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13.3.5. Ecology of Northern Prairie Wetlands

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Glaciated wetlands of the prairie pothole region are among the most productive of ecosystems. In terms of primary productivity (vegetation) they rank with the tropical rain forests (Fig. 1). Wetland productivity is controlled by water levels that fluctuate over time. However, primary productivity is highly variable for a variety of reasons including the variance in annual precipitation, the nature of the glacial till, the salinity of the water, the relation of the basin to the groundwater, and the temperature extremes typical of a continental climate.

My purpose is to review the basic patterns that contribute to the productivity of prairie wetlands

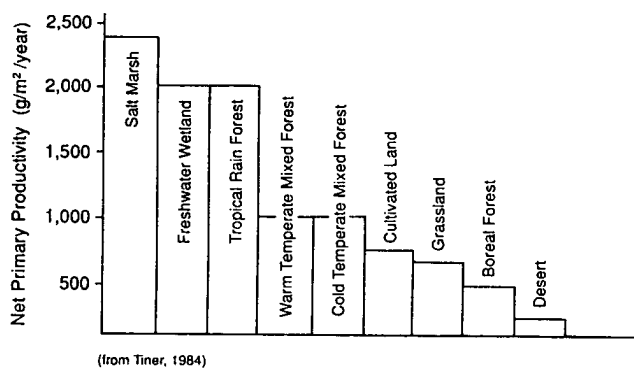


Fig. 1. Net primary productivity (vegetation) of selected ecosystems (from Tiner 1984).



with the goal of duplicating some of the essential ingredients in managed marshes. The most effective strategy for meeting this goal is through community management. This requires a basic understanding of the dynamics of the marsh ecosystem.

Influence of Climate

The first axiom of marsh management could be derived from Weller (1978) when he observed, "Stability seems deadly to a marsh system." This is primarily because the community of plants and animals typical of any marsh has adapted to the highly variable and unpredictable annual precipitation in the prairie pothole region. The variance in precipitation results in dynamic water level changes in individual basins over time and is reflected in the annual pond count conducted by the United States and Canada (Fig. 2). Only ponds that contain water are counted; as a result, there are more ponds in years when precipitation is above average, than in dry years. The key to understanding a prairie wetland lies in its water dynamics.

Influence of Geology and Hydrology

The reason that wetlands reflect variability in precipitation can be found in the nature of wetland basins. As the last glacier receded about 10,000 years ago, it left large chunks of ice in the glacial till. As these ice chunks melted, shallow depressions were formed. These depressions soon became wetlands because the till in this region is composed

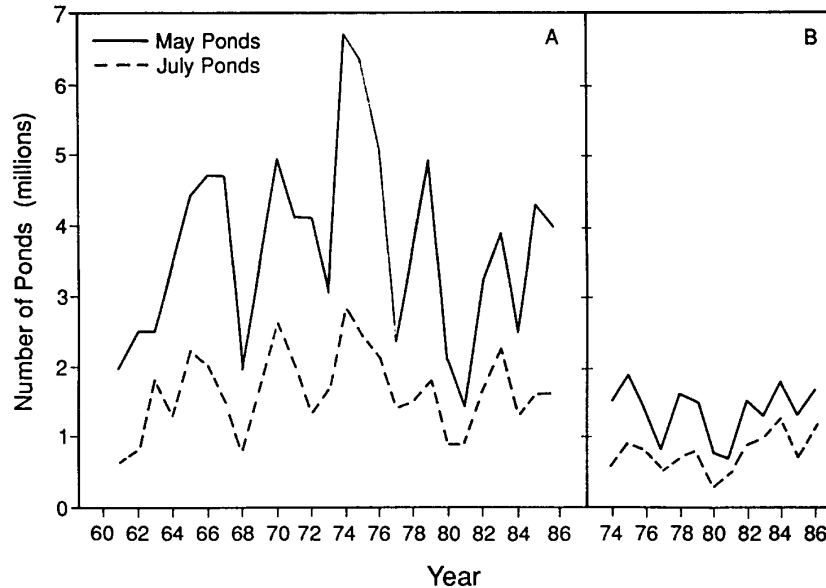


Fig. 2. Pond survey results conducted annually by the United States and Canada.

primarily of impermeable silt and clay. The last glacier was a fairly recent event in geologic time and since its departure, there has not been sufficient time to erode watersheds connecting many of the basins. As a result, the basins fill in response to precipitation in the area and changes in the ground water flow. They drain slowly, often holding water independent of surrounding wetlands.

