DESCRIPTION OF A DYNAMIC ECOTONE IN THE PANTANAL OF MATO GROSSO, BRAZIL

Charles W. fieldman*
Universidade Federal de Mato Grosso, CCBS, Av. Fernando Corrêa de Costa, s/n, 78.103 Cuiabá - MT, Brazil

Abstract. During the course of the seasonal succession in the Pantanal of Mato Grosso, a large wetland under the influence of the tropical wet-and-dry climatic zone, an asynchrony between the terrestrial and aquatic habitats develops that moves across the floodplain maximizing a more or less continuous succession of plant and animal species. This dynamic asynchrony develops only during the dry season as the water level rapidly falls, and no apparent phenomenon was observed during the rainy seasons, when floodwaters advance across the landscape. The species that arrange themselves in distinct zones within the ecotone include many short-lived annual plants geographically confined to South American wetlands, rapidly developing larvae of insects and amphibians, and a few predators that follow the receding water. The characteristics of such a lane-mapping system at the land-water interface within a wetland ecosystem subject to a seasonal succession have not been previously described. Accepted 18 March 1997.

Key words: dynamic wetlands, Amphibia, Nematoda, terrestrial nearwetland, seasonal succession, tropical wet-and-dry climate, water levels, wetlands.

INTRODUCTION

During a study of the Pantanal of Mato Grosso, a large wetland in the tropical wet-and-dry climatic region that is still relatively little-influenced by human activity, a dynamic asynchrony was observed. This remarkable phenomenon deserves closer study. According to Odum (1971), an ecotone is "a transition between two or more diverse communities..." Generally, ecotones are fairly static, at least over periods of a few years. When one community enlarges at the expense of another, such as during a seasonal succession, there is a gradual movement of the edge species along the advancing front. This is generally apparent only over a period of several years, and the changes are slow.

* Present address: Institut für Hydrobiologie und Pflanzen- wissenschaft, Zeitenweg 9, D-22763 Hamburg, Germany

One distinguishing characteristic of a seasonal succession is its annual repetition. Other kinds of succession usually result in permanent changes (Andersen 1986). Because the diverse communities appear repeatedly, the ecotone often appears seasonally as well. Most ecotones between seasonal communities are static, appearing at approximately the same time year after year. Hence, ecotones are usually studied as static transition zones, and because of their rarity, descriptions of obviously dynamic ecotones have not previously appeared in the literature.

The dynamic asynchrony described in this paper develops during a seasonal succession and moves rather rapidly across large areas. The species aggregations differ from those in typical successional stages by displaying not only a sequential development but also a continued occupation of new areas as they become available, relinquishing others to different
METHODS

The characteristics of the dynamic ecotone were observed during a study of the Pantanal of Mato Grosso over a period of more than three and one-half years, with interruptions of several weeks during absences about twice each year. The movements of the ecotone were observed and photographed in the field during weekly visits to various sites at which water samples were analyzed chemically and plants and animals collected for identification. The methods and the vegetation in order to elucidate the seasonal succession are described by Prado et al. (1994); while the locations of the sampling sites are shown in Heckman (1994a).

To document the events in the seasonal succession of macrophytes, an area 50 x 50 m was divided into 100 sub-units, each 5 x 5 m, and all macrophyte species present in each sub-unit were recorded once during each season. In addition, their relative abundances in each sub-unit were used. The results were then correlated with the water-level changes (Prado et al. 1994). During these investigations, as well as during the weekly faunal and floral surveys, it was noted that the dominant plant aggregations of the rainless seasons, consisting mainly of very shoal-land annuals, move along with the receding water. To describe this phenomenon of a moving cymatium, a composite transect was formulated for the four dry-seasons of the study. Because the area of the floodplain subject to desiccation varied considerably from year to year, with the entire area drying up in late 1991 and several hundred square kilometers at the time of flood throughout 1994, the area across which the cymatium moved also varied. The entire area of the floodplain in the region was extensive, and several square kilometers were regularly observable from the 50 x 50 m experimental plot.

