

Capítulo 2

Connectivity processes as a basis for the management of aquatic plants¹

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Introduction

Is it possible to anticipate the occupation of a reservoir or channel by aquatic plants? Can we predict which plant bioforms will occupy this environment and at which stage the reservoir will have operational problems because of the massive development of plants?

If we answer these questions affirmatively, we will be admitting that the environment has a high degree of determinism, and that there is an unequivocal adjustment between causes (environmental factors) and effects (plant assemblages). It also implies that the environment is mainly conditioned by physical and chemical variables. On the other hand, if we deny the possibility of predicting the spatial and temporal development

¹ Contribution of the Projects PIP 4242/96 and PIP 0815/98 of the National Council of Scientific and Technical Research (Argentina).

of aquatic plants in a reservoir or channel, we would be postulating a total randomness and a low or null connection between the distribution and abundance of plants and the factors that condition them.

In this contribution, an eclectic approach is presented, which postulates the possibility of anticipating the future conditions of a floodplain lake, reservoir or channel using knowledge of the connectivity that links plants of a determined geographical region with the central factors that condition them. Therefore, the degree of precision of the model depends on existing experience, as well as on information on causes and effects for each bioform or plant species at each phase of their biological cycle. This could be represented by a multidimensional matrix, almost infinite due to the multiple stage variables of the different populations of each species and the links of these different stages to n species, with the multiple environmental conditions in a time series. However, we know that in an environment neither the present and expected number of species nor the possible stages of growth/development are infinite, and that the environment which contains them has a certain order over time.

Connectivity analysis is frequently considered within the disciplines dedicated to systems analysis and especially landscape ecology, where this concept has been used to explain the interdependencies between patches within a landscape and the elements which integrate it. Connectivity has been understood as a condition of transfer of organisms, matter and energy between the river course and the floodplain (Ward; Stanford, 1995; Ward; Tockner; Schiemer, 1999) and horizontal connection between patches.

A different perspective on river connectivity was presented by Heiler, Hein and Schiemer (1994), who remarked on the importance of the hydrological regime as regulator of limnological processes on a Danube River floodplain (transfer of nutrients and composition of the plankton).

Connectivity processes as a basis for the management of aquatic plants

This contribution is conceptually very valuable, although it did not result in a quantitative analysis of the relationship regarding the parameters that compose the pulses that measure connectivity.

In this contribution, connectivity is understood as a link between the elements and processes of a system, which is defined by its state variables in space and time.

The study of connectivity allows the definition of the "*normal*" (expected) condition of the aquatic vegetation for a determined space, time and stage of environmental variables and the establishment of the extreme condition (limit configuration) for the system. The analysis of connectivity also allows the evaluation of the influence of environmental perturbations and disturbances on the distribution and abundance of plant populations².

Studies on connectivity generally evaluate the central factors (i.e. key factors) and elements (e.g. geofoms, plants, animals) which contain the greatest information on the relationships between plant assemblages. This allows the complexity of the natural system (i.e. indicator species) and the environmental factors that have the highest weight as determinants of the vegetation to be known.

The use of indicator populations and the environment in which they live allows the elaboration of tendency models on the most probable characteristics of the aquatic vegetation³. This information allows inferences on the possible colonization of the studied site by plants and their future dynamics or even other inferences that would make reconstruction of the past environment possible.

² We use the term **perturbations** to define the extreme levels naturally reached by a factor or complex of factors (e.g. flood or extreme drought). **Disturbances** refer to extreme limiting situations for organisms, generally not predictable, produced by man (e.g. pollution).

³ In this contribution, we consider aquatic vegetation to be those plants (including herbaceous plants, bushy plants or trees fixed to the substrate, free floating or mobile

Aquatic vegetation in lakes and reservoirs

In lakes, models have been used to explain the possible occurrence of submerged plants due to light. Knowing the transparency of lakes, a predictive model of the area which could be occupied by these plants in a lake or reservoir could be built.

