HYDROLOGIC CYCLE AND DYNAMICS OF AQUATIC MACROPHYTES IN TWO INTERMITTENT RIVERS OF THE SEMI-ARID REGION OF BRAZIL

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(With 5 figures)

ABSTRACT

The dynamics of aquatic macrophytes in intermittent rivers is generally related to the characteristics of the resistance and resilience of plants to hydrologic disturbances of flood and drought. In the semi-arid region of Brazil, intermittent rivers and streams are affected by disturbances with variable intensity, frequency, and duration throughout their hydrologic cycles. The aim of the present study is to determine the occurrence and variation of biomass of aquatic macrophyte species in two intermittent rivers of distinct hydrologic regimes. Their dynamics were determined with respect to resistance and resilience responses of macrophytes to flood and drought events by estimating the variation of biomass and productivity throughout two hydrologic cycles. Twenty-one visits were undertaken in the rewetting, drying, and drought phases in a permanent puddle in the Avelós stream and two temporary puddles in the Taperoá river, state of Paraíba, Northeast Brazil. The sampling was carried out by using the square method. Floods of different magnitudes occurred during the present study in the river and in the stream. The results showed that floods and droughts are determining factors in the occurrence of macrophytes and in the structure of their aquatic communities. The species richness of the aquatic macrophyte communities was lower in the puddles of the river and stream subject to flood events, when compared to areas where the run-off water is retained. At the beginning of the recolonization process, the intensity of the floods was decisive in the productivity and biomass of the aquatic macrophytes in the Taperoá river and the Avelós stream. In intermediate levels of disturbance, the largest values of productivity and biomass and the shortest time for starting the recolonization process occurred.

Keywords: stream, disturbance, flood, drought, aquatic macrophyte.

RESUMO

Ciclo hidrológico e dinâmica de macrófitas aquáticas em dois rios intermitentes da região semi-árida do Brasil

A dinâmica de macrófitas aquáticas em rios intermitentes está relacionada com as características de resistência e resiliência das plantas as perturbações hidrológicas da cheia e da seca. A região semi-árida do Brasil apresenta rios e riachos intermitentes, com ocorrência de eventos de perturbação em diferentes graus de intensidade, freqüência e duração ao longo de um ciclo hidrológico. O objetivo deste estudo foi determinar a ocorrência e variação de biomassa de espécies de macrófitas aquáticas em dois rios intermitentes de regime hidrológico distintos. A dinâmica foi determinada pelas respostas de resistência e resiliência das plantas aos eventos de cheia e de seca, através da variação da biomassa e produtividade ao longo de dois ciclos hidrológicos. Foram realizadas 21 visitas de campo durante as fases de reinundação, vazante e seca, em uma poça permanente localizada no riacho Avelós e duas poças temporárias no rio Taperoá, estado da Paraíba, Brasil. A amostragem foi feita de acordo com o método dos quadrados. Durante o estudo ocorreram cheias de diferentes magnitudes no rio e no riacho. Os resultados mostram a cheia e a seca como fatores determinantes na ocorrência e na estrutura da comunidade de macrófitas aquáticas. A riqueza da comunidade de macrófitas aquáticas foi menor nas poças do rio e riacho, sujeitos a eventos de cheia, quando comparada com a área de retenção de água, formada principalmente por escoamento superficial. A intensidade das cheias foi determinante no início da recolonização, na produtividade e na biomassa das espécies de macrófitas aquáticas no rio Taperoá e no riacho Avelós. Os maiores valores de produtividade, biomassa e o menor tempo para o início da recolonização ocorreram em níveis intermediários de perturbação.

Palavras-chave: riacho, perturbação, cheia, seca, macrófita aquática.

INTRODUCTION

Processes of natural disturbances are important phenomena in the dynamics of ecosystems and are known for causing fluctuations in the biological community and acting as a selective strength in the evolution of the species (White, 1979). Disturbance can only be defined as an event that generates unpredictable modifications in the environment and frequent alterations are considered as normal events (Resh *et al*., 1988); or it is a predictable event causing modifications in individuals or populations and creating opportunities for new groups to be established, as proposed by Sousa (1984) and accepted in the present study. The different intensity degrees, duration, frequency, and predictability of the disturbances are decisive throughout the ecological succession and in the establishment of biodiversity (Fisher *et al*., 1982). Biodiversity variations during succession are mainly due to different strategies of the species in response to disturbance regimes (Smith & Huston 1989), as reported in several ecological models (Southwood, 1977). Many studies have reported that the largest values of biodiversity occur in environments with disturbances in intermediate levels of magnitude and frequency, and with moderate levels of productivity (Dobson, 1994).

The stability of an ecosystem is determined by the resistance (proportional change) and resilience (potential of subsequent recovery) responses of the communities and populations to disturbance events (Pimm, 1991). Floods in rivers and streams act as a disturbance for aquatic macrophytes and riparian vegetation because they break and retreat plants, and remove sediments (Bilby, 1977). Recurrent floods open new areas and form a mosaic of environments in different recolonization levels (Dawson *et al*., 1978), influencing the abundance and distribution of species, and the availability of environmental resources (Barrat-Segretain & Amoros, 1995). The hydrologic drying and dryness phases also represent a disturbance for organisms of intermittent environments, and the magnitude of the events is a determining factor of the structure and functioning of ecosystems (Stanley & Fisher, 1992). Trémolières *et al*. (1994) suggested that organisms and communities of streams present evolutionary responses to disturbance events.

