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

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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 ecotone between the terrestrial and aquatic habitats develops that moves across the floodplain maintaining a more or less constant zonation of plant and animal species. This dynamic ecotone develops only during the dry season as the water-level rapidly falls, and no equivalent phenomenon was observed during the rainy seasons, when floodwaters advance across the floodplain. 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 fast-moving ecotone 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: Aquatic macrophytes, Amphibia, Heteroptera, terrestrial macrophytes, seasonal succession, tropical wet-and-dry climate, water birds, 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 ecotone 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 seral 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.

One distinguishing characteristic of a seasonal succession is its annual repetition. Other kinds of succession usually result in permanent changes (Anderson 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 sites 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 ecotone 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 continual occupation of new areas as they become available, relinquishing others to different

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groups of species and causing the entire ecotone with its complex system of zonation to move as the season progresses.

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 used to study 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 noted. 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 short-lived annuals, move along with the receding water. To describe this phenomenon of a moving ecotone, 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 meters of it remaining flooded throughout 1994, the areas across which rhe ecotone moved also varied. The entire area of the floodplain in the region was extensive, and several square kilomerers 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 Brazilian state of Mato Grosso, bring about a pronounced seasonal succession, which was studied extensively over a four-year period (Heckman 1994a, Prado *et al.* 1994, De-Lamonica-Freire & Heckman 1996, Hardoim & 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 lowest elevations on the floodplain. Unlike the well-described static ecotones that characterize many littoral biotic 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 dynamic rather than static, and the position of its distinct zones at any one time depends upon how low the water-level has 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 movement 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 pseudoterrestrial 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 densities of the species that are adapted to fluctuations between flood and very dry conditions are often remarkably high (Heckman 1994b). Prado *et al.* (1994) recorded the presence of 48 species of macrophyte on the 50 x 50 m experimental area. Most of these had life-cycles rimed to give them a temporal niche in the seasonal succession, but they were not directly involved in the dynamic ecotone 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

