ABSTRACT

A conceptual ecosystem model illustrates principles of ecosystem management in wetlands. Wetlands are excellent systems for the development of ecosystem management principles because they are relatively simple ecosystems and respond quickly to changes in their environment. The model shows stressors and subsidies as the driving forces of wetland ecosystems. Ecosystem management focuses on wetland functions and uses the driving forces of ecosystems to achieve desired goals. Fire is an example of a wetland stressor that also acts as a subsidy. Fire accelerates, arrests, or redirects succession, favors certain species, mineralizes nutrients, and consumes biomass. Wetland management will evolve towards a greater emphasis on ecosystem manipulation to achieve specific wetland functions regardless of species composition. Such types of ecological engineering depend on the preservation of wetland biodiversity and will result in wetland ecosystems with new combinations of species.

INTRODUCTION

Wetlands are ecosystems adapted to stress. They exhibit common characteristics with other stressed ecosystems, including low plant species diversity, specialized physiology, dominance of age classes, and pulsed processes. However, in contrast to stressed ecosystems, many wetlands can be highly productive, exhibit fast rates of succession, and maintain high biomass. This apparent paradox is due to their close association with hydrologic phenomena. The material, energy, and biotic fluxes of wetlands are very open and provide natural inputs or subsidies (e.g., nutrients, sediments, kinetic energy) that counteract the costs of stressors. As a result, wetlands exhibit a large variance in most of their structural and functional parameters, a condition that limits the usefulness of generalizations and management solutions to other common problems. Because wetlands experience a large variety in the number, intensity, and periodicity of stressors and subsidies, it is necessary to always relate research findings and management recommendations to specific types of wetland ecosystems.

WETLAND STRESSORS

Most wetlands function under the influence of one or more of the most severe stressors that affect ecosystems on Earth. These are: salinity, anoxia, drought, frost, and fire. Wherever these stressors occur on the planet, major discontinuities occur in species richness, and ecosystem structure and function. Salinity causes the discontinuity between halophytes and glycophytes; anoxia causes the discontinuity between aerobic and anaerobic metabolism; drought causes the discontinuity between xeromorphic and hygromorphic; frost causes the discontinuity between tropical and temperate biomes; and fire causes discontinuities between pyric and non-pyric ecosystems. These five factors, alone or in concert, contribute to delimitation of life zones, biomes, or plant as-
sociations; as well as zonation and sharp ecotones in many ecosystems.

Salinity, anoxia, drought, frost, and fire are not the only stressors of wetlands. Other stressors of wetlands include long hydroperiods, winds and storms, oligotrophic conditions, poor substrates, and many others. These stressors interact in complex patterns that include additive, synergistic, negative, and even compensatory relationships that are poorly understood (Lugo 1978). Moreover, stressors can be chronic or acute and occur on a variety of time scales or pulses. Although we lack complete understanding of the spatial and temporal complexity of the action of stressors on wetlands, it is axiomatic that simplification or stabilization of the wetland environment is counter to the natural adaptations of the ecosystem. The same is true about the nature, action, and function of wetland subsidies.

WETLAND SUBSIDIES

Hydrologic phenomena regulate wetland structure and function. Water causes stress when hydroperiods are long or anaerobic conditions develop, but it is also a main subsidy of wetlands. Depending on hydrological conditions, wetlands can either accumulate nutrients and organic matter or export them. Water is a carrier of nutrients and sediments that subsidize the productivity of wetlands. Water can also relieve the stress of salinity by diluting salt. Water in motion oxygenates the ecosystem and acts as a subsidy by mitigating the effects of low oxygen, high salinity, or oligotrophy.

In some instances, a wetland can function on substrates that normally would not support much biotic activity because water flow provides the essential nutrients and organisms. An example is the lacrimitic wetlands on rocky surfaces by waterfalls. In many instances where a given site is inherently favorable for plant production but is subject to a strong stressor such as fire or salinity, a few species with high productivity dominate; a situation that illustrates the interplay between the stressor and subsidy of wetlands.