Canfield *et al.* (1985) provided an equation to estimate the maximum depth of colonization (mDC) by submerged macrophytes from Secchi disk measurements. We tested Canfield's equation (proposed for tropical lakes in Florida) on some subtropical lakes in Argentina (Neiff *et al.*, 2000):

$$\text{Log mDC} = 0.42 \log \text{SD} + 0.41$$

However, the maximum depth for submerged plants (mDSP) is determined by many other factors, such as water pressure and sediment texture. Thus, Canfield's equation is rarely useful to explain the distribution and abundance of aquatic plants in shallow floodplain lakes.

Different equations have been used for northern hemisphere lakes to relate the biomass of submerged plants with the morphometry of lakes. Assuming that a slope of 5.33% limits the development of this vegetation, Duarte and Kalf (1986) developed two equations:

$$\text{Slope} < 5.33\%$$

$$\text{MSMB} = -29.8 + 1.403 \text{ slope}^{-0.81}$$

$$\text{Slope} > 5.33\%$$

$$\text{MSMB} = 13.2 + 3.434 \text{ slope}^{-0.8}$$

in rivers, lakes and wetlands) which need soil permanently or temporarily covered by water to fulfil some of their vital functions.

Connectivity processes as a basis for the management of aquatic plants

Where: MSMB (maximum submerged macrophyte biomass, in grams of fresh weight/m²).

It is necessary to introduce a correction in this model in relation to the height above sea level at which the lakes are found. In mountain lakes, the atmospheric pressure is much lower than in other lakes; therefore, submerged plants can reach higher depths. *Egeria najas* has its distribution limit at a depth of 5 m in lakes found up to 70 m a.s.l. (above sea level), but reaches a depth of 18 m in tropical lakes in Colombia found at 900 m a.s.l.

These models have not yet been tested in warm South American environments, where water turbidity can cause the model to overestimate expected macrophyte biomass.

The relationship between populations of floating plants and the environmental factors which limit them is very complex, especially because floating meadows are limited by some factors of stochastic behavior (e.g. wind).

Free-floating plants are very sensitive to waves, which damage them and submerge them. Wind makes great energy waves. Moreover, frequency, wind direction and reservoir morphology have great importance in the elaboration of predictive models. The potential effect of the wind on the water surface was estimated for Yaciretá Dam from satellite images (Neiff *et al.*, 2000), considering the frequency and velocity of the wind and the distance over which the wind had blown without being interrupted by land (fetch). The height of the highest waves was calculated from statistical records of wind velocity and the fetch. The equation proposed by Saville, McClendon and Cochran (1962) was used:

$$Z_w = 0.005V_w^{1.06} F^{0.47}$$

where:

Z_w = height of the highest waves (in m)

V_w = wind velocity (in km²/h)

F = fetch (in km)

The flooded areas (at different depths) were estimated using the GIS IDRISI. Based on the planimetry, hypsographic curves of the lake surface were plotted and the Digital Elevation Model (DEM) was obtained. After a field survey of the reservoir had been done, map curves were adjusted.

We concluded that when the wind reaches 40 km/h and the fetch surpasses 4 km, it is possible that waves larger than 50 cm are formed. These waves control the development of free-floating vegetation naturally in Yaciretá Reservoir (Neiff *et al.*, 2000). In spite of this, models that predict vegetation cover and density in lakes and reservoirs should be used carefully, because the wind is changeable (Håkason, 1993).

Marshy plants that live in the littoral zone of most lakes in the world are found in a fringe not exceeding a depth of 2 m, since at least part of their leaves and inflorescences must remain emergent. Many of them have even more precise distribution limits, so that the area potentially colonized by these plants could be established with an error lower than 30% in some reservoirs. However, the distribution limit also depends on the position of the lakes regarding sea level (atmospheric pressure). The geophyte *Schoenoplectus californicus* has its mDC at 2 m in lakes of the Paraná-Paraguay riverine system (up to 70 m a.s.l.), while in lakes and wetlands of the Benni (Bolivia), near the Andes, this species reaches a depth of four meters⁴ (verbal information).