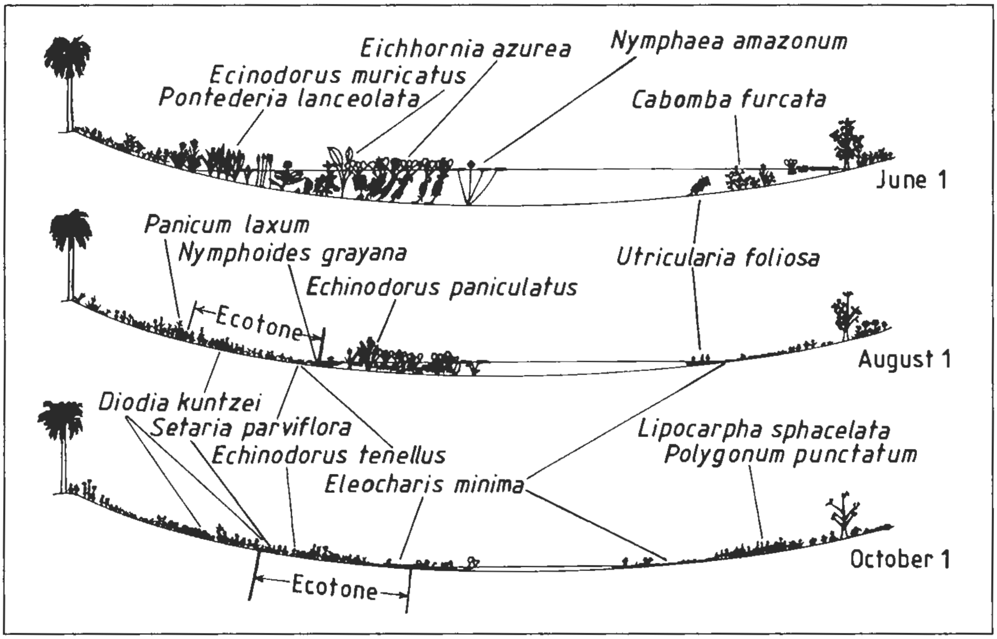

FIG. 1. Diagram illustrating the formation and movement of the dynamic ecotone on the floodplain of the Pantanal of Mato Grosso. On June 1 (above), the water is only about 50 cm below its highest level, and the floodplain is dominated by aquatic plant species. By August 1 (middle), the level has receded considerably, and a typical transition zone dominated by short-lived wetland plants has developed between typical dry season floodplain aggregations and the dying aquatic vegetation. By October 1 (below), the water has approached its lowest level of the year, and most of the vegetative parts of the aquatic macrophytes have died off. The transition zone occupied by the same species as those present on August 1 is now located on a lower-lying area of the floodplain, and its earlier position is occupied by different plant species. The downward movement of this transition zone continues until the water-level begins to rise again.

littoral zone. Hence, the description focuses on those relatively few species which are characteristic of the dynamic ecotone.

Vegetation. The mainly terrestrial species aggregations belong to two general classes. Above the high water-level of the floodplains are small patches of woodland, which are islands during the flood period. The characteristic edge species of the static ecotone separating the wooded islands from rhe floodplain is *Bromelia balansae* Mez. Slightly below this level are areas covered by drought-resistant 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 bicornis* Linnaeus and *Andropogon hypogynus* Hackel in Martius. As the water recedes from those areas inundated for longer periods of time, the dynamic ecotone species first appear.

As the water-level continues to fall, a few species of the littoral ecotone first begin to grow at the edges of the water. This group is dominated by such plants as *Diodia kuntzei* Schumacher, an upright flowering form of *Hydrolia spinosa* Linnaeus, and *Polygonum punctatum* Léveillé. However, these first appear as part of a succession that seems static because there is no zonation or dying off of the plants before the onset of the next rainy season. Other prominent species of this aggregation include *Alternanthera philoxeroides* (Martius) Grisebach, *Hyptis lorentziana* O. Hoffmann, *Bacopa myriophylloides* (Bentham) Wettstein, *Reussia subovata* (Seubert) Solms-Laubach, *Leersia hexandra* Swartz, and *Panicum laxum* Swartz. These species are very abundant on the floodplain as

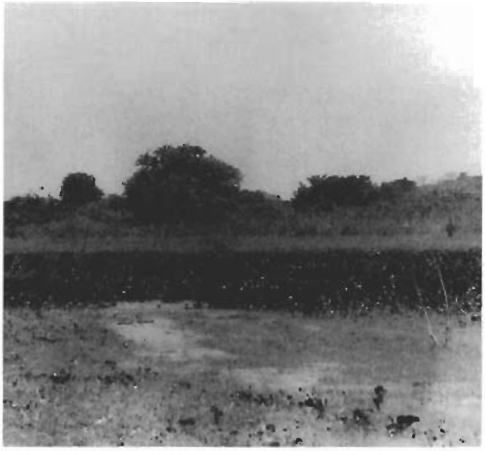

FIG. 2. An area on which a dynamic ecotone is developing after the receding flood waters have exposed large areas of the Pantanal floodplain. The open area in front of the hummock in the background is occupied by a large bed of *Eichhornia azurea* on an area still covered by shallow water. The small, fast-growing annuals of the ecotone can be seen developing in the foreground among a few dying aquatic species. If the dryness persists, they are, in turn, replaced by terrestrial plants.

long as the soil remains moist, and they also grow in many locations where no dynamic ecotone appears.

The species of the dynamic ecotone 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 *Echinodorus tenellus* (Martius) Buchenau, 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 *Diodia kuntzei*. As the *E. tenellus* at the upper end of the ecotone 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 ecotone appears, the terrestrial form of *Eleocharis minima* Kunth 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. minima* 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 periods, the areas they occupied are infiltrated by *Diodia kuntzei*, *Polygonum punctatum*, and the other plants of the uppermost zone of the ecotone. In the zone of transition between the upper two plant aggregations, other small herbs appear, such as *Lipocarpha sphacelata* (Vahl) Kunth.