Rivers and streams of arid and semi-arid regions are characterized as being systems of high resilience, with a high recovery capacity after abiotic disturbances (Dudley & Grimm, 1994). In temporary environments, aquatic macrophyte communities are characterized as having low competition and great occurrence of vegetative reproduction (Lippert & Jameson, 1964). Aquatic macrophytes in rivers and streams present morphologic plasticity in relation to variations of the water level and current speed (Allan, 1995). Flash-floods act as dispersion factor for aquatic macrophytes (Lokker *et al*., 1997). Fox (1994) states that the dispersion rate is determined by the size and weight of the propagules and by the water movement strength. The recruitment and the density of annual species are determined by the variation of the hydrologic conditions, which allow the plants in the environment to be established and regenerated. (Bonis *et al*., 1995).

In the semi-arid region of Brazil most of the rivers and streams present intermittent hydrologic regimes with periods of flash-floods and prolonged droughts. Floods and droughts act as agents of hydrologic disturbance and have a strong influence on the way the environment functions, causing alterations to the dynamics of aquatic macrophytes (Maltchik & Pedro, 2001). The aims of the present study are (within the conceptual approach of the stability and hydrologic disturbance of communities: 1) to evaluate the occurrence of aquatic macrophytes in two intermittent rivers (ephemeral and temporary) of the semi-arid region of Brazil throughout the hydrologic cycles of 1999 and 2000; and 2) to estimate the biomass variations of the plants facing floods and drought.

MATERIAL AND METHODS

Study area

The study was carried out in a permanent puddle in the Avelós stream and in two temporary puddles in the Taperoá river. The river and the stream are located in the sub-basin of the Taperoá river and in the basin of the Paraíba river in the semi-arid region of Northeast Brazil (Fig. 1). Field work was carried out according to the hydrologic regime of the region at the beginning of the rain period of each year. Twenty-one visits were undertaken during the hydrologic cycles in 1999 and 2000. The semi-arid region spreads over *ca*. 800,000 km^2, and it has a hot semi-arid climate with summer rains (BSh) and a bioclimatic sub-desert hot zone with a tropical tendency (2b). The mean annual temperature varies between 25 °C and 30 °C and the rainfall varies between 200 mm and 800 mm/year, distributed mainly from January to June. The evaporation rate is high (IBGE, 1977). The vegetation close to the study area is composed predominantly of a caatinga, deciduous savannah-like vegetation, with thorny shrubs and stunted trees, with small and subdivided leaves, or an absence of leaves. Among the most common species there are *Caesalpinia pyramidalis* Tul., *Cereus jamacaru* DC, *Cereus squamosus* Guerk, *Pilosocereus gounellei* Weber, *Zizyphus joazeiro*