For rooted plants with floating leaves (*Nymphaea* spp; *Nymphoides* spp; *Victoria* spp), the bottom should have muddy-sandy-clayey

⁴ Personal Communication of Dr. Stefan Beck, Museum of Natural History, La Paz (Bolivia).

sediments, since they rarely grow on a stony bottom. They are found at a depth of up to 3.5 m, since the laminae and floating petioles are drawn upwards; and when the water column is equal to or higher than 3.5 m, leaves are broken in the lower part, close to the bottom, and the plants die (Neiff, 1978; Neiff *et al.*, 2000).

The potential surface area of the littoral zone which rooted plants can colonize depends on two morphometric features of the lake -- shore development, which is the relationship between the shoreline of the lake and its area, compared with the circumference of a circle that has the same area as the lake, and shore slope. Both were obtained directly using a Kontron planimeter.

Contrary to what is expected, there is a poor correlation between the development of free-floating plants and the concentration of nutrients in lakes and reservoirs (Thornton, 1987; Bond; Roberts, 1978), although a higher concentration of nitrogen and phosphorus favors their growth (Carignan; Neiff, 1992; Carignan; Neiff; Planas, 1994).

The nutrients limit the growth of the aquatic plants. Thus, macrophyte growth has been associated with phosphorus concentration in temperate lakes and nitrogen availability in some tropical lakes. Still, when explosive growth of aquatic plants (e.g. Harbeespoort) is recorded in hypereutrophic lakes (Scott *et al.*, 1977), growth of aquatic macrophytes is not exclusively related to nutrient enrichment in tropical man-made lakes (Thornton, 1987). The highest colonization of *Salvinia molesta* in Lake Kariba (21% of the surface area) occurred when the nutrient levels did not exceed 25 $\mu\text{g.l}^{-1}\text{P}$ and 0.02 $\text{mg l}^{-1}\text{N}$. In addition, Marshall and Junor (1981) report no significant relationship between *Salvinia* growth and lake nutrient status.

If the rate of water renewal is high in lakes and reservoirs with low nutrient concentrations, plants could cover their nutrient needs and reach high production values. Moreover, nutrient fluxes could occur from

the sediments, especially in shallow lakes, where plants use water nutrients as much as those from sediments.

In northeastern Argentina there are lakes that, because of their nutrient concentrations, could be categorized as oligotrophic, in which luxuriant aquatic and marshy vegetation is developed. In these lakes, macrophytes have a high turnover and, when decomposing, release nutrients that become available for new plants, thus favoring growth in the occupied area.

Some other considerations are necessary to explain and predict macrophyte colonization in lakes and reservoirs. As Thomaz and Bini (1998, 1999) pointed out, the role of the regional biological processes (species pool in surrounding area, dispersion and invasion rates by non-native species) is one of the main factors that control species composition and abundance.

Aquatic vegetation in large rivers and their floodplains

Plants that live temporarily or permanently in rivers have undergone a process of long-term adaptive selection, adjusting their populations to the hydrological variability at different levels (e.g. metabolism, individuals, bioforms, species, size structure) (Neiff, 1978; Joly; Crawford, 1982; Irgang, 1999; Thomaz; Bini, 1999).

Seeds of most plant species found in the Paraná River Basin do not germinate in the flooded soil, i.e. the plain could be interpreted (for this process) as a binary system. If there is a low water phase (emergent soil), germination occurs. If the water remains on the ground, it does not. Inhibition of successive seasonal germination periods could determine the recession of many species, which would not be able to replace the young strata of the population (Table 1).