In the areas still covered by about 1 to 5 cm of water, other aquatic plants begin to produce their short-lived terrestrial forms. *Nymphoides grayana* (Grisebach) Kuntze, referred to as *Villarsia kirkii* (N.E. Brown) De Wit by various authors (Prado *et al.* 1994), produces its last seeds, and its typically aquatic leaves die off leaving a root system in the mud and small rosettes 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 *Echinodorus tenellus* and *E. minima* is the small grass, *Setaria parviflora* (Poiret) Kerguélen. Dense monospecific beds of newly sprouted seedlings appeared on areas that completely dried up only during 1991, the driest year. They did not sprout when the areas

FIG. 3. An area covered by shallow water and moribund aquatic plants. As they die off, ecotone species quickly sprout from the wet sediment. The large plants in the center of the photo are *Eichhornia azurea*. Also apparent are the rosettes of *Ludwigia sedoides* and the emergent shoots of *Ludwigia inclinata*, together with several other species.

remained flooded throughout the dry season, as in 1992, 1993, and 1994. This speaks for an annual deposition of seeds in the soft sediments of the floodplain and the sprouting 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. As the *S. parviflora* matured and began to flower, the species that had first appeared in the upper parts of the ecotone began to infiltrate the stands of this grass.

At the lower end of the ecotone are the moribund 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 ecotone, diagrammatically illustrated in Fig. 1 and discussed by Prado *et al.* (1994), include *Salvinia auriculata* Aublet, *Ludwigia inclinata* (Linnaeus filius) Gomer, *Ludwigia sedoides* (Humboldt & Bonpland) Hara, *Caperonia castanaeifolia* (Linnaeus) Saint Hilaire, *Myriophyllum mattogrossense* Hoehne, *Cabomba furcata* Schultes & Schultes filius, *Justicia laevilinguis* (Nees) Lindau, *Hyptis lorentziana* O. Hoffmann, *Utricularia foliosa* Linnaeus, *Utricularia poconensis* Fromm-Trinta, *Echinodorus muricatus* Grisebach, *Echinodorus paniculatus* Micheli, *Hydrocleys commersonii* L.C. Richard, *Limnocharis flava* (Linnaeus) Buchenau, *Pontederia lanceolata* Nuttal, *Eleocharis elegans* (Kunth) Roemer & Schultes, *Eleocharis acutangula* (Roxburgh) Schultes, *Sagittaria guyanensis* Kunth, and *Hymenachne amplexicaulis* (Rudge) Nees. In addition, *Ricciocarpus natans* (Linnaeus) Corda is an aquatic liverwort that is often found at the waterline of the receding water during the dry season. Generally, plants such as *Myriophyllum mattogrossense* and *Cabomba furcata* 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 intensively until the plants have died off. *Ludwigia sedoides* persists only while the sediment remains damp, while *L. inclinata*, *Hyptis lorentziana*, and *Justicia laevilinguis* develop terrestrial forms which often remain viable on low-lying areas until the next flood period. Most of the rest of the aquatic plants are annuals that produce spores or seeds to survive the dry period. A few of them, including *Eichhornia azurea* (Swartz) Kunth, survive vegetatively in low-lying areas for at least two years if the drought is not too severe.

As the dry season continues, this entire ecotone gradually moves across the floodplain from the higher to the lower-lying sites. An essential requirement for niche-occupation in one of the intermediate zones of the ecotone is the production of seeds or vegetative propagules within a period lasting no more than a few weeks.

Fauna. In addition to the vegetation, there are a few animal species typically associated with the dynamic ecotone. They have the advantage over the plants of being able to move actively with the receding water, and most of them are able to survive both on land and on or below the surface of the water.

One prominent species in this ecotone is the toad bug, *Gelastocoris flavus* (Guérin-Méneville, 1835), a predatory heteropteran 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 dipteran species also congregate in the retreating littoral zone. The adults are observed at the margin of the water, sometimes in large numbers, and the larvae develop in waterlogged detritus, mainly decaying plants and manure from the cattle that come to the water to drink. Most prominent among these are detritivorous species of the family Ephydridae and Sphaeroceridae and predatory dolichopodids. The adults of these dipterans are seldom if ever encountered during the rainy season.

