A COMPARISON OF DISPERSAL, GERMINATION AND ESTABLISHMENT OF WOODY PLANTS SUBJECTED TO DISTINCT FLOODING REGIMES IN BRAZILIAN FLOOD-PRONE FORESTS AND ESTUARINE VEGETATION*

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Resumo:
"Estudo comparativo da dispersão, germinação e estabelecimento de plantas lenhosas sujeitas a diferentes regimes de inundação em algumas florestas inundáveis e vegetações estuarinas brasileiras"
        Embora intrinsecamente tolerante à falta de oxigênio decorrente da inundação, uma dada espécie vegetal pode sofrer reveses durante os processos de dispersão, germinação e estabelecimento, e/ou ser mais sensível à inundação enquanto semente e/ou plântula, impedindo sua fixação em áreas inundáveis. Aspectos ecológicos e ecofisiológicos de modo reprodutivo, dispersão e germinação de sementes e estabelecimento de plântulas foram comparados para espécies lenhosas brasileiras sujeitas a distintos regimes de inundação (fluvial sazonal na Amazônia; de maré em estuários; e freática permanente em pântanos fluminenses). As diferenças encontradas pareceram constituir respostas às diferenças em sazonalidade e previsibilidade entre os habitats. Propagação vegetativa destacou-se nos pântanos onde inundação não é sazonal e o ambiente é de baixa previsibilidade. O sucesso da propagação por sementes nos habitats com freqüência foi associado à dispersão aquática eficiente de frutos e/ou sementes, à combinação de dormência pré- e pós-dispersão e a plântulas criptocotiledonares. Dispersão em duas fases foi comum e vantajosa. Na fase aquática, encontrou-se frutos e sementes flutuantes assim como aqueles que afundam. Flutuação se associou com heterogeneidade na duração da dormência de sementes de uma mesma coorte, e afundamento com dormência prolongada. Plântulas criptocotiledonares de crescimento rápido predominaram, porém fanerocotiledonares de crescimento lento também ocorrem.

Abstract:
        Flood-tolerance does not guarantee successful colonization of flood-prone habitats, since a given species might undergo a number of hazards during the processes of seed dispersal, germination and seedling establishment; or else, be flood-sensitive as seed and/or seedling. I compare the ecological and ecophysiological aspects of reproductive mode, seed dispersal, germination and seedling establishment in some woody Brazilian species from distinct habitats subjected to distinct flood-regimes (seasonal river flooding in the Amazon; tidal flooding in estuaries; and permanent phreatic flooding in the swamps of southeastern Brazil). Differences in regeneration strategies seem to be responses to variations in habitat seasonality and predictability. Vegetative propagation was common to many species in swamps where safe unflooded patches are unpredictable in space and time. Seed propagation success in the various habitats was often related to an efficient fruit/seed water dispersal, to a combination of pre- and post-dispersal dormancy and to cryptocotylar seedlings. Two-phase dispersal (another agent besides water itself) was often found. In the aquatic phase, both buoyant and submerged fruit/seeds were found. Buoyancy was related to heterogeneity in the duration of dormancy among seeds of a same cohort, and submergence to prolonged dormancy. Fast-growing cryptocotylar seedlings were common among the species studied.

Introduction

The past thirty years have seen a number of studies on the biochemical and ecophysiological basis of flooding and anoxia tolerance (see Lobo & Joly, 1998; and Pimenta *et al.*, 1998 in this volume) and on seed dispersal, germination and seedling establishment in tropical ecosystems (see Ng, 1978; Bazzaz, 1991; Fleming & Estrada, 1993; Vázquez-Yanes & Orozco-Segovia, 1993; and Chambers & McMahon, 1994 for reviews). Curiously however, the ecological information available on dispersal (eg. Cook 1987), germination of seeds and establishment in riverine, estuarine and floodplain habitats is still limited. Processes of seed bank renewal in temperate wetlands are better understood than colonization and establishment. Tropical and subtropical wetlands clearly lack information on seed banks, germination and seedling establishment (Garwood, 1989; Leck, 1989). More basic information on seed and seedling biology of tropical plants is particularly necessary for tropical wetlands and could be highly relevant to the management of tropical vegetation (Bawa *et al.*, 1990; Terborgh, 1990).