Connectivity processes as a basis for the management of aquatic plants

Table 1. Process associated to the pulse regime

Limnophase (period in which the river course remain isolated from the floodplain) Associated *FITRAS* attribute (*) Author

Increase in nutrient concentration in floodplain lagoons	amplitude +	1
Germination phase	magnitude - amplitude + seasonality +	6
Flowering of submerged plants	magnitude - amplitude + seasonality +	4-6
Dispersion of fruit and seeds	magnitude - frequency - or +	4-6
Increase in primary productivity in floodplain lakes	amplitude +	1
Colonization of exposed sediments by woody vegetation	amplitude + tension +	1
Fragmentation of floodplain aquatic habitats, replacement of lotic communities by lentic communities, particularly aquatic invertebrates and their predators (other invertebrates, amphibians)	amplitude + intensity + tension -	1

POTAMOPHASE

(time lapse in which bodies of water (wetlands, lakes) are connected to waters of the river course)

Transport and deposit of seeds on the floodplain	intensity + amplitude +	5,6
Decomposition of terrestrial organic matter, detrital accumulation and increase in bacterial activity in sediments	intensity + amplitude +	2
Connection of floodplain aquatic habitats, predominance of reophile communities in water courses	amplitude + intensity + tension +	1,5
Increase in dissolved organic carbon in the river	intensity + amplitude - frequency +	2
Germination of plants from seeds	amplitude - intensity - seasonality +	4-6
Abundance of phytophile invertebrates	Intensity -	3

The symbol + or - refers to the estimated or inferred correlation between the event and the attribute.

1. Neiff (1990, 1996), Neiff *et al.* (1985)- 2. Paolini (1990)- 3. Poi de Neiff and Bruquetas de Zozaya (1989)- 4. Irgang (1999)-5. Colonnello (1995)-6. this study.

(*) The attributes of **FITRAS** are defined as:

Frequency for certain reference level (overflows level), number of times that floods or droughts have occurred in a decade (e.g. floods of 6 m on the hydrometer of Porto São José in the last century).

Magnitude (or intensity reached by a drought or inundation) could temporally exclude determined populations or sizes of plants or animals that live in the wetlands.

Tension or value of the standard deviation from the maximum or minimum means in a curve of pluriannual hydrometric fluctuation establishes the variability of floods and droughts.

Recurrence is the statistical probability that a flood or drought of a determined magnitude will occur within a century or millennium.

Amplitude of the phase is the duration of droughts and floods of a determined magnitude in a determined place on the floodplain.

Seasonality is the seasonal frequency with which the droughts and floods occur.

This change in the hydrological periodicity of the river also affects animals associated to vegetation (e.g. foraging, pollination, dispersion and seed germination). In turn, changes in vegetation produce variations in the habitat offer for animals which frequent these environments (e.g. using them for feeding, refuge or reproduction) (Poi de Neiff; Bruquetas de Zozaya, 1989; Beltzer; Neiff, 1992).

Many biogeochemical processes, such as leaf litterfall, organic matter decomposition, nutrient availability, and flux and retention of sediments on the floodplain are closely related to the alternation of droughts and floods, i.e. the frequency, intensity, duration and seasonality of connectivity between the floodplain and the fluvial course (Neiff ; Poi de Neiff, 1990; Poi de Neiff *et al.*, 1994).

Undoubtedly, of all factors controlling the distribution of plants, the pulse regime is the most important macro-factor (Lewis; Franceschi; Prado, 1987; Franceschi; Prado, 1989; Junk; Bailey; Sparks, 1989; Neiff, 1990, 1996, 1997; Colonnello, 1995; Malvarez, 1997; Bini; Thomaz; Souza, 2001). Another group of dependent variables (e.g. current velocity, water transparency and nutrient content) is also associated to the pulse and an even wider array of variables is associated to each one of them (Neiff, 1997; Bini *et al.*, 1999).

As Bini, Thomaz and Souza (2001) pointed out, at high water phase horizontal fluxes of individuals along the floodplain river course disrupt the dissimilarity in the landscape and increase the similarity of assemblages between bodies of water and the river as a whole. This periodical homogenizing process (Thomaz; Roberto; Bini, 1997) has been shown in other communities (Poi de Neiff; Bruquetas de Zozaya, 1989; Bonecker; Lansac-Tóha; Rossa, 1998).

However, is it possible to quantitatively analyze the variability of distribution, abundance and growth of plants in relation to parametric variables such as the hydrometric regime of a river?