Wetland ecologists have not developed comprehensive paradigms for evaluating the additive or synergistic effects of stressors and subsidies on wetland function (Lugo 1978; Lugo et al. 1990). The lack of such understanding limits our ability to manage these ecosystems with greater certainty. Part of the problem is that wetlands respond very well to single factors and this has led to numerous studies that focus on one factor at a time. The situation is changing with new approaches to ecological studies, i.e., long-term analysis, historical reconstructions of ecosystems, modeling, and spatial analysis. A holistic approach to managing wetlands may lead us to consider environmental factors as being both stressors and subsidies of ecosystem function.

THE RESPONSE OF WETLANDS TO FIRE

The association of wetlands and fire is not intuitive; one would not expect wetlands to burn. However, the moisture regime of many wetland ecosystems is variable and includes conditions which support fire, from those that burn frequently such as marshes to those that burn seldomly such as some forested wetlands. Moreover, wetland fires can range widely in both intensity and degree of combustion, i.e., plant tops, tree canopy, soil organic matter, dead material, or combinations of the above. The literature on the response of wetlands to fire, though fragmented, is quite extensive. Primarily only qualitative information was available as recently as the 1970's (Robertson 1962; Kozlowski and Ahlgren 1974; Little 1974; Komarek 1974).

While the southeastern United States appears to lead the nation in fire research, the fraction of studies dedicated to wetlands is small (Christensen 1985). I will concentrate on the fire aspects of southeastern wetlands but it is not my intention to conduct a comprehensive review. Instead, I used recent citations in Biosis to survey topics of research attention, and grouped them into four subject areas: (1) long-term, large scale reconstruction of fire history and its effect on wetland area and succession (historical ecology); (2) effects of fire on wetland plants; (3) effect of fires on soils and nutrient cycling; and (4) the interaction of fire and other stressors on wetlands. My interest in the review was to seek elements for a new paradigm of ecosystem management using fire and wetlands as the example.

Historical Ecology

Reconstruction of past landscapes using a variety of techniques, has led ecologists to recognize the close relationship between ecosystem types and the synergy between natural- and human-induced disturbances. The history of Atlantic White Cedar in the Carolinas (Little 1974; Frost 1987) is an example. Without human intervention this wetland maintained deep organic soils, stable hydrology, and low fire return frequencies (Little 1974). Technological innovations such as tools for digging ditches, followed by steam dredges, and later by fossil fuel subsidized technology incrementally modified the hydroperiod and consequently the fire frequency such that the ecosystem was eliminated from large areas where conditions for growth were otherwise optimal (Frost 1987). Furthermore, frequent re-harvesting affected natural regeneration of this forested wetland (Little 1974;
Frost 1987). Changes in the fire regime has led to a different behavior of Atlantic white cedar in the southern states (Ward and Clewell 1989).

Reduction of fire frequency in non-wetland ecosystems did not severely affect wetlands of central Florida, although some species were able to migrate outside the wetland into areas where fire had excluded them (Peroni and Abrahamson 1986). Hamilton (1984) found the same results in the Okefenokee Swamp. In these instances, the long-term effect of management of wetlands is due to secondary effects of logging practices and changes in hydrologic conditions.

Land conversion practices and plowing for establishment of fire lines have an impact on the ecotones between wetlands and other ecosystems. Taylor and Gibbons (1985) and Frost et al. (1986) documented this effect for the southeastern United States. In these examples, fire management activities had an indirect effect on wetland ecosystems.

The timing of fires has critical implications for wetlands. Those that occur during dry conditions as in Cumberland Island, Georgia (Turner and Bratton 1987) have different effects than those that occur during wet seasons as in south Florida (Wade et al. 1980; Kushlan 1990). In both examples the natural cause of the fire was lightning, but the compartments affected are different because in Florida the natural fire burns the vegetation but not the soil whereas in Georgia the drier conditions associated with the fire, can allow it to consume litter and soil organic matter.