Soil flooding brings up a number of hazards not overcome by most terrestrial vascular plants. Root oxygen deprivation is probably the most obvious adverse effect of flooding. Hendry & Crawford (1994) argue that what determines the form of anoxia survival is a complex adjustment of anatomy and biochemistry which is achieved on a limited scale by plants. Nevertheless, a plant can be intrinsically tolerant to flooding and still be unable to establish in a given wetland due to dispersal, germination or young-age hazards (Scarano & Crawford, 1992). Many species rated as flood-tolerant may be quite sensitive in the seed (Scarano *et al.*, 1997) or seedling stage (Kozlowski *et al.*, 1991). Thus, from an ecological viewpoint, plant colonization of tropical wetlands is a matter that still demands a lot of research effort.

Kubitzki & Ziburski (1994) have recently given a key contribution to the understanding of tree regeneration ecology and evolution of hydrochorous dispersal systems by comparing phenology, dispersal and regeneration of hydrochorous tree species in Amazonian seasonally flooded forest with their congeners in flood-free sites (*terra-firme*). Here, I discuss some ecological aspects of seed dispersal, germination, asexual propagation and seedling establishment by comparing some tree species of different Brazilian flood-prone habitats subjected to distinct flooding regimes. Plant regeneration strategies are analysed in regard to flooding seasonality and predictability. Diversity of flood-prone forests in Brazil (World Conservation Monitoring Centre, 1992; Junk, 1993) allows for a comparison between the strategies of species subjected to seasonal, permanent or tidal flooding.

Seasonal floodplain forests of the Amazon

These include the seasonal *várzea* (flooded by "white-water", nutrient-rich rivers) and seasonal *igapó* ("black" and "clear-water", nutrient-poor, low pH rivers) forests (*sensu* Prance, 1979) which, despite the differences in water quality, invariably

subject marginal vegetation to 6-8 months flooding which may reach over 10 m deep, submerging entire trees (Furch & Otto, 1987).

Successful regeneration processes in these plants face at least two problems: 1) **fruits and seeds** matured during the flood season are likely to be shed on water (Kubitzki & Ziburski, 1994) which means a high degree of risk due to the unpredictability of timing **and** landing site; 2) seedling establishment during the dry season has to be such that allows the individual to withstand, a few months later, full submergence for 6 months or more.

Fruit and seed dispersal

Fruits and seeds shed on flood-water will either float, sink or be eaten by fish.

Carapa guianensis Aubl. (Meliaceae) is a tree species common to seasonal *várzeas*, estuarine *várzeas* and flood-free sites (*terra-firme*) in the Amazon (Pennington *et al.*, 1981; Scarano *et al.*, 1994). The large seeds of this species float. Scarano & Pereira (1994) showed experimentally that within the same seed lot, some remained dormant for at least 2.5 months of buoyancy and others germinated while buoyant. Seed viability during flotation depended on the length of the buoyancy period, and death was possibly due to lack of essential nutrients or exhaustion of stored reserves provided by the endosperm (see Manasse, 1990). The plants which germinated while floating grew roots and shoots, although at a slower rate than plants germinated on flood-free soil. In nature, these structures are bound to suffer mechanical injury during the dispersal process. Throughout these experiments, whenever damage took place, the propagules regenerated new shoots and roots. The ability to keep roots and shoots alive until water level drops may favour plant anchoring and rapid establishment.

Hopkins & Hopkins (1983) argue that *Parkia discolor*´s indehiscent pods drop into the Rio Negro (seasonal *igapó*) at maturity and float away. When the water level drops, many of the previous season´s pods are found on the high water mark of the flood, often disintegrating but with some seeds still inside. The seeds released from the pods prior to anchoring will sink but remain viable for up to 6 months due to their impermeable seed coat (Coutinho & Struffaldi, 1971).