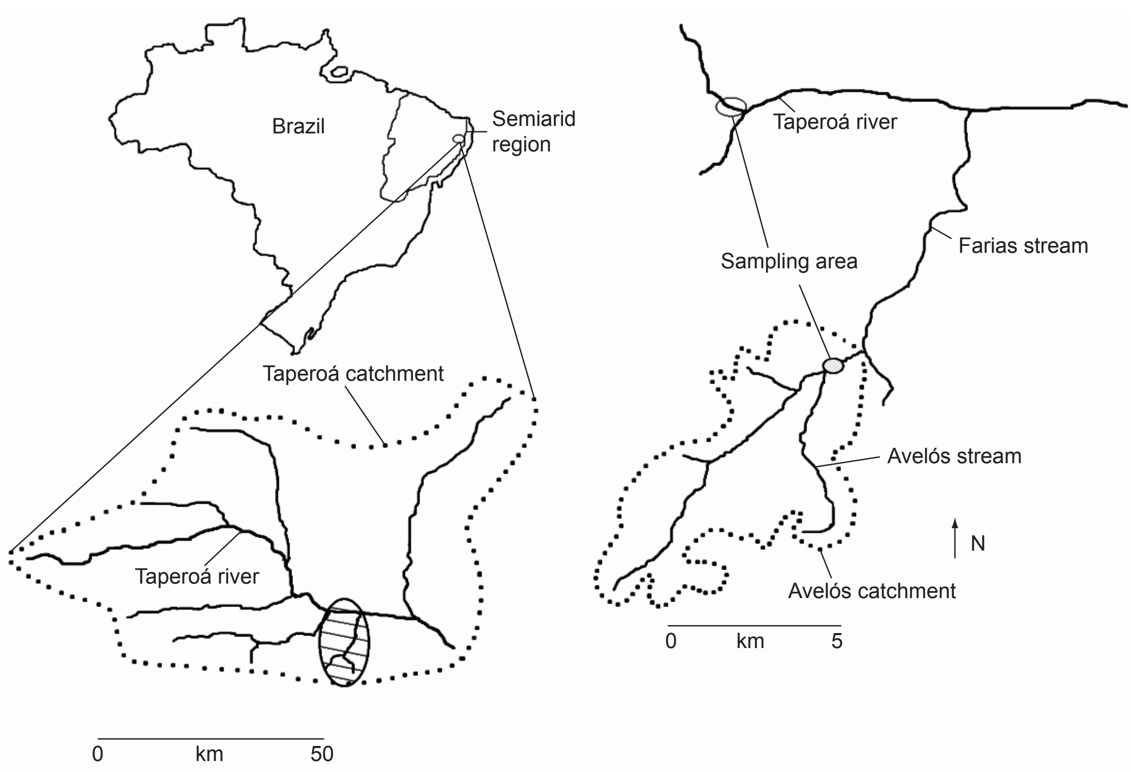

Fig. 1 — Geographical localization of drainage basins and sampling areas in the Avelós stream (7° 28' 08" S and 36° 31' 17" W), and in the Taperoá river (between 7° 00' S and 7° 30' S, and 37° 00' W and 36° 10' W) in the semi-arid region of Brazil.

Mart., *Delicate verrucosa* Benth, *Prosopis juliflora* DC, and *Opuntia ficus* Mill. The soils are of metamorphic origin (gnaisses, migmatites, and schists), shallow, rocky and with low permeability. The drainage system is totally intermittent (Rizzini & Mors 1976; Bigarella *et al*., 1985) (Fig. 1).

The Avelós stream is an ephemeral river of 2nd order (Graff, 1987), *ca*. 8 km extension, medium steepness of 9.7 m/km and a drainage area of 42 km^2. Its source is at 576 m above sea level; it runs northwards in a narrow channel formed by sand and stones discharging its water into the Farias stream. On the bed of the stream, there is an area with permanent superficial water, resulting from a positive exchange of underground water with the surface. This site is unique in the region located at 7° 28' 08" S and 36° 31' 17" W, 14 km distant from the municipality of São João do Cariri. The area was distinct as being a puddle without water flowing superficially during the drought phase and was stored in the river bed. The total area of the environment, formed by the water surface plus the ecotone is *ca.* 5,300 m^2 including the fluvial and parafluvial zones of the stream. The area of the ecotone is formed mainly by stones and it is under effect of the floods and of the run-off water. The substratum of the puddle consists of sand, pebbles, and granite.

The Taperoá river is a temporary river of the 6th order (Graff, 1987), whose water remains for several months throughout the year. Its source is at 720 m above sea level; it runs eastwards with a medium steepness of 2.2 m/km discharging its water into the Boqueirão dam. It extends for 133 km, with a drainage basin of 5,664 km^2 located between lat 7° 00' and lat 7° 30' S and between long 37° 00' and long 36° 10' W (IBGE, 1977). The sediment of the river mainly consists of sand, gravel and pebbles with granite outcrops. Two temporary puddles in the Taperoá river were also studied, one located on the left margin and the other on the river bed. The study places are about 5 km from the municipality of São João do Cariri. The width and length measurements of the puddles were taken with a tape measure (m) considering the largest extremities of the puddles. The areas of the puddles were determined by drawing their forms on millimeter paper on a proportional scale. Measurements in the depth of water and the deposited sediment were obtained by recording the distances between the nylon line, and the surface of water and between the line and the substratum. Three transects perpendicular to stream flow were selected in the same area where macrophytes were collected. For each transect, a nylon line was tied to two wooden stakes on each stream bank. The first measurement between the nylon line and the substratum was established as being zero, and the subsequent measurements were reported as positive or negative changes from the baselines.

The growth of aquatic macrophytes was also observed in an area of retention of water, which appeared during the construction of the highway that crosses the area, formed mainly by run-off water. The flooded area was monitored in the hydrologic cycle in 2000, acting as a reference environment for the growth of aquatic macrophytes in places with no disturbances of floods. The rainfall was recorded at the Hydrological Station of the Federal University of Paraíba located in São João do Cariri.

Biomass of aquatic macrophytes

The variation of biomass of the aquatic macrophytes was determined using the square method (Nogueira & Esteves, 1990). Samples were taken in ten transects perpendicular to the margins, ten metres distant from each other, starting at the front part of the puddle up to the back part. In each transect, five sites of samples were randomly selected (Titus, 1993) making a total of 50 samples in each visit. All plants found in a square of 25 cm x 25 cm were collected above the water surface. They were stored in polythene bags and maintained refrigerated until they were washed in running water, drained for 15 min, separated by taxon and oven-dried at 60 °C for 72 h or until the weight loss stabilized. The results are expressed in gDW/m^2 (Esteves, 1988). The existence of significant differences in the biomass means of the aquatic macrophytes, between consecutive visits was statistically dealt with using a *t*-test (Anderson & Kalff, 1986). The productivity of the plants was estimated by considering the increase of biomass means over consecutive samples related to the time between the samples and expressed in gDWm^{-2}.day^{-1}. The richness of the species was estimated as the number of existent species in the environment at each visit we undertook. The species were identified by Dra. Maria Regina Barbosa and comparisons were made with exsiccata deposited in the botany collection of the Department of Systematics and Ecology at the Federal University of Paraíba.