Connectivity processes as a basis for the management of aquatic plants

Relationships between aquatic plants and environmental factors have different characteristics in rivers and lakes. In rivers, it rather depends on the group of regional characteristics and management of the hydrographic basin, the replacement of natural forest by crops or the regulation of the river regime by dams.

Moreover, spatial heterogeneity is greater in rivers than in lakes. Sites which are adjacent to the floodplain or separated by a few meters could differ in the number of days that they remain connected to the fluvial course and could have marked differences in the distribution and abundance of many aquatic communities (Neiff, 1979, 1997; Thomaz; Roberto; Bini, 1997). This relationship has not been quantitatively studied to explain the structure and dynamics of vegetation patches and the aquatic fauna of rivers.

When a connectivity model is used, it is important to analyze the geographical context in which the study area is found. A reservoir or channel depends on the feeding basin and on its hydrological functioning. If the study area is found in the low part of a basin that has extensive lakes colonized by plants at its heads, the result would depend to a great extent on the area of contribution (Thomaz; Bini, 1999). If, on the contrary, the contributions of the drainage basin (e.g. nutrients, plants and seeds) are low, plant development in this reservoir would mainly depend on the characteristics of the lake (e.g. sediments, transparency, winds, etc.). Thus, connectivity models should associate physical and chemical parameters with plant development.

If we know the hydrological range in which a determined species is found, the possibility of finding it in one or another hydrological phase can be inferred, as can its survival after low water or floods of extraordinary duration and magnitude. Knowledge of its phenology in both phases (floods and droughts) allows inferences about whether such

a species could remain in the system if the seasonal periodicity of the hydrological regime is altered.

When considering the floodplain topography, most species have very wide distribution ranges. This means that these organisms also have wide niches and are able to withstand very limiting environmental conditions in the extraordinary droughts and floods⁵.

Floods occur with different intensity and duration over several decades. In the Lower Paraná River, for example, the "annual" floods (with a typical alternation of flood and drought phases) occurred with a certain recurrence until the beginning of the 1970s. Since then, the overflow has progressively increased, with very short and slightly pronounced limnophases. Compared to the magnitude recorded at the beginning of the century, the potamophases have acquired a progressively higher duration (with an extreme value of 15 months in 1983/84 -- our example).

This drastic change in the periodicity of the system produced a natural perturbation of great magnitude, which in turn produced a drastic modification in the organization of the landscape, with changes in the proportion of typically aquatic species, species that can live alternatively in aquatic or terrestrial environments and species that need to fulfil an emergency phase to complete determined biotic functions. In the Lower Paraguay River, between 40 and 60 % of the fluvial forests died during the 1982/83 flood (Neiff *et al.*, 1985).

⁵ To explain the limits of the distribution of aquatic plants, the extreme conditions of the system should be defined. In the Lower Paraná River (after its confluence with the Paraguay), for example, **extraordinary floods** are those exceeding 7.5 m on the hydrometer of Corrientes Port, Argentina. **Extraordinary droughts**, for the same system, are those in which the river course does not overflow its channel (low waters) for more than 10 months.

Guidelines for the analysis of vegetation and pulse attributes

The landscape components and elements (e.g. trees, algae, vertebrates) have a different degree of connectivity with the river course, according to the position they occupy on the plain and their possibility of avoiding the critical periods of floods or droughts (e.g. migration). Not all landscape elements are equally sensitive to the different pulse attributes.

For the above reason, indices could be used to infer which pulse attributes (e.g. frequency, intensity, tension, regularity, amplitude, seasonality) produce changes in community integration, phenological characteristics or determined population growth. They could also be used to obtain synthetic indicators of the relationships between plants and the environment in which they live.

The connectivity amplitude, for example, taken here as the percentage of time (days/year or days/decade) that a lake is found connected to the river course along a time series, is an indicator of the continuity in the information fluxes (e.g. nutrients, sediments, organisms) between both subsystems (lake and river) and can be compared with species number, abundance or plant size. Growth of *Eichhornia crassipes*, for example, is limited by nitrogen. Thus, floodplain lakes with low connectivity would be expected to have scarce development of this species.

