUSION

Disturbance is a short-lived event that removes biomass, causing a measurable change in the properties of an ecological community. We have seen that disturbance can have major effects upon wetlands and at many scales. Droughts, fires, floods, ice, logging, and winds are but a few of the factors that can quickly change the type of wetland community in a landscape. At smaller scales, when small patches are disturbed, disturbance increases the heterogeneity of the habitat, and sets up a system where patches are being created and recovering from disturbance. Species may then disperse among those patches. Managers can deliberately make disturbances that vary in duration, intensity, frequency, or area to create desired kinds of habitats.

One way to further summarize this chapter and combine the many types of disturbance in nature is to select two of the four measurable properties, intensity and area, as in Figure 4.25. At the upper left are disturbances that are generally of low intensity in small patches, such as grazing. Ice scour is a disturbance that still may occur in small patches, but with much higher intensity. Atmospheric deposition of pollutants (not shown) may produce

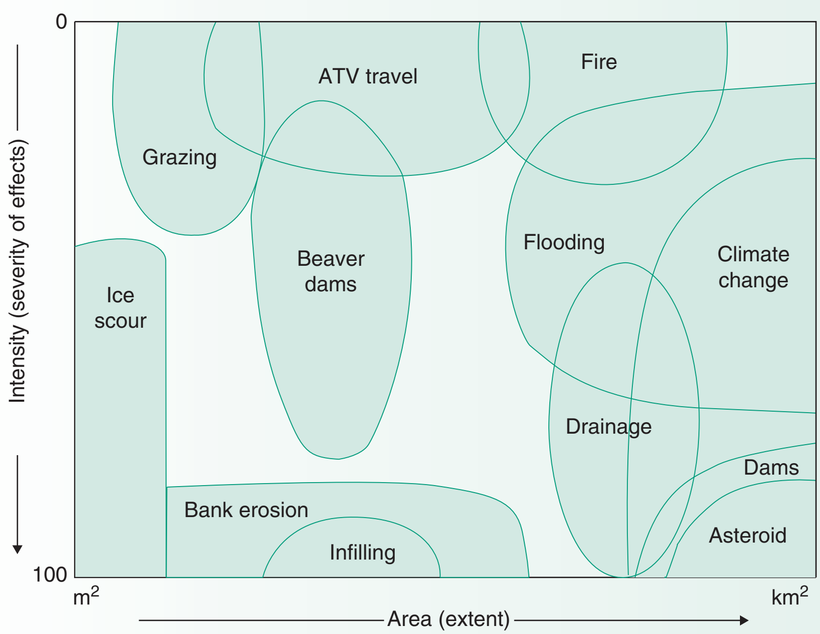


FIGURE 4.25 Intensity and area plotted for an array of natural disturbances in wetlands.

only small changes in composition, but these may cover very large areas. Finally, there are events like the construction of hydroelectric dams which have high intensity and affect large areas.

These kinds of disturbances play an important role in determining the area and species composition of wetlands. They also interact with other factors including fertility, competition, and herbivory. Hence they are important, and often overlooked, factors that affect vast areas of wetland. They also provide, when used wisely, important tools for managing and restoring wetlands to achieve specific conservation objectives, such as maintaining habitat for rare species of wildlife.