There is considerable variation between basins in any given area in terms of water permanence and quality. Some wetlands are ephemeral, holding snowmelt only in the spring before the frost leaves the ground. Temporary and seasonal wetlands usually dry by the end of each season. Semipermanent wetlands retain water for a period of years, and permanent wetlands retain their character for decades except in years of extreme drought. Salinity for wetlands usually increases with water permanence.

In a given area, some wetlands may be dry while others are full. Variation in water retention in neighboring wetlands increases habitat diversity for wildlife. The variation can be explained in part by the relation of the basin to the groundwater system. This relation is usually complex and often determines the salinity and permanence of water in the basin. In general, the water level in the basin reflects the local water table. Glacial till is fairly impermeable and as a result, groundwater flow is slow and often uneven. Several patterns in the configuration of groundwater flow have been observed in the prairie pothole region.

- Fairly permanent, saline wetlands result when the water table slopes into a wetland on all sides, and water seeps into the basin but not out. The only way for water to leave is through evaporation or transpiration. As a result, minerals accumulate and the wetland can become very saline.
- When the water table slopes away from the wetland, water leaves the basin and enters the water table, usually in the shallow edges of the basin. This type of wetland contributes to groundwater and is fairly fresh and temporary.
- When the water table slopes into the basin on one side and away from the basin on the other side, the water is brackish and the wetland is semipermanent.

Although these generalized patterns explain some of the variation in wetlands in a particular area, the complete effect of groundwater on wetlands is very complex involving several layers of groundwater flow systems that can extend 10,000 feet below the ground. Other regional climatic patterns also influence salinity in the prairie pothole region. Because the western portion of the region has a drier climate than the eastern portion, evaporation in western wetland basins is greater and, as a result, they become increasingly more saline.

The overriding result of these relations for most wetlands is dynamic fluctuation in water levels and high variance in wetland types within an area. Because basins respond to groundwater, which varies locally, wetlands cycle from wet to dry periods inde-

pendently. As a result, a group of wetlands in an area forms a diverse set of habitats known as a wetland complex.

Vegetation Structure

Plant species reflect water fluctuations by forming characteristic associations known as zones. Plants within the zones have similar requirements for germination and persistence, and they have similar tolerances for water level permanence and chemistry. For example, in permanently flooded portions of a wetland, submergents such as the widgeongrass, pondweed, and muskgrass dominate. In semipermanently flooded portions, emergents that require mudflats to germinate but that tolerate flooding dominate. Species such as bulrush and cattail are common. In seasonally flooded portions, moist-soil plants such as burreed, smartweed, white-top, and spikerush dominate, whereas in ephemeral or temporarily flooded areas, species typical of a wet prairie dominate, such as bluestem and prairie cordgrass.

Several basic patterns in the zones can be observed in prairie wetlands.

- The number of zones usually increases with the size of the basin and the time it holds water during the season, so that ephemeral and temporary wetlands may only have one or two zones, whereas larger, semipermanent wetlands may have all of the zones.
- In most wetlands, the height of the emergent vegetation increases in areas where water is more permanent (saline wetlands are an exception).
- The number of different plant species in the zone decreases in areas where water is more permanent.

The plant zones provide structural diversity within the marsh and several zones are more beneficial to vertebrate wildlife than are homogeneous stands. The edge between zones is particularly important; more edge is better for waterfowl because nesting cover becomes more accessible, vegetation diversity increases, and macroinvertebrate production is greater. Macroinvertebrates are particularly important because they are the dominant food of laying hens and broods in wetlands managed for waterfowl production.

Several basic patterns have been reported in plant and invertebrate associations: (1) Invertebrates are more abundant in vegetated areas than in areas devoid of vegetation; (2) invertebrates increase proportionately with plant material, averag-

ing approximately 1 g animal matter to 100 g of plant material; (3) plant species with extensive invertebrate associations are not always the species that ducks consume. Elodea is an example. This plant ranked very low as a food item for waterfowl but was extremely high as a source of cover and habitat for invertebrates (Krull 1970). The plants with more surface structure seem to be ideal for invertebrates.

Vegetation Dynamics and the Food Web

High primary productivity combined with dynamic water fluctuations and severe climate result in rapid nutrient cycling in prairie wetlands. The emergent vegetation acts as a nutrient pump, drawing nutrients from the soil beneath the wetland floor. Much of the aboveground vegetation dies during the winter, so in spring a flush of nutrients enters the wetland in the form of detritus and soluble water-borne nutrients. In addition to seasonal flushes, annual variation in water permanence in the basins results in multi-year variation in nutrient cycles. As the marsh changes, the composition of plant zones changes as plants die and enter the detrital layer.