Natural cycles of precipitation induce fire cycles to which vegetation adapts over large portions of the landscape. In Cumberland Island, for example, wetland vegetation was more stable than terrestrial vegetation because fire had less effect than hydrology (McPherson and Bratton 1991). Izlar (1984) related the survival of swamp and marsh vegetation in the Okefenokee Swamp to the 25-30 year cycle of drought and fire.

Brenner (1991) related long-term wildfire activity in Florida to the presence of the El Niño Southern Oscillation. The same correlations have been shown for southwestern United States (Swetnam and Betancourt 1992) and for streamflow in western United States (Cayan and Webb 1992) and elsewhere (Diaz and Markgraf 1992). Such a relationship underscores the predictability of fire occurrence when viewed on an evolutionary scale. Predictability facilitates evolution. However, Snyder (1991) analyzed fire regimens over the last few thousand years in south Florida and discovered that human-induced fires were becoming more prevalent than lightning-induced ones. Snyder noted the difficulty in establishing the pre-Columbian fire regimen and suggested to managers that it was more important to use fire regimens that resulted in the desired effects as opposed to recreating a specific fire regimen. Hermann et al. (1991) reached the same conclusion when they studied fire regimens of peat-based marshes in the Okefenokee and Dismal swamps. They discussed how different intensities of fire result in different types of wetlands and pointed out that high fire frequency can have the same results as less frequent but more intensive fire. Moreover, severe or frequent fires can cause a change in the wetland type, while light and moderate ones maintain a specific wetland type (c.f. Christensen 1988).

Fire Effects on Plants

Fire killed or set back aboveground plant growth in the freshwater marshes of Cumberland Island. However, within two years the marshes had recovered their pre-fire physiognomy, plant cover, and species composition (Davison and Bratton 1988). Schmalzer et al. (1991) found similar results in various marshes in the Kennedy Space Center, Florida. They also noted that the ratio of live to dead biomass increased after the fire. In south Florida, where flooding can follow fire, Herndon et al. (1991) found that the height of surviving plant clumps in sawgrass marshes was critical for surviving flooding. Shorter clumps could not grow fast enough to keep up with rising waters. In pine-wiregrass savannas of the Green Swamp, Walker and Peet (1983) observed that fire disturbance favored high herbaceous plant species richness and high aboveground production.

Fire favors populations of the pitcher plant Sarracenia in southeastern United States (Schnell 1992). Schnell found that the plant also responded well to increased light and lower competition following brush cutting in a pocosin but perished due to drought as a result of ditching. These responses occurred over a period of time with the positive response occurring first and the negative effect last. Use of fire, ditching, and brush cutting in tandem are tools to either increase or decrease the abundance of Sarracenia populations. Experience with Sarracenia demonstrates the possibility of using fire and other management tools to favor particular species, including endangered or endemic species (c.f. Kirkman et al. 1989).

Fire Effects on Soils and Nutrient Cycling

After reviewing the literature, Christensen (1987) suggested that oligotrophic ecosystems burned more readily than eutrophic ones. The reason is that they tend to accumulate fuel because of low litter quality and slow decomposition rate. However, wetlands are generally very combustible (particularly non-forested wetlands) even
though they are relatively eutrophic. Nevertheless, fire
frequency in wetlands does appear to have a relationship
with hydroperiod and soil fertility in that ombrotrophic
peatlands experience fire more regularly than say, allu­
vial swamps (Ewel 1990). Total ecosystem biomass and
species richness appear to be inversely related to fre­
quency of fire (Ewel 1990).