RESULTS

The rainfall between February and July in 1999 and 2000 had different magnitudes (Fig. 2) in the drainage basin of the Taperoá river causing floods with different frequency, intensity degrees, and duration in the rivers and streams of the region. The hydrologic phases of floods and droughts were determining factors in the formation and functioning of permanent and temporary puddles, and the formation of flooded areas in the region. Nine species of aquatic macrophytes were found in the studied environments: *Echinodorus macrophyllus*, *Eleocharis interstincta*, *Eleocharis* sp, *Elodea* sp, *Heteranthera limosa*, *Hydrocleys nymphoides*, *Najas marina*, *Najas* sp, and *Nymphaea lingulata*.

Permanent puddle in the avelós stream

The puddle had rewettings in the hydrologic cycle in 1999 (14 Mar) and in the cycle in 2000 (20 Feb). They were of the flash-flood type and the run-off water was interrupted quickly after the events. The hydrologic phases of rewetting, floods and drying then occurred, but not the drought phase. The puddle had a mean area of 2,177 m^2 (± 837), the mean water level was 14.3 cm (± 10) and the mean deposited sediment was 12.6 cm (± 12). The community of aquatic macrophytes consisted of two species from distinct environments: *Najas marina* occurring largely in the fluvial area distributed in stands in the whole puddle and *Eleocharis interstincta* of scarce and limited occurrence in the parafluvial area.

The mean biomass of *Najas marina* was 62.3 g/m^2 (± 78) and the mean productivity was 2.4 gDW m^2.day^{-1}, which had significant alterations throughout the hydrologic phases of the puddle (Fig. 3). In the 1999 cycle, the species showed resistance and high resilience. The recolonization of *Najas marina* was noted 38 days (21 Apr) after rewetting. The biomass increased significantly (n = 2, $P < 0.047$) in the flood phase of the puddle (18 Mar – 14 Apr), with a rise of 443% and a mean productivity of 5.5 gDW m^{-2}.day^{-1} (± 2.9). In the drying period (3 Jun, 1999 – 11 Feb, 2000), the biomass decreased significantly (n = 4, $P < 0.025$),

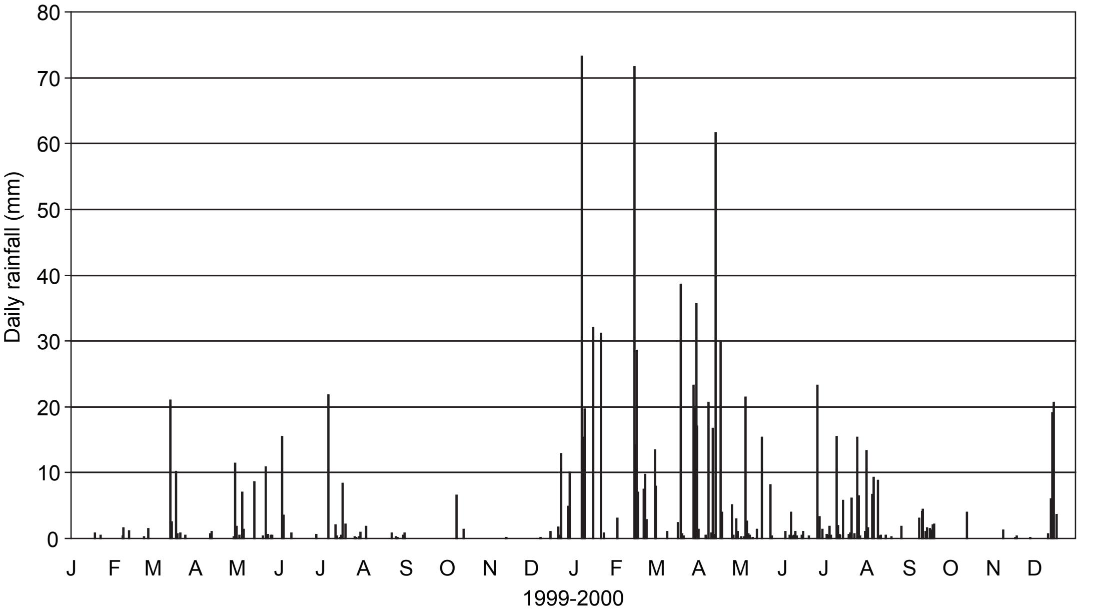

Fig. 2 — Daily rainfall (mm) recorded at the Hydrologic Station in the municipality of São João do Cariri, state of Paraíba, Brazil, throughout 1999 and 2000.