Some authors have speculated upon fish dispersal of Amazonian tree species (Gottsberger, 1978; Goulding, 1980), and also of riverine tree species of southern Brazil (Souza-Stevaux *et al.*, 1994). This has often been based on finding viable seeds in the fish's stomach and/or intestine as in the case of *Cecropia* sp dispersal by *Auchenipterichthys longimanus* in the Trombetas (clear-water) river in the Central Amazon region (Bevilacqua *et al.*, 1995). Little is known however about the efficiency of this process from a seed viewpoint. However, Kubitzki & Ziburski (1994) already pointed out 3 obligate fish dispersed plant species and 5 other likely candidates, which is clear evidence of the evolution of this dispersal syndrome in the Amazon. Furthermore, they also provide the most up-to-

date review of ichthyochory in the Amazonian floodplains. If seed dispersal by fish is at all efficient, the seed will either float or sink after being eliminated in the fish's feces, and then go through a phase of water dispersal before anchoring at a safe germination site.

Germination and seedling establishment

Germination and establishment are, thus, the next hurdles to be faced by these water and/or fish dispersed propagules. The large-seeded *C.guianensis* and the small-seeded *P.discolor*, which show distinct dispersal strategies as seen above, also resort to different germination and establishment strategies. *C.guianensis* seeds produce cryptocotylar seedlings (seedlings which remain attached for longer periods to a hypogeal, reserve-rich cotyledon; *sensu* Duke, 1969) which may form shoots c. 60 cm long 10 days after shoot emergence (Scarano & Pereira, 1994). Mc Hargue & Hartshorn (1983) reckon that large seed reserves may be important in getting the seedlings' leaves above the normal water level. Although this is probably true for seedlings growing in tidal *várzea* forests, this is clearly not the case for those growing on seasonal *várzeas*, where water level may rise up to 10 m or more above normal. This fact suggests the existence of an additional tolerance mechanism for seedlings of this species.

Parkia discolor, on the other hand, has slow-growing phanerocotylar seedlings (epigeal, leafy cotyledons; *sensu* Duke, 1969) which must rely on their own photosynthesis and soil nutrient uptake in the shaded and nutrient-poor soil of the *igapó* forest floor (Hopkins, 1986). However, saplings of this species withstand long-term submersion (Coutinho & Struffaldi, 1971) unlike their *terra-firme* counterpart *Parkia pendula*. Despite the tolerance to long-term submersion and anoxia of the hard-coated seeds, the latter has seedlings which are intolerant to a couple of weeks of root flooding, which accounts for the almost complete absence of *Parkia pendula* from flood-prone sites (Scarano & Crawford, 1992).

Estuarine vegetation

Dalbergia ecastaphyllum (L.) Taubert is a widely distributed perennial shrub commonly found on the central-western coast of Africa and on the eastern coast of the American continents, from southern Florida to the extreme south of Brazil (Hoehne, 1941; Carvalho, 1989). This species has a habitat-preference for flood-prone areas on the banks of water courses whereby its seeds are dispersed (Lima, 1989). The unpublished experiments described below were conducted with seeds collected at the Reserva Biológica Estadual da Praia do Sul, on Ilha Grande, a coastal island in Ilha Grande bay, on the southern coast of Rio de Janeiro state. A random collection of 162 seeds was made on a sand bank in the estuary of a natural canal connecting two inland saline lagoons to the sea, under the limbs of the parent plants, which suggests that they had recently been shed. Fifty-seven seeds were randomly collected on nearby sandy beaches (Praia do Sul and Praia do Leste). The latter group of seeds was obviously carried by the canal into the sea and then thrown onto

the beach by waves. This species is hardly ever present in the beach vegetation of Ilha Grande, so it could not possibly reach the beach by wind dispersal of its winged seeds.