Studies of the effects of fire on wetland soils are few
and usually focus on short-term effects, i.e., one year
(Schmalzer and Hikle 1992). The results are difficult to
interpret in light of the paucity of data and the chemical
complexity of wetland soils. However, pulses in the con­
centrations of cations and anions occur in the upper soil
horizons consistent with the transformation of organic
matter to ash (Wilbur and Christensen 1983). The return
of nutrient concentrations to pre-burn levels depends on
hydrology, type of soil, and vegetation growth rate. Rich­
ter et al. (1982) found limited effects of prescribed fire
on soils, nutrient cycling, and hydrologic systems across
the southeastern United States. The environmental cost
in terms of impacts on water quality is low in proportion
to the benefits of the management procedure. This is not
surprising in ecosystems adapted to fire where one ex­
pects adaptive responses to conserve nutrients in the
biotic and abiotic system (c.f. Riekerk 1985). Moreover,
control of fire frequency allows regulation of the amount
of fuel on the ground, the speed of fire movement, and
the amount of heat it generates. The result is that the
fraction of the nutrient pool that circulates due to fire is
small. It appears that losses of nutrients are smaller than
inputs from rain and dust (Christensen 1987). Long-term
monitoring allows better measures of the cumulative
effect of fires on ecosystems.

One aspect of burning wetlands (and other ecosys­
tems) that is increasingly gaining in importance is the
volatilization of gases such as N₂, N₂O, CH₄, CO₂ and
other greenhouse gases, i.e., those that contribute to global
warming. Measurement of these gases is important for
a better understanding of nutrient balances in the burned
system, and to estimate the effect of combustion on
greenhouse gas emissions to the atmosphere. Studies in
Florida wetlands document the importance of wetlands
in these gas emissions during burning events (Levine et
al. 1990; Cofer et al. 1990). They also show the impor­
tance of combustion efficiency in the production of gases.
Emission of many of the gases is reduced when the com­
bustion efficiency is high. The release of nutrients to
wetland soils can also promote biogenic formation of
greenhouse gases. Thus, the fertilization effect of burning
occurs at the microbial as well as the macrophytic level.
Hogg et al. (1992) showed that not all wetlands peat will
be respired at faster rates under scenarios of global
warming with greater drought and fire frequency. Again,
the variability of wetland conditions preclude simple
generalizations to particular phenomena.

Interaction between Fire and Other Stressors

Fire, drought, and changes in drainage are wetland
stressors commonly considered in tandem. Their rela­
tionships are fairly obvious and are difficult to separate
when considering their effects on wetland ecosystems
(c.f. Lowe 1986). Today, the future of wetland ecosys­
tems under scenarios of climate change depends on eval­
uations of these factors (Hogenbirk and Wein 1991).
There are many other synergistic relationships occurring
in wetlands and these also require consideration when
evaluating management alternatives.

For example, the construction of fire plows to pre­
vent fires in marsh wetlands of south Florida introduced
numerous unexpected stressors to the wetland (Taylor
and Gibbons 1985). Plow lines affected soil, redirected
succession, created habitat suitable for the invasion of
exotic species, altered drainage and micro-topography,
changed the hydroperiod, and affected microbial popu­
lations.

A fundamental question regarding the action of
multiple stressors on wetlands is whether their effects
are additive or not. This question was addressed exper­
imentally by Turner (1986; 1987; 1988) in wetlands of
Cumberland Island. She tested grazing, clipping, tram­
ping, and a late winter burn on a salt marsh. Clipping
and trampling had additive effects on aboveground bio­
mass, but a combination of fire, clipping, and trampling
had less effect than expected by addition. Clipping and
trampling or clipping and burning resulted in greater
impact on net aboveground primary productivity than
expected by addition alone. The effect of trampling and
burning on net aboveground primary productivity was
additive.

There are two observations with management im­
plications that emerge from these experiments. First,
they show that the same stressor can have different ef­
ects on different components of the wetland ecosystem.
Second, all three stressors had their main effect on the
structure of the wetland, i.e., the immediate effect of the
stressor was to remove biomass. The question still re­
mains as to the interaction between this type of stressor
and another that affects other sectors of the ecosystem,
i.e., root physiology (oxygen availability) or photosyn­
thetl capacity (below zero temperatures).

FIRE AS A STRESSOR AND SUBSIDY

Fire has a multiplicity of effects on ecosystems (Ta­
ble 1). Its primary effect is to remove biomass and min­
eralize nutrients. However, such effects result in many
other modifications of the biotic and abiotic environ­
ment and these also affect ecosystem function. Fire ef­
Table 1. The ecological role of fire (Wade et al. 1980).