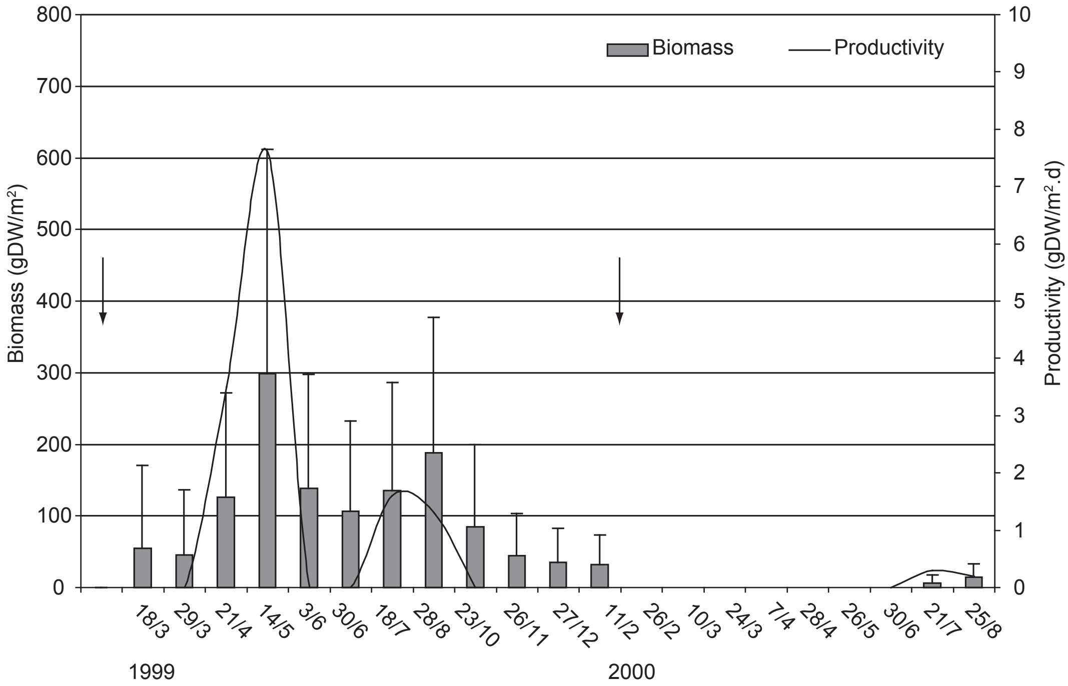

Fig. 3 — Mean biomass (gDW/m^2), standard deviation, and productivity (gDW m^{-2}.day^{-1}) of the aquatic macrophyte *Najas marina* in the permanent puddle of the Avelós stream (7° 28' 08" S and 36° 31'17" W) in 21 field visits carried out during the hydrologic cycles of 1999 and 2000. The arrows indicate the occurrence of floods.

with a loss of 89.2%. In the 2000 cycle, *Najas marina* showed a low resistance to the flood and drought and its biomass decreased by 100% ($P < 0.010$) and its mean productivity was 0.25 gDW m^{-2}.day^{-1} (± 0.1). This species showed a low resilience potential. The recolonization followed the pattern of occupation from the margins to the centre of the puddle.

Temporary puddle on the margin of the Taperoá river

The Taperoá river had two short floods (22 days) in the 1999 cycle (14 Mar and 12 May) and one long flood (47 days) in the 2000 cycle (20 Feb). The drying phase occurred after the interruption of the continuous run-off water, forming temporary puddles on the margins and in the river bed. The river presented a mean water level of 51.3 cm (± 7.3) and a mean deposited sediment of 11.8 cm (± 10.4).

The temporary puddle on the margin was formed over the three rewetting phases of the river (29 Mar – 21 Apr and 3 Jun – 28 Aug, 1999; 7 Apr – 26 May, 2000). The puddle on the margin had a mean area of 77.0 m^2 (± 59.0), a mean water level of 33.9 cm (± 10.9) and a mean deposited sediment of 7.3 cm (± 9.6). The community of aquatic macrophytes consisted of the dominant species *Najas* sp, with a fluvial development on the margins of the puddle, and *Echinodorus macrophyllus* was represented by only one specimen in the parafluvial area of the puddle. The mean biomass of *Najas* sp was 64.7 gDW/m^2 (± 53.6) and the mean productivity was 2.2 gDW m^{-2}.day^{-1}, with strong variations during the study period (Fig. 4). The colonization began between days 38 and 68 after the rewettings. The resilience was significant in the beginning of the three drying periods (21 Apr and 30 Jun, 1999; 28 Apr, 2000), with a mean productivity of 3.3 gDW m^{-2}.day^{-1} (± 0.7). During the drying phases the biomass of the macrophytes increased up to 65% and the mean productivity was 1.2 gDW m^{-2}.day^{-1} (± 0.3). *Najas* sp presented a low resistance to drought, which caused the total loss of biomass. *Echinodorus macrophyllus* maintained the rhizomes in the soil but its aerial part was totally lost during the dry period.