RESULTS

Seasonal cycle: Water-level changes exceeding 1.5 m in the northern part of the Pantanal, in the Brasili- an state of Mato Grosso, bring about a pronounced wet-season succession, which was studied extensively over a four-year period (Heckman 1994a, Prado et al. 1994, De-Lamounna-Feine & Heckman 1996, Fletcher & Heckman 1996). During the season of little rainfall, generally from May through November, the water level progressively falls, leaving most of the floodplain dry. At this time, an ecotone develops between the dry, hard-baked sediment supporting a few drought-resistant terrestrial plants and the remaining water bodies at the lower elevations on the floodplain. Unlike the well-described static ecotones that characterize most limnic and brackish communities in all parts of the world, the ecotone in the drying wetlands of the Pantanal moves steadily with the receding water. Thus, it is a dynamic rather than static, and the position of its various areas at any one time depended upon how low the water-level had fallen. Because the absolute minimum water-level varies considerably from year to year, the ecotone, which nevertheless always appears in certain areas, does not always move the same distance.

The general structure and morphology of the ecotone is illustrated in Fig. 1. At its terrestrial end is a temporary community of drought-resistant annual plants that develop and produce seeds within a period of more than six months before the area becomes inundated during the subsequent season of flooding from about January through March (Fig. 2). At its aquatic end is a community of submerged and emergent vegetation (Fig. 3) together with a typical aquatic fauna, including that in the pseudomembranous community, as described by Heckman (1994b). The species in the intermediate zones of the ecotone are mainly very short-lived wetland annuals, terrestrial forms of aquatic plants, and animals that follow the moving shoreline.

The floodplain in the northern part of the Pantanal is characterized by large numbers of relatively few species, mainly fast-growing plants and animals with very high rates of reproduction. Hence, species diversity is low, but population density of the species that are adapted to fluctuation between flood and very dry conditions are often remarkably high (Heckman 1994b). Prado et al. (1994) recorded the presence of 48 species of macrophytes on the 50 x 50 m experimental area. Most of these had life-cycles that gave them a temporal niche in the seasonal succession, but they were not directly involved in the dynamic cymatium because their growing period was too long to permit the movement of their populations with the receding water. They were either aquatic or wetland terrestrial annuals, or amphibious perennials. Similarly, the members of the fauna are predominantly aquatic or terrestrial, and only a few species have found a niche in the rapidly moving...
litoral zone. Hence, the description focuses on those relatively few species which are characteristic of the dynamic ecosystem.

Vegetation. The mainly terrestrial species aggregations belong to two general classes. Above the high water-level of the floodplain are small patches of woodland, which are islands during the flood period. The characteristic edge species of the unvegetated separating the wooded islands from the floodplain is *Bromelia balansae* Miq. Slightly below this level are areas covered by drought-tolerant terrestrial species, which die off during the short period of flooding. Several species introduced to the Pantanal from other parts of the world are dominant within this vegetation, such as *Andropogon gayanus* Lam. and *Andropogon hygrophilus* Hackel in Minas. As the water recedes from these areas (standard for longer periods of time), the dynamic ecosystem species that appear.

As the water-level continues to fall, a few species of the littoral zone first begin to grow at the edges of the water. This group is dominated by such plants as *Diospyros kaki* Schumacher, an upright flowering form of *Hycoma pseudolimosa* and *Polycnemum punctatum* L. (Agliph). However, these first appear as part of a succession that seems erratic because there is no transition as dying off of the plants before the start of the dry rainy season. Other prominent species of this aggregation include *Alternanthera philoxeroides* (Marin) Grisebach, *Hypno leonardiana* O. Hoffmann, *Aegagropila leptocarpa* (Lam.) Wettstein, *Rumina salvinii* (Seubert) Solms-Laubach, *Lecidea lepidota* Swartz, and *Phragmites communis* Trin. These species are very abundant on the floodplain as
long as the soil remains moist, and they also grow in many locations where no dynamic system appears.

The species of the dynamic system first begin to appear after the water level has dropped below the annual median level. One of the first species of this group to begin growing near the edge of the receding water is Eleocharis trinervis (Mottam) Buchanan, which apparently grows from seeds left from the previous year and usually reaches a height of less than 10 cm. While the sediment remains rather moist, these plants sprout, flower, and produce seeds, and as the sediment dries up, they die off and are displaced by the more stable aggregation dominated by Cyperus kauaiensis. As the E. trinervis at the upper end of the ecosystem are dying off, new individuals are just beginning to grow near the edge of the receding water. Just after this first species of the dynamic system appears, the terminal form of Eleocharis trinervis Kunitz begins to grow just below the surface at the water’s edge. This species grows from thick underwater stems that persist as aquatic plants through the flood period. E. trinervis produces dense tufts of tiny leaves, usually under 5 cm in height, with inflorescences at the tip. These produce seeds during a period of a few weeks after the water has receded from the area and the sediment is still damp. As these plants approach the end of their short growth period, the areas they occupied are infiltrated by Cyperus kauaiensis, Polygonum punctatum, and other plants of the uppermost zones of the ecosystem. In the zone of transition between the upper two plant aggregations, other small herbs appear, such as Lippia argyrophylla (Valle) Kunitz. In the area still covered by about 1 to 5 cm of water, other aquatic plants begin to produce their short-lived terrestrial forms. Nymphoides peltata (Cúití-s) Kunz, referred to as Vallisneria spiralis (PNM) Brown, De We by various authors (Frids et al. 1994), produces in large size, and its typically aquatic leaves die off leaving a non-system in the mud and small remains of very thick, succulent leaves, which apparently store water over the dry weeks and permit the plant to remain in its vegetative state on the dry ground until the flood waters return.