Germination percentage (at 30°C, 8-hours light per day, 100 $\mu mol.m^{-2}.s^{-1}$ light intensity, assessed periodically over an 80-day period after which no more seeds were viable) was higher for seeds collected under the parent plants (84.6%) than for those which underwent an unknown period of sea dispersal and landed on the beach (43.9%). The timing for the beginning of the germination process varied a great deal among the individual seeds tested. For the seeds collected below the parent plants, germination (assessed by the evidence of radicle protrusion) was observed from 3 to 79 days after incubation. For those collected on the beach after sea dispersal, individual seed germination ranged from 3 to 55 days after incubation. Table 1 shows that despite the differences in viability, there is a considerable similarity in terms of pattern of timing of germination between the two groups of seeds. The percentage of seeds germinated in the period from 0 to 10 days after incubation was higher both for seeds collected under the parent plant and for seeds subjected to a period of sea dispersal. In the subsequent day-intervals, in both cases, germination percentage gradually declined.

Table 1. Timing of germination of *Dalbergia ecastaphyllum* (L.) Taub. seeds under controlled conditions (30°C; 8-hours light per day; 100 $\mu mol.m^{-2}.s^{-1}$) as seen by the percentage (number) of viable seeds germinated per day-interval. Seeds collected in two different situations: under the parent plants in a sandy mangrove and on the beach after an unknown period of sea dispersal.

day-interval for germination	percentage (number) of viable seeds germinated	
	sandy mangrove (below parent plants)	beach (after sea dispersal)
0-10	43.8% (60)	52.0% (13)
10-20	37.3% (51)	24.0% (06)
20-30	10.9% (15)	16.0% (04)
30-60	5.8% (08)	8.0% (02)
60-90	2.0% (03)	0.0% (00)
germinated seeds	84.6% (137)	43.9% (25)
non-germinated	15.4% (25)	56.1% (32)

Seed dispersal and seed dormancy

These results could be attributed, at first glance, to variation in seed dormancy within a single fruit. Koller (1972), for instance, refers to the desert legume *Medicago turbulenta* as having seeds with varying degrees of dormancy inside their legumes before shedding. Carvalho & Nagakawa (1988) explain that in some species the seed as a whole may reach maturity and be detached from the fruit, without the embryo being fully developed however. After shedding, these seeds, at adequate temperature and humidity conditions, can possibly proceed with the development of their embryos, which are fed

through the endosperm to the point where they are finally able to germinate. However, this alone does not explain the similar pattern of timing of germination under controlled conditions for seeds collected immediately after shedding and those collected after an unknown period of sea dispersal, since the germination percentage of sea-dispersed seeds per day-interval coincides with that of the seeds collected prior to sea dispersal. Our hypothesis is that a great number of seeds are shed at different embryo maturity stages. When these seeds fall into the water course, there is the onset of quiescence, irrespective of maturity stage. As they reach land again, the maturation process is resumed for those seeds which did not reach this stage before shedding, and germination finally takes place. However, loss of viability is a risk for seeds that take a long time to land or land on unfavourable sites such as the beach.

Seedling establishment

Lee (1988) argues that while a broad seed rain (see Harper, 1994) allows escape from predators or colonization of microsites that are more favourable for establishment, fitness may be enhanced by differential fruit maturation. It may be true, as it appears from the present results, that differential seed dormancy levels or embryo maturation at the moment of shedding also enhances fitness. Successful establishment of this species is also possibly favoured by its seedling type. Lima (1989), for instance, suggests the existence of a possible adaptive relationship between the species' crypto-hypogeal seedling type and its fixation on flood-prone habitats.

Koller (1972) suggests that the creation of dense, uninterrupted canopy by individuals of a same species growing side by side, which is typically the case of *Dalbergia ecastaphyllum*, filters out photosynthetically active radiation excluding newcomers, characterising a competition-avoidance mechanism.