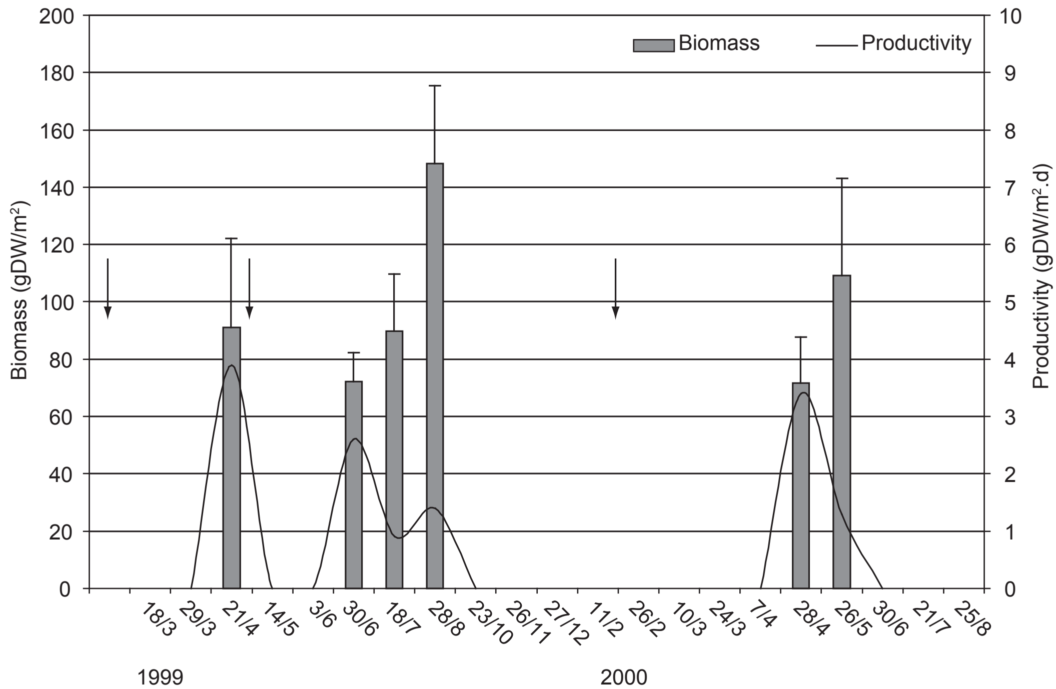

Fig. 4 — Mean biomass (gDW/m^2), standard deviation, and productivity (gDW m^{-2}.day^{-1}) of the aquatic macrophyte *Najas* sp in the marginal temporary puddle of the Taperoá river (between 7° 00' S and 7° 30' S and 37° 00' W and 36° 10' W) in 21 field visits performed during the hydrologic cycles of 1999 and 2000. The arrows indicate the occurrence of floods.

Temporary puddle in the bed of the Taperoá river

The temporary puddle was formed only after the second rewetting of the river, in the 1999 cycle (3 Jun – 28 Aug). The puddle in the bed had a mean area of 465 m^2 (± 680), a mean water level of 20.5 cm (± 8.2), and a mean deposited sediment of 3.0 cm (± 2.6). The bed was consisted of sand and small stones. The puddle was colonized only by the aquatic macrohyte *Najas* sp, 67 days after rewetting. Colonization occurred on the margins of the puddle. The mean biomass of the species was 35.1 gDW/m^2 (± 51), which had a significant increase ($P < 0.001$) of 232% in 41 days and its mean productivity was 1.8 gDW m^{-2}.day^{-1} (Fig. 5). *Najas* sp had a total loss of biomass throughout the drought phase.

Area of water retention

A flooded area was formed in the hydrologic cycle of 2000 mainly due to the run-off water from the rain. The area remained flooded for 131 days. It had a mean area of 2,680 m^2 (± 1,016) and a mean water level of 10.8 cm (± 7.6). Eight species of aquatic macrophytes were recorded in the environment, 96 days after rewetting: *Echinodorus macrophyllus*, *Eleocharis interstincta*, *Eleocharis* sp, *Elodea* sp, *Heranthera limosa*, *Hydrocleys nymphoides*, *Najas* sp, and *Nymphaea lingulata*.

DISCUSSION

Hydrologic disturbance and species richness

The occurrence of rains, mainly from March to August, in the 1999 and 2000 cycles (Fig. 2), causing floods of different characteristics, confirm the predictability of flood and drought events for rivers and streams of the studied region (Maltchik & Pedro, 2001). The frequency of floods showed to be related to the size of the drainage basins. The temporary river, with a larger drainage basin had a larger number of floods (n = 3) than the ephemeral stream (n = 2) with a smaller drainage basin. The amount of floods altered the amplitude of the hydrologic phases. The ephemeral stream had a longer drought phase, with longer intervals between floods (335 days) than in the temporary river (276 days) (Figs. 3 and 4). Despite the