We also propose here the Fluvial Connectivity Quotient (*FCQ*):

$$FCQ = FD/ID$$

where FD= number of flooding days (potamophase)

and ID= number of isolated days (limnophase)

This quotient can be calculated for each pulse and compared with the population values (bioforms, density, biomass and size classes) corresponding to that pulse. Or, the mean FCQ could be used for a time series, if the tension values (see definition at Table 1) were lower than 20 % for the maximum and minimum means, respectively.

Using data obtained in Paraná River floodplain lakes, we compared tree sites located along the geomorphological gradient from October 1997 to August 1998. Site A was connected with the main channel for 404 days (Table 2), site B was flooded 520 days and site C remained isolated.

The mean FCQ calculated from the FCQ for each pulse divided by the number of pulses (Figure 1 and Table 2) was 4.1 (Site B), 4.2 (Site A) and 0 (Site C).

According Neiff, Poi de Neiff and Casco (2001), the mean leaf length frequency of water hyacinth was higher in the floodplain lake connected to the main river channel (most prominent leaf mode = 90 cm and 105cm) than in the isolated condition (most prominent mode = 65cm). The FCQ index for this period demonstrated the effect of flooding on the growth responses of *E. crassipes*.

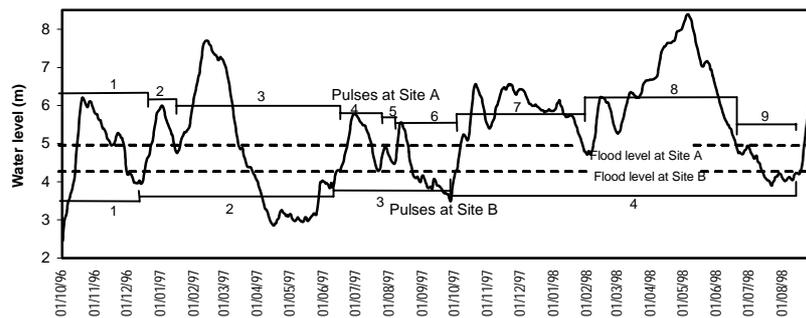


Figure 1. Water level of the Paraná River showing pulses and flood levels at different floodplain sites. Numbers indicate pulses

Connectivity processes as a basis for the management of aquatic plants

Table 2. Duration of the low and high water phases and number of pulses between October 1996 and August 1998 (Neiff; Poi de Neiff; Casco, 2001)

Site A					Site B				
Pulse	Start date	Time	Low water phase (days)	High water phase (days)	Pulse	Start date	Time	Low water phase (days)	High water phase (days)
1	14-Oct-96	68	25	43	1	12-Oct-96	65	16	49
2	22-Dec-96	27	5	22	2	17-Dec-96	181	81	100
3	18-Jan-97	154	98	56	3	17-Jun-97	108	20	88
4	22-Jun-97	35	12	23	4	3-Oct-97	318	35	283
5	28-Jul-97	10	9	1					
6	8-Aug-97	58	48	10					
7	6-Oct-97	121	7	114					
8	5-Feb-98	144	10	134					
9	27-Jun-98	52	51	1					

It is probable that similar relationships between biotic complexity and pulse amplitude would be found for plankton and other communities (Frutos, 1993; José de Paggi, 1993; Zalocar de Domitrovic, 1993; Pagioro; Roberto; Lansac-Tôha, 1997). Measurement of connectivity helps explain the microsuccessions, although this perspective has not yet been analyzed in the fluviology.

Since the hydrological regime of the river is regulated by natural phenomena (like the "El Niño" floods), and by reservoirs and other hydraulic forces, FCQ values can change and be changed. Modifications in the assemblages of floodplain plants and animals can also be expected. The FCQ can thus be used to compare partial periods within a time series to look for changes in the communities as a consequence of natural or anthropogenic modifications in the hydrological regime of rivers.