Swamp forests of southeastern Brazil

The Atlantic rainforest's freshwater swamps, in southeastern Brazil, are flooded by a superficial water table which rises up to 30 cm above soil level depending on local rainfall. In Poço das Antas Biological Reserve (Silva Jardim county, Rio de Janeiro state), one finds a gradient from a periodically flooded site to a permanently flooded site. However, both consist of mosaics of flooded and unflooded patches. The former, dominated by tree species of Clusiaceae, has a slightly irregular soil which provokes marked differences of flooding duration between neighbouring patches (from 0 to 300 days a year). In the latter, which is mono-dominated by *Tabebuia cassinoides* DC., safe germination sites are not found on the soil which is fully covered by a water layer up to 30 cm deep, but in the leaf-tanks of terrestrial bromeliads of the understory. The latter have wide open rosettes which trap litter and provide a "suspended soil" whereupon seeds germinate and establish.

Seed germination and vegetative propagation

Scarano *et al.* (1997) showed that *Symphonia globulifera* L., *Tovomitopsis paniculata* and *Tabebuia cassinoides* reproduce sexually and vegetatively. *Calophyllum brasiliense* Camb. reproduces only by seeds. The fruits of all these species float, except for those of *T.paniculata* which sink and rapidly rot. As a result *T.paniculata* is significantly more frequent on unflooded than on flooded patches. However, on the flooded patches, a significantly higher number of *T.paniculata* regenerants (<1.0 m tall) originate from vegetative organs than from seeds, which indicates that for this species vegetative reproduction may favour colonization of lower sites where flooding lasts longer and seedling establishment is less successful. On the other hand, *C.brasiliense* reproduces only by seeds but occurs indistinctly on both types of patches which shows that, in some cases, reproduction by seed alone may be successful irrespective of site.

In the stagnated water of the swamps, seed buoyancy does not play a role in dispersal but, instead, it allows the formation of "floating seed banks" as Marques (1994) described for *C.brasiliense*. Although floating germination is insignificant and ten weeks floating reduces seed viability for this species, the seeds show two types of dormancy: one imposed by the endocarp (pre-dispersal dormancy) and another which manifests itself, even in the absence of endocarp (post-dispersal dormancy), by provoking different timing of germination among seeds collected within the same population which may favour germination of some when the water table recedes, a common strategy for many swamp tree species (Kozlowski *et al.*, 1991). Endocarp-dormancy is possibly affected during bat-dispersal, often the first phase of dispersal for this species, which imposes different patterns of endocarp removal on the seeds (see Garwood, 1989) and may contribute to seed polymorphism in the second dispersal phase. Thus, for a given seed group dispersed by bats, the greater the variation in dormancy among them the greater the chance that some will become successfully established in a given soil patch.

Seedling establishment

Seedling tolerance of flooding is apparently common in the dominant species of this site. *C.brasiliense* seedlings, for instance, showed no significant difference in shoot extension and leaf emission of flooded and control seedlings after 12 weeks (Scarano *et al.*, 1997). Seed germination seems to be more of a problem since it depends on safe sites. In the permanently flooded edge of the gradient in this swamp forest safe sites are provided by tank bromeliads. It appears that for seedlings grown in lateral tanks, gradual death of external leaves of the bromeliad rosettes may favour fixation on the swampy ground thus constituting a key-factor for the success of seed propagation in this habitat. This is particularly true of the dominant genus at this site, *Tabebuia*, found in large numbers in the bromeliad rosettes.

Discussion

The woody plants described occur in flood-prone habitats which differ in many characteristics. Each of these species shows a different combination of dispersal, germination and establishment strategies which possibly respond to substrate heterogeneity in time (seasonality) and in space (predictability). In a seasonal floodplain forest, in most cases a given plant will produce seeds which will be shed on a predictable substrate: water (if dispersed during the flooding season) or on soil (if during the dry season). In a tidal forest, the substrate where upon seeds are shed is less predictable in time, varying according to tidal movement, but still, at a given moment, a seed will be shed upon water or soil. On the other hand, a swamp, as the one studied here, is the most unpredictable of all three from a spatial viewpoint. Since this site is a mosaic of flooded and unflooded patches, a seed, at a given moment in time, will be shed upon one or the other. In these areas there is also some degree of seasonality, although not as marked as in the seasonal or tidal flood-prone forests, which may turn an unflooded patch into a flooded one and vice-versa (except when the unflooded patch is a bromeliad tank).