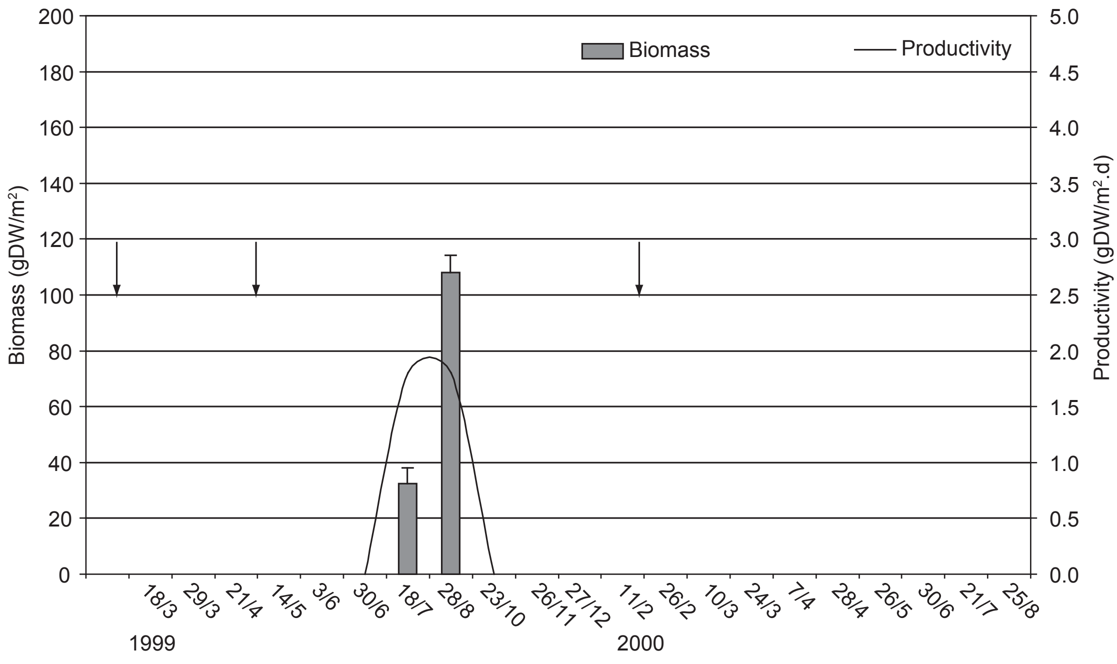

Fig. 5 — Mean Biomass (gDW/m^2), standard deviation, and productivity (gDW m^{-2}.day^{-1}) of the aquatic macrophyte *Najas* sp in the temporary puddle in the bed of the Taperoá river (between 7° 00' S and 7° 30' S and 37° 00' W and 36° 10' W) in 21 field visits carried out in the hydrologic cycles of 1999 and 2000. The arrows indicate the occurrence of floods.

adaptations, the aquatic plants of temporary rivers have to survive in dry environments; the length of the drought phase is an important factor for the survival of different groups of species and for determining the structure and functioning of communities in temporary aquatic environments (Stanley & Fisher, 1992).

The results showed low species richness in the aquatic macrophyte communities in the temporary river (n = 2) (Taperoá river) and in the ephemeral stream (n = 2) (Avelós stream) when compared with the species richness of the retention area (n = 8). These results suggest that the flood is an important disturbance agent and a highly selective agent for most of the studied aquatic macrophytes. The communities of plants in rivers are composed of few species with evolutionary adaptations to flood and dry events (Dawson *et al*., 1978), which act as agents of natural selection in the life history of the species (Henry *et al*., 1996). However, temporary ponds formed only by run-off water in the semi-arid area showed a high species richness (n = 7) (Maltchik & Pedro, 2000), a result similar to the species richness in the retention area of the present study (n = 8).

Resistance

The present results showed that in the permanent puddle of the Avelós stream, *Najas marina* was resistant in the 1999 cycle, maintaining a biomass of 55 gDW/m^2 and a decreased resistance in the 2000 cycle, with a total loss of biomass (Fig. 3). The different resistance responses estimated from the remaining biomass after the floods, showed that the population of *Najas marina* suffered larger disturbance (in intensity) in the flood of the 2000 cycle than in the flood of the 1999 cycle. Sousa (1980) observed that the extension of changes caused by a disturbance in a community can be related to the intensity of the disturbance. *Najas marina*, a species with low competitive ability, is a submersed and attached macrophyte that is easily removed from the substratum (Muenscher, 1967). Floods have been reported as agents of changes and removal of aquatic macrophytes (Bilby, 1977) and as a direct source of spacing heterogeneity in the vegetation. The opening of new areas in the plant communities allows for the expansion of vegetative growth forms and the opportunity of recruiting species with sexual reproduction (Henry *et al*., 1996). The distribution of aquatic macrophytes in rivers and streams has been described as segmented in mono-specific patches, resulting from vegetative growth of the species (Husband & Barrett, 1998). *Eleocharis insterstincta* presented a low resistance capacity and a low recolonization potential, after the 2000 cycle, with a total loss of biomass and lower recruitment in the post-disturbance period.

In the temporary puddles of the Taperoá river, *Najas* sp presented a total loss of biomass in the drought phase (Figs. 4 and 5). Bianchini-Júnior & Toledo (1996) state that the contribution of aquatic plant debris in different magnitudes and forms can generate significant alterations in the physical, chemical and biological characteristics of the water and sediment. *Echinodorus macrophyllus* was resistant in the marginal puddle, maintaining the rhizomes and losing the aerial part during the drought phase of the 1999 hydrologic cycle. This species is described as amphibious and tolerant to stress (Kautsky, 1988).