Fire influences the physical-chemical environment by:

● Directly releasing mineral elements as ash
● Indirectly releasing elements by increasing decomposition rates
● Volatilizing some nutrients (N, S)
● Reducing plant cover and thereby increasing insolation
● Changing soil temperatures because of increased insolation

Fire regulates dry-matter production and accumulation by:

● Recycling the stems, foliage, bark, and wood of plants
● Consuming litter, humus layers, and occasionally increments of organic soil
● Creating a large reservoir of dead organic matter by killing but not consuming vegetation
● Usually stimulating increased net primary production at least on short time scales

Fire controls plant species and communities by:

● Triggering the release of seeds
● Altering seedbeds
● Temporarily eliminating or reducing competition for moisture, nutrients, heat, and light
● Stimulating vegetative reproduction of top-killed plants
● Stimulating the flowering and fruiting of many shrubs and herbs
● Selectively eliminating components of a plant community
● Influencing community composition and successional stage through its frequency and/or intensity

Fire determines wildlife habitat patterns and populations by:

● Usually increasing the amount, availability, and palatability of foods for herbivores
● Regulating yields of nut and berry-producing plants
● Regulating insect populations which are important food sources for many birds
● Controlling the scale of the total vegetative mosaic through fire size, intensity, and frequency
● Regulating macroinvertebrate and small-fish populations

Fire influences insects, parasites, fungi, etc., by:

● Regulating the total vegetative mosaic and the age structure of individual stands within it
● Sanitizing plants against pathogens such as brownspot on longleaf pine
● Producing charcoal which can stimulate ectomycorrhizae

Fire also regulates the numbers and kinds of soil organisms; affects evapotranspiration patterns and surface waterflow; changes the accessibility through, and aesthetic appeal of, an area; and releases combustion products into the atmosphere.

Effects on wetlands can be both positive (subsidy) and negative (stressor). The nature of the effect depends on the affected ecosystem compartment and whether it has or not adaptations to fire. Because the ecosystem effects of fire are not all negative, it is possible to understand why the stressor turns into a subsidy or positive force of ecosystem recovery following the immediate instantaneous “negative” effect. For this to occur without a transformation of species composition, the burned populations must possess adaptations to fire. If they don’t, fire selects for new species and changes the composition of the ecosystem.

MANAGING STRESSORS AND SUBSIDIES OF WETLANDS

There are some wetland stressors whose presence or effects are unmanageable. For example, frost, drought, storms, or anaerobic conditions are difficult or too costly to manipulate. Fire and hydroperiods are examples of manageable stressors. Before manipulating a stressor it is important to have an understanding of how the stressor affects the ecosystem and how it interacts with other stressors or wetland subsidies. Another management strategy is the suppression of stressors using subsidies (Lugo 1987).

Figure 1 illustrates the point of attack of stressors on wetland ecosystems. It helps explain why wetlands recover faster from some stressors than they do from others. Stressors that attack the conversion of solar energy to photosynthate (type 2) have longer lasting impacts on the ecosystem than those that remove biomass (type 4). For example, a hot fire that kills roots has a longer impact than a cool one that only burns above-ground biomass. Most management situations involve acceleration of ecosystems as opposed to slowing them down. These accelerations facilitate rehabilitation, restoration, mitigation, or production schemes. For this reason, stressors of type 4 are the most versatile to use in wetlands. In addition, they are cheaper to use than stressors of type 1 which are those that change wetland conditions i.e., canalization, drainage, or dams. Fire is particularly useful for management because it can suppress certain organisms, modify the environment, and create conditions favorable for ecosystem recovery. In short, fire can act as a stressor of types 2–5 or as a subsidy. Managers have then an opportunity to direct succession towards a desired goal.