It is commonly thought that wetland food chains are detritus-driven. In fact, the detritus may function as a substrate for colonizing microorganisms such as various algal types that obtain necessary nutrients directly from the water. The algae are then consumed by larger invertebrates. These larger aquatic invertebrates are the key to the secondary productivity of the marsh ecosystem.

Invertebrates may be divided into a variety of functional groups depending on how they process litter. Shredders and grazers, such as scuds and snails, break up the larger pieces of plant litter. The fine particles of dead plant material are consumed by filter feeders and collectors. Midge larva (Chironomidae) specialize in both functional groups. Some investigators are convinced that these invertebrates consume the detritus to obtain microorganisms, because detritus that is heavily colonized is more rapidly consumed by larger, foraging invertebrates.

In summary, emergent vegetation is high in nutrients, which enter the water column through leaching from standing vegetation that dies, from gradual breakdown of plant litter by larger foraging invertebrates, and from decomposition by microorganisms. There is a flush of nutrients entering the

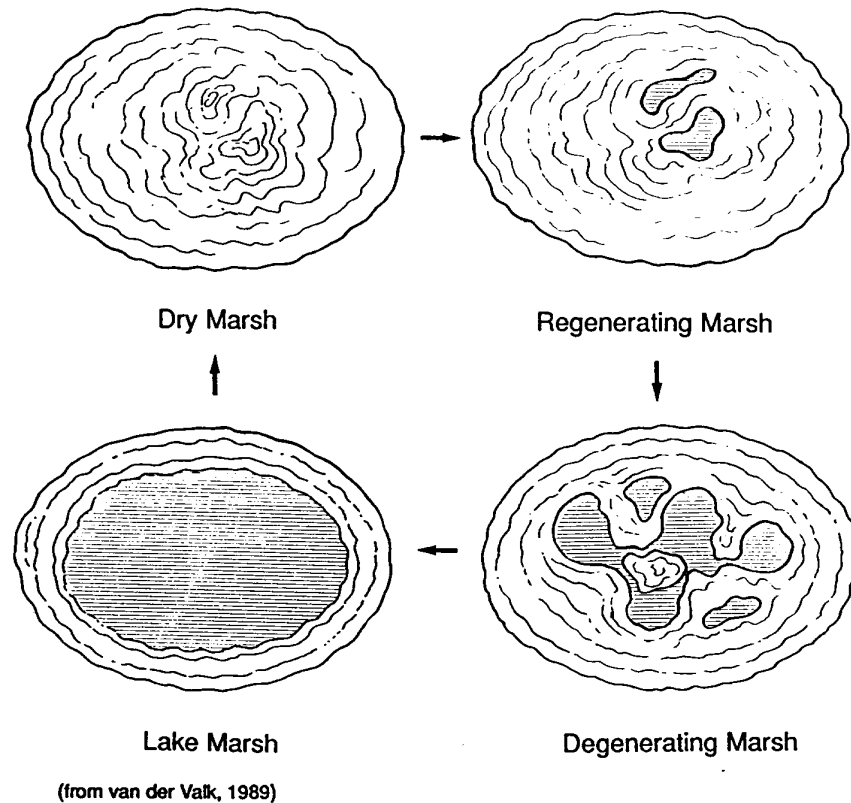


Fig. 3. The four stages of a marsh during a standard wet and dry cycle. Lines represent vegetation zones that become apparent in the regenerating marsh stage, and black represents open water (adapted from van der Valk 1989).

water in the spring, as well as a multi-year nutrient cycle as the vegetation zones respond to changes in the wet and dry cycle.

The vegetation in a marsh responds to dynamic water fluctuations in characteristic ways. This is particularly true for semipermanent wetlands with a capacity to hold water to a depth of 1 m. Four idealized vegetation stages have been identified that correspond to the way the vegetation responds to a typical wet and dry cycle (Fig. 3). Given the variability inherent in the prairies, a typical cycle may be interrupted at any time, but the following stages can be used as a general guide.

Dry Marsh Stage

In the dry marsh stage, a drought exposes part or all of the marsh bottom and many species of annual and perennial emergent plants germinate on the mudflats. Emergents such as cattail require moist mudflats to germinate. As a result, a dense stand of annuals and perennials forms in the wetland basin during a dry year. During this stage, invertebrate production is minimal or nonexistent and the marsh receives relatively little use by wild-

life except as a source of cover or for the browse and seeds produced by the annuals.