Resilience

The results (Figs. 3, 4, and 5) showed that variations of productivity and biomass of the aquatic macrophytes at the beginning of recolonization in the permanent puddle of the Avelós stream and in the temporary puddles of the Taperoá river are directly related to the occurrence and resistance of the species to floods of different intensity which occurred during the present study. The long time recorded for recolonization in the permanent puddle, as well as in the temporary puddles, suggests that the flood of the 2000 hydrologic cycle was more intense during the whole study period. In the low intensity of the 1999 hydrologic cycle, the beginning of the recolonization of *Najas marina* was noted 38 days after the flood, as well as the maximum productivity (7.6 gDW $m^{-2}.day^{-1}$) and the maximum biomass (299 gDW/m^2) when compared to the preceding hydrologic cycle. The intensity of the flood altered the beginning of recolonization, productivity, and biomass of the species.

The low recruitment and slow growth after the flood of larger intensity was observed, which indicates the areas of refuges suitable for the growth of *Najas marina*, at the time the run-off water was maintained and the disturbance was of low level intensity. Bilby (1977) reported that puddles and ponds along the rivers act as refuge areas and are important in the processes of recolonization of aquatic macrophytes. The least disturbed margins can also act as refuges and as regeneration niches for a lot of species (Henry *et al*., 1996). Our results show that *Najas marina* persisted during the flood disturbances in the two hydrological cycles, presenting resistance and a high resilience potential (> 37%) (Pimm, 1991) after intermediate disturbances, and slow recolonization with low resilience potential after disturbances of larger intensity (Fig. 3).

Najas sp showed three recolonization periods in the marginal puddle during the drying phases of the Taperoá river, two in the 1999 hydrologic cycle and one in the 2000 cycle (Fig. 4). Johnson (1994) reported the growth of some species of aquatic macrophytes in intermittent rivers beginning at the end of the rain period, when the flow of run-off water is interrupted and the formation of puddles occurs along the rivers (drying phase). Recolonization began earlier in the 1999 hydrologic cycle (floods of smaller intensity), despite the largest frequency of floods. *Najas* sp was noted 38 days after the first flood, 49 days after the second and 68 days after the third flood (larger intensity). In the puddle located in the bed of the Taperoá river the recolonization of *Najas* sp was noted 67 days after the second flood, with 18 days of delay in relation to the puddle on the margin (Figs. 4 and 5).

The difference in the mean productivity of *Najas* sp in the marginal puddle (2.2 gDW $m^{-2}.day^{-1}$) and in the puddle in the river bed (1.8 gDW $m^{-2}.day^{-1}$) indicates that the latter has a lower resilience potential for that species. The largest values of productivity recorded at the beginning of the recolonization phase and of biomass at the end of this phase in the margin and bed puddles (Figs. 4 and 5), suggest a strategy of rapid growth and biomass accumulation. Menezes *et al*. (1993) state that the increase in productivity can lead to a biomass increase of aquatic macrophytes. Despite many aquatic and riparian species being adapted to current speed, the productivity of aquatic macrophytes in streams can be up to three times lower than the productivity in ponds (Pastore *et al*., 1995). The values of maximum biomass and maximum productivity of *Najas* sp in the marginal puddle were similar in the two hydrologic cycles, showing that the flood intensity did not alter the productivity and biomass of the river species, except at the beginning of the recolonization.

The occurrence of *Najas* sp in the three rewettings of the temporary puddle on the margin, and in the puddle of the bed of the Taperoá river, shows the persistence and the high resilience potential (> 37%) (Pimm, 1991) of the species in the temporary river with a higher frequency of floods. The results of occurrence of *Najas* sp after puddles being formed in the drying phase suggest the species is a pioneer plant (Connell & Slatyer, 1977), an *r-strategist*. Penha *et al*. (1998) state that in environments subject to floods, populations guarantee their persistence through *r-strategy*. A lot of macrophyte species in rivers possess reproductive strategies strongly adapted to the disturbance regime (White, 1979; Trémolières *et al*., 1994; Barrat-Segretain & Amoros, 1995), being highly dependent on such events.

The species *Najas marina* and *Najas* sp recorded in the Avelós stream and in the Taperoá river varied with respect to their productivity and the maximum biomass they could achieve. The occurrence and persistence of macrophytes species in intermittent rivers of the semi-arid in Northeast Brazil, are a consequence of their resistance and resilience responses to different intensities and frequencies of the hydrological disturbances of floods and droughts.

CONCLUSION

The present study showed the hydrologic variability of two intermittent rivers and the resistance and recolonization responses of aquatic macrophytes to the events of disturbance of flood and drought. The different rainfall regimes in the drainage basins determined the length of the hydrologic phases, and the ephemeral stream presented a longer drought phase than the temporary river. The flood limited the occurrence of aquatic macrophytes in the river and in the stream, whose communities of aquatic macrophytes showed a lower species richness than the communities of the retention area with no floods.

The largest frequency of floods in a hydrologic cycle did not retard the beginning of recolonization by aquatic macrophytes. The effect of the flood intensity on the community of aquatic macrophytes could be evaluated from the resistance of the plants and the time of recolonization after the disturbance. Flood intensity affected the beginning of recolonization, the productivity and the maximum biomass of aquatic macrophytes in the river and in the stream. The largest values of productivity and biomass, and the shortest time for the beginning of recolonization occurred at intermediate levels of disturbance, whereas in the event of larger magnitude, such values were smaller, with a longer time of recolonization.

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