The distribution of rooted aquatic plants (including trees) on a floodplain can be represented on an axis of Cartesian coordinates (Figure 2). The topographic position (altitude) of the sectors that integrate the river floodplain is placed in the abscissa. These points can be referred to as values of the hydrometric ruler at the nearest port, or to the altitude in relation to sea level. The percentages of occurrence of each species for each topographic position represented in the abscissa are placed in the

ordinate. Generally, each plant species is represented by a Gaussian curve showing the chance of occurrence of a given species at each point of the topographic gradient.

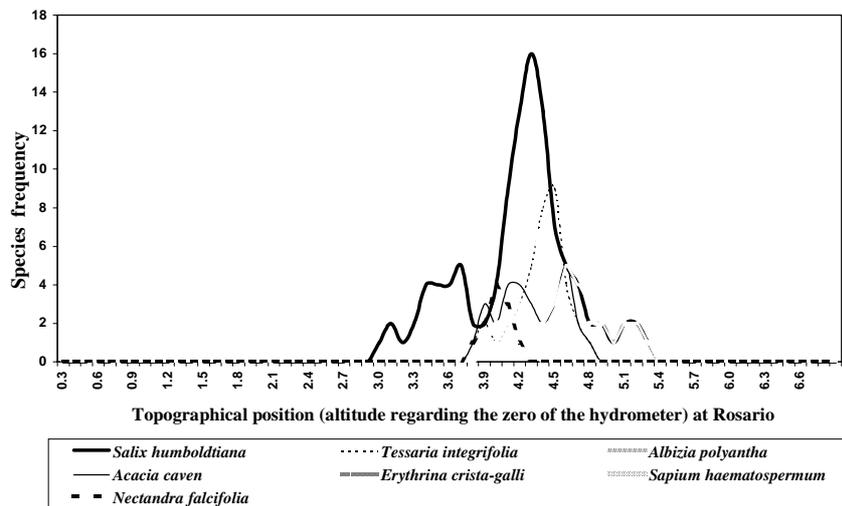


Figure 2. Distribution of some species of trees in the delta of the Paraná River

Plants have very different curves. The most plastic or eurytypical plants have platykurtic curves with an indistinct mode. They are adapted to live at sites with a high pulse fluctuation, while stenotypical plants are represented by leptokurtic curves with a well-defined mode. We propose a eurytypical index (Ei), which relates the height of the population mode (or the mean of the modes) with the amplitude of values in the abscissa:

$$Ei = \text{value of the mode on the } Y \text{ axis} / \text{range of } X \text{ values on the curve}$$

Values of Y are expressed as frequency values, and those of X are expressed in meters (equivalent to the time of flooded soil).

The seasonal connectivity index (SCI) represents the phenological recurrence of a population (e.g. florescence phase, fructification, fertility, or maximum population value) in relation to the period in which floods occur in a time series, expressed as a percentage of this. In other words, it indicates the degree of adjustment of the biological phases in relation

to the hydrological events. If, for example, the fertility period of a plant frequently occurred during the period of flooded soil, we would confront a disarrangement phenomenon between the biological and physical variables. Such plants could not renew their populations and would be segregated from the system in the future. SCI is given by:

$$SCI = \frac{FSd \times 100}{FeD}$$

where:

FSd= flooding seasonality (in days)

FeD= length of the fertility period (in days)

Conclusions

It is possible to define a probable setting for the presence or absence of aquatic plants in a determined environment for which some simple models can be assayed. The validity of these approximations depends to a great extent on the available knowledge of the limits of the environmental tolerance of populations and the variability range of the limiting environmental factors. Models are only useful tools and cannot explain more than probable situations. The best knowledge of the ecological connectivity between aquatic vegetation and the environment results from great interest in the management of plants in lakes, reservoirs and rivers, especially in predicting changes.

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Ecologia e manejo de macrófitas aquáticas

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Connectivity processes as a basis for the management of aquatic plants

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Ecología e manejo de macrófitas acuáticas

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