Regenerating Marsh Stage

In the regenerating marsh stage, water returns to the basin, drowning the moist-soil annuals, but the perennial emergents continue to spread through vegetative propagation. The typical vegetation zones that are characteristic of wetlands develop during this stage. Litter from the annual plants provides an influx of nutrients to the marsh. Some of the soluble nutrients are leached into the water, while other nutrients are consumed by various plankton and detritivores. The emergent stand does not completely close and shade the marsh bottom, so algae flourish on the litter from the dead annuals. The annual litter on the bottom also provides habitat and food for invertebrates such as midges and as a result, invertebrate populations increase. In fact, the substrate and food source provided by the litter from annuals explain the flush of productivity common to newly flooded basins. The rapidly expanding emergent beds also provide

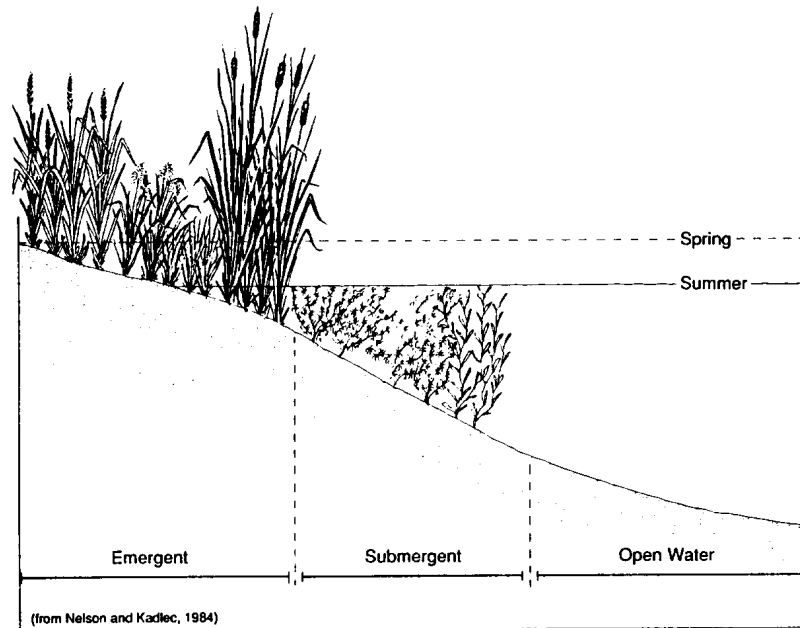


Fig. 4. Seasonal water level changes influence water temperature and create a nutrient-rich current between emergent and submergent vegetation (adapted from Nelson and Kadlec 1984).

food for larger herbivores such as muskrats and as a result, their populations increase.

Degenerative Marsh Stage

After the water has remained in the wetland for several years, the emergents become stressed from water, insects, and senescents. In many areas, muskrats also create openings in the emergent stands. The marsh is in the "hemimarsch" stage when there is a 50:50 ratio of emergent vegetation and open water. At this stage, edge between emergent and submergent vegetation is plentiful, invertebrate populations peak, and waterfowl and other wetland birds respond dramatically. This is the most productive stage of the marsh cycle.

The importance of the edge between emergent and submergent vegetation is particularly relevant for management (often this appears to be the edge between emergent stands of vegetation and open water). Waterfowl prefer the cover provided by a hemimarsch and overwater-nesting birds prefer the isolation provided by the mixture of vegetation; however, they also prefer these marshes because invertebrates are readily available. Invertebrate response is due to the cover provided by the vegetation and to the dynamics of the current at the edge between emergent and submergent vegetation.

Differences in temperature between emergent and submergent vegetation establishes a current between the two areas that is rich in small organic particles from the decomposing vegetation. Many invertebrates forage on algae and fine organic particles and concentrate in edge areas because the current there brings them a rich food supply.

One explanation for this phenomenon is that in spring, when wetlands are flooded, litter accumulates in the emergents and provides structure and substrate for algae and a source of fine organic particles (Fig. 4). As spring progresses, the water recedes and warms. Decomposition accelerates and water quality in the emergent litter deteriorates (reduced oxygen and higher temperature). Invertebrates move to the flooded openings where the growing, submerged vegetation provides substrate and the currents provide a source of organic food particles. As a result, invertebrate populations tend to congregate at the edge between submerged and emergent vegetation. More edge means more invertebrates for waterfowl that rely on invertebrates for food during spring and early summer.