Figure 2 illustrates the use of environmental factors to accelerate ecosystem growth. This approach uses the opposite strategy as the one illustrated with stressors. The idea is to relieve stress to accelerate ecosystem re-
Fig. 1. Simplified diagram of an ecosystem showing the point of attack of five types of stressors. A stressor such as fire can function as more than one type of stressor. Type 1 stressors change the energy sources or fundamental environmental conditions of ecosystems. For example, removing water from wetlands. Type 2 stressors reduce the input of energy or materials to the ecosystem. For example, reducing the input of water to a wetland. Type 3 stressors affect the primary productivity of ecosystems. For example, removing plants from the system. Type 4 stressors reduce soil organic matter or nutrients from the ecosystem. Type 5 stressors attack animals and other consumers, thus impacting respiration and other roles that these organisms play in the ecosystem (Lugo 1978).

Fig. 2. Simplified diagram of an ecosystem as depicted in Figure 1 but with the addition of subsidies to overcome the effects of stressors. Type 1 subsidy suppresses the effects of stressors 3, 4, and 5. An example would be fire suppression. Type 2 subsidy adds organisms or nutrients to the ecosystem. Type 3 subsidy accelerates the rate of ecosystem processes. An example is use of fire to accelerate nutrient cycling. Type 4 subsidy suppresses the effect of stressors 1 and 2. An example would be the opening of a dam or breaking a dike to restore the hydroperiod of a wetland. Type 5 subsidy restores the energy sources of the ecosystem. Restoring a fire frequency and intensity regime would be an example (Lugo 1988).

MANAGING WETLANDS IN THE 1990'S AND BEYOND

The social environment for wetland management is changing and will continue to change as the resource base of the world shrinks and we must “do more with less.” From the 1970's to the 1980's the predominant interest in wetlands focused on their loss and protection from total extermination. A philosophy of preservation and restoration addressed this early goal. In the 1980's and 1990's we have experienced a shift to mitigation of wetland loss. This required a more proactive management of these ecosystems and a philosophy of rehabilitation and wetland creation. At the present time, we are feeling the need to step up the level of management of wetland ecosystems. The focus will be ecological engineering where we attempt a tighter match between the needs of society and the conservation of nature.

With ecological engineering we need to use natural phenomena to achieve specific management objectives. This is not new. All strategies of wetland management have always been present and will continue to be part of the tool box of managers. What changes are the emphases and the ease with which society accepts certain approaches to landscape management. Wetlands will always require preservation for their value in supporting biodiversity, conserving water, protecting coastlines, and providing innumerable services to humans. However, in the future wetlands will be required to increasingly act as ecotonal ecosystems in an increasingly urban world. Their role for absorption of waste, food and commodity production, and hydrologic buffers will certainly increase in the future. This changing demand on wetland ecosystems will require wetland managers to change the focus of their management as well.

I visualize a greater emphasis on manipulation of the forcing functions of wetlands. Increasingly the objective will be to direct ecosystem development to desired states irrespective of species composition. Wetland function will be the criteria of management success in an era of ecological engineering. Does the system store carbon? Does it preserve a given set of organisms? Does it store water? Does it clean water? Can it store heavy metals? What stressors or subsidies can be used to accomplish these goals? The flexibility of fire as a stressor-subsidy will make it an ideal tool for managing wetlands and other ecosystem types.

The key to success will be the self-design of ecosystems or the ability of combinations of species to respond to specific inputs of energy and materials and...
function in predicted ways. This is the essence of ecosystem management. For this approach to work, we must be successful in the preservation of wetland species and types of ecosystems because it is from these natural reservoirs of biodiversity that the managers of the future will draw the biotic capital needed to make ecological engineering approaches and self-design work. Finally, we need to recognize that with increasing human control of the environment, new conditions for wetland establishment will occur. For example, wetlands under artificial hydroperiods, human-controlled, fire regimens, and altered water qualities. Ecosystem self-design will lead to novel combinations of species and it will be necessary for managers and regulators to accept these “new wetland ecosystems” as an additional wetland type worthy of our attention, use, and conservation. This pragmatic approach will allow society to benefit from wetland functions in altered environments and relieve pressure on natural wetlands.

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