The dynamic ecotone is used by the large toad, *Bufo paracnemis* Lutz, 1925, for breeding. The eggs are deposited in shallow areas of receding water. The vast numbers of tadpoles generally remain together in large schools, forming extensive black patches on the sediment. 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 Bufonidae generally complete larval development from eggs to adults in only a few weeks, and the toadlets are, as a rule, relatively small compared to the adults. The rapid evaporation endangers those 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 dying siblings, tiny toadlets, some still with the stump of a tail, can be seen hopping away from the water and toward the denser plants in the upper zones of the ecotone.

Most of the large water birds feed on fishes and snails in the shallow pools, but a few of the smaller species are typically observed seeking food in the ecotone at the water's edge. One of the most common of these is the wattled jacana, *Jacana jacana* (Linnaeus, 1766). In the terrestrial zones of the ecotone, the southern lapwing, *Vanellus chilensis* (Gmelin, 1789), is frequently observed, and chicks appear during the dry season.

DISCUSSION

The dynamic ecotone 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 aggregations in each zone of the former 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 terrain differences. The species aggregations in classical static ecotones, especially those in the littoral zones of more stable marine and freshwater bodies, are not encountered at different locations on the substrate according to season.

Although the dynamic ecotone appears as part of a seasonal succession in the Pantanal, individuals of the same species do not all appear at the same time of year. The ecotone 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 intermediate zone between the upper and lower changes its size continually according to the terrain features. For example, at the site investigated by Prado *et al.* (1994), it occupied a strip only two to three meters wide when it first appeared early in the dry season, increasing its width to nearly 50 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 littoral zone has a moderately steep gradient. The movement of the ecotone is made possible by the very short life spans of the dominant plant species or of their reproductive growth stages, particularly *Echinodorus tenellus*, *Eleocharis minima*, *Lipocarpha sphacelata*, and *Setaria parviflora*. 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 ecotone 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 terrestrial 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 actively remained exclusively in the littoral zone. Among the water plants, there is a permanent zonation 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 azurea*, a dominant deep-water species of the floodplain, may increase at the expense of *Pontederia lanceolata*, an abundant shallow water species, during a series of particularly wet years and decrease again during dry ones. Although the dynamic ecotone 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 qualitatively by year to year variations in the minimum water-level.

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REFERENCES

Anderson, D.J. 1986. Ecological succession. Pp. 269–285 *in* Kikkawa, J., & D.J. Anderson (eds.). Community ecology: Pattern and process. Melbourne.

De-Lamonica-Freire, E., & C.W. Heckman. 1996. The seasonal succession of biotic communities in wetlands of the tropical wet-and-dry climatic zone: III. The algal communities in the Pantanal of Mato Grosso, Brazil. Int. Rev. ges. Hydrobiol. 81:255–282.

Hardoim, E.L., & C.W. Heckman 1996. The seasonal succession of biotic communities in wetlands of the tropical wet-and-dry climatic zone: IV. The free-living sarcodines and ciliates of the Pantanal of Mato Grosso, Brazil. Int. Rev. ges. Hydrobiol. 81:367–384.

Heckman, C.W. 1994a. The seasonal succession of biotic communities in wetlands of the tropical wet-and-dry climatic zone: I. Physical and chemical causes and biological effects in the Pantanal of Mato Grosso, Brazil. Int. Rev. ges. Hydrobiol. 79:397–421.

Heckman, C.W. 1994b. New limnological nomenclature to describe ecosystem structure in the tropical wet-and-dry climatic zone. Arch. Hydrobiol. 130:385–407.

Odum, E.P., 1971. Fundamentals of ecology. Philadelphia.

Prado, A.L. do, Heckman C.W., & F.R. Martins. 1994. The seasonal succession of biotic communities in wetlands of the tropical wet-and-dry climatic zone: II. The aquatic macrophyte vegetation in the Pantanal of Mato Grosso, Brazil. Int. Rev. ges. Hydrobiol. 79:569–589.