Lake Marsh Stage

As time passes, the wetland lake enters the lake marsh stage where only a ring of emergents remains around the outside of the basin. Floating algae may be the dominating vegetation and midge

larvae the dominating macroinvertebrate. The marsh may continue at this stage for many years until a drought, begins the cycle again.

Marsh Management

Managed wetlands with water control can hedge against drainage and drought in surrounding land. In wetlands on floodplains, water control can mitigate against damage caused by flooding and fish invasion. Marsh management in impoundments with water-control capability should duplicate the water dynamics of a natural prairie wetland. The basic goals of wetland management for a semipermanent wetland are as follows:

- Cycle the wetland through drawdown, dense marsh, and open marsh phases.
- Fluctuate water levels to maximize the amount of edge between vegetation zones for increased invertebrate productivity. The ratio of interspersion between emergent and submergent vegetation should be about 50:50 for as long as possible (2 to 5 years on the average). Many semipermanent wetlands do not have natural openings in the the emergent of vegetation stands because the basin is too shallow to drown out cattails and because muskrats are not common enough to create openings. In these impoundments, artificial openings can be created through grazing, burning, or tillage.
- When conditions in the basin deteriorate, cycle the water back as rapidly as possible, depending on the cycle of other basins in the complex.

This water regime outline is typical for semipermanent wetlands; however, a wetland complex includes a variety of wetland types. Seasonal and temporary wetlands can be created by cycling the water each year and allowing the wetland to slowly dry in summer. Water can be returned to the basin in the fall or the following spring. The plant zones will be simple and the invertebrates that inhabit the basin will differ depending on when the water is returned. These seasonally managed wetlands can be very productive and provide an excellent invertebrate food source for waterfowl.

On refuges, the key to successful water management is to provide a variety of wetland habitats. Water levels in a managed complex should be fluctuated so that basins cycle into the most productive stages asynchronously to provide some optimum habitat each year. The management of a group of wetlands should duplicate the diversity

and variation common to a prairie wetland complex by cycling the drawdowns at different times and with differing durations.

The techniques for using drawdowns vary with the area and the latitude of the basins. For example, in the North, nutrient cycling in wetland basins may take longer and the basins may be more vulnerable to damage from overwinter drawdowns, such as invertebrate die-off. In addition, the soil freezes to the surface layer of ice and, in spring, if water returns to the basin before the thaw, the frozen soil will float with the ice. As the ice melts, the soil settles in an unconsolidated layer to the bottom, where it will cause increased turbidity and loss of vegetative growth.

The following guidelines may serve to improve management results:

- Increase water levels slowly after germination in late summer or fall. Flooding during the growing phase clouds the water and decreases light penetration. This approach has the added advantage of providing easy access to annual seed production for fall migrating waterfowl.
- Encourage establishment of the hemimarsch stage by artificially clearing trails in dense stands of emergent growth or by encouraging muskrat populations to increase naturally. If muskrats are present, they will harvest the emergent vegetation for lodges and food.
- Establish submergents vital to invertebrates by allowing several years of stable water levels of moderate depth.

Effective evaluation is the most important aspect of any marsh management program. Evaluations should include inventories of wildlife response to vegetation and of invertebrate response within each managed basin. Overviews and summaries of wildlife response at a refuge may be helpful; however, a basin-specific evaluation will reveal if a management regime is working. The common denominator of all wetlands is variation, so management in each area must vary as well. If management is not accompanied by evaluation, it will be impossible to know if the management regime is providing the habitat necessary for wildlife.

Suggested Reading

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Appendix. Common and Scientific Names of Plants and Animals Named in the Text.

Plants

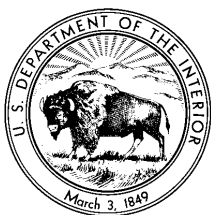
Widgeongrass	<i>Ruppia</i> spp.
Pondweed	<i>Potamogeton</i> spp.
Elodea	<i>Elodea</i> spp.
Muskgrass	<i>Chara vulgaris</i>
Bullrush	<i>Scirpus</i> spp.
Cattail	<i>Typha</i> spp.
Burreed	<i>Sparganium</i> spp.
Smartweed	<i>Polygonum</i> spp.
Whitetop	<i>Scolochloa festucacea</i>
Spikerush	<i>Eleocharis</i>
Bluestem	<i>Andropogon</i> spp.
Prairie cordgrass	<i>Spartina pectinata</i>

Invertebrates

Scuds <i>or</i> Side-swimmers	Amphipoda
Snails	Gastropoda
Midges	Insecta, Diptera, Chironomidae

Vertebrates

Muskrats	<i>Ondatra zibethicus</i>
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