A species that appears on some areas in place of Eleocharis trinervis and E. trinervis is the small grass, Stipa pumilifolia (Vale) Kangalov. Dense mono-specific beds of newly sprouted seedlings appeared on areas that completely dried up only during 1991, the driest year. They did not occur when the areas
remained flooded throughout the dry season, as in 1992, 1993, and 1994. This speaks for an annual deposition of sediments in the soft sediments of the floodplain and the spraying of these seeds only when the sediment becomes exposed to the air. Therefore, on areas that do not usually dry up completely, these seeds may accumulate in increasing numbers from year to year and all of the viable seeds sprout only during the infrequent years of particularly low water levels, like the S. parviflora matured and began to flower; the species that had first appeared in the upper parts of the corms began to infiltrate the stands of the grass. At the lower end of the corms are the more robust aquatic plants, many of which go through a period of intensive flowering and seed production before their vegetative parts die off. The aquatic species most abundant at the deepest end of the corms, diagrammatically illustrated in Fig. 1 and discussed by Prado et al. (1994), include Salvinia auriculata Aubl., Ludwigia adscendens (Linnaeus) F. & G. Garner, Ludwigia sedifolia (Yamato & Becc.)Honda, Ceratophyllum demersum (L.)Ellis, Myriophyllum verticillatum Hay, Callitriche serrata Schultes & Schultes, Illia, Jussiaea lenticulata (Nees) Lindau, Hydrilla verticillata O. Hoffm., Utricularia pulchra Linnaeus, U. macronervis Fontenay-Trevisan, Eichhornia crassipes G. G. Weber ex Schultes, E. triglacheta Kunth, Pistia stratiotes (L.) K. Schum., Sparganium erectum (L.) Scop. and Trapa natans (L.) K. Schum. As is often noted at the weir site of the excising water during the dry season. Generally, plants such as Myriophyllum verticillatum and Callitriche serrata die off well before the water has completely receded, while Utricularia species generally die when the receding water leaves them exposed to the air, and flowering often continues intermittently until the plants have died off. Ludwigia sedifolia persists only while the sediment remains damp, while L. inclinata, Hydrilla verticillata, and Jussiaea lenticulata develop terrestrial forms which often remain viable for low-water areas until the next flooded period. Most of the rest of the aquatic plants are annuals that produce seeds or seeds to survive the dry period. A few of them, including Eichhornia azurea (Swartz) Kunth, survive vegetatively in low-water areas for at least two years if the drought is not too severe. As the dry season continues, this entire cormes generally moves across the floodplain from the higher to the lower-lying areas. An essential requirement for niche-occupancy is one of the interconnecting cormes of the cormes in the production of seeds or vegetation propagules within a period lasting no more than a few weeks. In addition to the vegetative stems, there are a few annual species typically associated with the dynamic cormes. They have the advantage over the plants of being able to move actively with the receding water, and none of them are able to survive both on land and in or below the surface of the water. One prominent species of this cormes is the round beak, Galerita flava (Sayce-Mitchell, 1855), a predatory hemipteran which is generally observed very close to the edge of the water, usually on the terrestrial side but sometimes in water a few millimeters deep. A number of dipneusts species also congregate in the receding littoral zone. The adults are observed at the margins of the water, sometimes in large numbers, and the larvae develop in water-laggregated detritus, mainly decaying plants and manure from the cattle that came to the water to drink. The most prominent among these are terrestrial species of the family Ephedridae and Sphaerocerae and predatory plecoptera. The adults of these dipneusts are seldom ever encountered during the rainy season. The dynamic cormes is used by the large bud, Bala pumicostata (Nakamura, 1925, for breeding. The eggs are deposited in shallow areas of receding water. The two hundred of tadpoles generally remain together in large schools, forming extensive black patches on the sediments. They grow very rapidly in the water at temperatures exceeding 30°C and begin their metamorphosis when the pools have nearly dried up. In contrast to many other families of anurans, members of the Podarcidae generally complete larval development from egg to tadpole in only a few weeks, and the tadpoles are, as a rule, relatively small compared to the adults. The rapid development enables these tadpoles that do not transform fast enough, and when many of these pools dry up completely, large masses of dead tadpoles are left behind. Nevertheless, many of the individuals do transform just in time, and near the masses of their dead and flying siblings, tiny tadpoles, some still with
the stomp of aвуl can be seen kcping away from the water and tord the danser plants in the upper ports of the ecrease.