.   *Reproductive mode*

Despite the commoness of vegetative reproduction among wetland plants (Abrahamson, 1980; Crawford,1992), vegetative propagation is quite irrelevant for woody species in Brazilian seasonal and tidal flood-prone forests (Table 2). Phenological adjustment of seed dispersal to a favourable season (Crawford, 1989) plus seed dormancy will be particularly successful strategies in seasonally predictable habitats (Colwell, 1974). Other seasonally flooded vegetation types, such as the Mediterranean temporary marshes (Grillas *et al.*, 1993), also show a higher investment in sexual rather than asexual reproduction. Spatial heterogeneity of the substrate seems to be related to reproductive mode, since in the swamp forests of Rio de Janeiro state, *Tovomitopsis paniculata* clearly resorts to vegetative propagation to colonize the flooded patches of the heterogeneous substrate (Table 2), which may also be true of *Symphonia globulifera* and *Tabebuia cassinoides* (Scarano *et al.*, 1997).

Calophyllum brasiliense exemplifies how seed propagation alone (irrespective of whether or not the seeds are apomytic) can also be efficient in colonizing patchy stressful environments such as these swamps. Although habitat patchiness and unpredictability are likely to bring about difficulties in the optimization of phenological timing (Colwell, 1974; Junk, 1989; Rees, 1994), seed reproduction stands a better chance of taking place at these sites than in a homogeneously inhospitable habitat (see Cook, 1980). The array of strategies shown by this species from dispersal to establishment (Table 2) is surely linked to its wide distribution in both seasonal and permanent flood-prone areas in South and Central America (Prance, 1979; Lacerda *et al.*, 1993; Oliveira-Filho & Ratter, 1995).

Table 2. Parameters of seed dispersal, seedling type, geographic distribution and preferencial habitat for Brazilian tree species from flood-prone habitats differing in spatial heterogeneity (patchiness) and seasonality of flooding phenomena. F = fruit; S = seed.

habitat	seasonality	patchiness	species	dispersal	seedling type	geographic distribution and preferred habitat
Várzea	High	High	Carapa guianensis	Buoyant/Rodent (S)	Cryptocotylar	Wide, neotropical, flooded and unflooded
Tidal Várzea	Intermediate	Intermediate				
Igapó	High	High	Parkia discolor	Buoyant(F)/Submerged (S)	Phanerocotylar	Restricted to this vegetation
			Cecropia sp	Wind/Fish(S)/?	Phanerocotylar	?
Estuary	Intermediate	Intermediate	Dalbergia ecastaphyllum	Buoyant(F)/wind	Cryptocotylar	Pantropical, mostly flooded in estuaries
Swamps	Low	High	Calophyllum brasiliense	Buoyant(F)/Bat	Cryptocotylar	Wide, throughout the Americas, mostly flooded
			Tovomitopsis paniculata	Bird (?)*	Cryptocotylar	Restricted to the Atlantic forest, flooded or not

* T. paniculata is the only one of the six species above to show vegetative propagation as well.

Seed dispersal, dormancy and germination

Buoyancy or sinking cannot be directly related to one forest type or another from the present data. However, it is true that buoyancy has a higher degree of unpredictability than sinking. Seeds that sink, as in the case of *Parkia discolor*, and do not loose viability after long-term submersion, often have dormancy imposed by a hard seed-coat. The main risk here is for the seed to sink and anchor at a site where the flood water does not recede, such as the bottom of a river.