Most of the large water feeds on fishes and smalls in the sh个e pools, but a few of the smaller species are typicaly observed seeking food in the c的声音 at the water’s edge. One of the more common of these is the waled jaguar, Isurus isurus (Linnnaeus, 1766). In the terrestrial zones of the eocene, the southern larvying, Vandalia chloe (Gmelin, 1789), is frequently observed, and which appear during the dry seasons.

DISCUSSION

The dynamic eocene differs from the more familiar static type, from which it, however, cannot be distinguished unless observed regularly over a period of at least several weeks (Fig. 1). The species aggregates in each zone of the bioria consist of short-lived species encountered at different locations from week to week but generally occupying the same relative positions to one another, subject to slight variations due to minor tems and variations. The species aggregates in this area could be observed, especially those in the littoral zones of more stable marine and freshwater bodies, are not encountered at different locations on the subaqueous substrate during seasons.

Although the dynamic eocene appears as part of a seasonal succession in the Pantanal, individuals of the same species do not appear at the same time of year. The eocene appears during the season of receding water-levels and begins a movement across the floodplain that continues at many locations throughout most of the dry season. During this movement, the upper zone with its fairly constant structure expands and does not give way to the drought-resistant grass aggregations which occupy the drier, usually unflooded parts of the floodplain. The lower zone of aquatic plants becomes progressively smaller. The intertidal zone between the upper and lower changes its size considerably according to the terrain features. For example, at the site investigated by Prado et al. (1994), it occupied a width of only 20 meters wide when it first appeared early in the dry season, increasing in width to more than 30 m on particularly flat areas of the floodplain. Encroachment by the plants of the upper zone later reduced its width to less than 10 m. An intermediate zone does not appear everywhere on the floodplain. It is absent where the intertidal zone has a moderately steep gradient.

The movement of the eocene is made possible by the very short life span of the dominant plant species or of their reproductive growth stage, particularly Eichhornia eucalyptus, Eleocharis minutana, Lipotesma pauciloba, and Stratiurus parviflorus. These species may begin blooming within a week of their first appearance and produce seeds within about three weeks. After six weeks they have usually died off.

The dynamic eocene occurs only while the water-level is falling. When it rises again no similar phenomenon is observed. There is instead a typical seasonal succession during which the seasonal plants drown and are rapidly replaced by typical aquatic species. There is no zone occupied by short-lived terrestrial or aquatic plants, and no animals were noted that activity remained exclusively in the littoral zone. Among the water plants, there is a permanent succession depending upon the depth during the high water period, but no regular advance or retreat of these zones during any given year was observed. Although the areas occupied by Eichhornia eucalyptus, a dominant shallow-water species, during a series of particularly wet years and decrease again during dry ones. Although the dynamic eocene is a result of the succession, and the areas it occupies may vary slightly from one year to the next, its characteristics are quite distinct from the well-known phenomena of static succession and are not affected positively by year to year variations in the minimum water-level.

ACKNOWLEDGEMENTS

This paper was prepared during a research project on the Pantanal at the Universidade Federal do Mato Grosso in Curitiba under the Governmental Agree-

ment on Technological Development between Germany and Brazil as part of the SMTF program financed by the Bundesministerium für Forschung und Technologie (BMFT), the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq), and the Instituto Brasileiro de Meio Ambiente e Recursos Naturais Renováveis (IBAMA). Thanks are due to Dipl. Biol. Michael Schell for providing information and additional plant specimens from various parts of the Pantanal, as well as to the taxonomic experts who identified plant specimens from the Pantanal: Stratiurus parviflorus by Mr. Steve Bremser, and Hypo incan-

sima by Dr. Raymond Hurky, both from the Royal
Braz. J. Biol. 61: 45-53.

REFERENCES