The species studied here which are capable of buoyancy (*Carapa guianensis, D. ecastaphyllum* and *Calophyllum brasiliense*) invariably show distinct timing of germination for seeds belonging to the same seed lot. Irrespective of whether this is due to different stages of embryo maturation at the time of shedding or different degrees of dormancy or quiescence, this characteristic is clearly an adaptation to the unpredictability of anchoring. Willson (1993) compared seeds with wind-dispersal mechanisms, with ballistic mechanisms and with no special mechanisms and found no clear trade-off between dispersal in space (long-distance) and dispersal in time (dormancy). Indeed, even in seasonal habitats (Colwell, 1974) seed dormancy may have evolved in response to environmental spatial variability and uncertainty (Evans & Cabin, 1995) which is often faced by water-dispersed seeds. In the case of a highly temporally heterogeneous habitat such as an estuary, abundant seed production as in *D. ecastaphyllum* is also an efficient strategy.

Curiously, all species listed in Table 2 also had another seed dispersor in addition to tide or flood water, and all, except the anemocorous *D. ecastaphyllum*, had a vertebrate as an associate. Although fish dispersal, as in *Cecropia* sp, still needs more studies to determine its ecological role, bat dispersal of *Calophyllum brasiliense* and rodent dispersal of *Carapa guianensis* are clearly advantageous. Dispersal vectors should differ in their relative contributions to risk reduction, escape from crowding, escape from sib interactions and directed dispersal (Venable & Brown, 1993).The recent development of techniques to study seed dispersal quality (*e.g.*, Bustamante & Canals, 1995) may now allow for more accurate assessments of efficiency (the probability that a seed dispersed by a given agent will land at a safe site and germinate) and effectiveness (the proportion of seedlings in a plant population that a particular seed vector is responsible for disseminating) as defined by Reid (1989). Measurements of these parameters for multi-phased and single-phased dispersed seeds of a given plant population in flood-prone habitats will be of great ecological interest.

Seedling establishment

Heterogeneity of germination timing among water-dispersed seeds is clearly a successful establishment strategy in all flood-prone habitats studied. Another key factor is seedling tolerance to flooding as shown by *P.discolor* and *C.brasiliense*. Seed-seedling

conflict (see Schupp, 1995) has been shown by Scarano & Crawford (1992) to be a possible reason for the noncolonization of flood-prone sites by the widespread *P. pendula* in the Amazon forest. The seeds of this species are tolerant of long-term submersion whereas its seedlings are highly intolerant of flooding. *T.paniculata* also shows seed-seedling conflict but in the opposite direction from *P.pendula*: it has flood-tolerant seedlings which germinate from flood-intolerant seeds, thus needing safe sites to accomplish seed germination or else resorting to vegetative reproduction. This is clearly not the case for *Calophyllum brasiliense*, *Carapa guianensis*, *P.discolor* and *D.ecastaphyllum* which combine seed and seedling flood-tolerance.

Cryptocotylar seedlings seem to be quite common in most flood-prone habitats. The main advantage of this type of seedling in shallow flood-prone habitats such as the tidal forests and the swamp forest is that in a few days after germination it may rid itself of full-submergence (provided that the seed did not fall in a submerged spot in the first place) by using seed reserves to quickly extend the shoot. This strategy may not be as efficient in a forest where flood water rises 10 m above normal levels. In this case, slow-growing phanerocotylar seedlings such as *P. discolor* are also found. Pearce & Jackson (1991) compare the different strategies of rice and *Echinochloa*, both successful wetland plants, where the former grows fast and avoids full submergence while the latter preserves a small, unchanging coleoptile even under the severest circumstances.

Final remarks

Studies on regeneration success and plant succession in Brazilian flood-prone habitats are currently lacking. The studies of Huenneke & Sharitz (1990) on the effect of different types of substrate on the regeneration of *Nyssa aquatica*; of Shipley & Parent (1991) on the germination attributes of 64 wetland herbaceous species; of Jones *et al.* (1994) on woody plant regeneration in four floodplain forests in South Carolina; and of ter Steege (1994) on tolerance of seeds and seedlings of two segregated *Mora* species in the Guianas; provide a wealth of novel approaches to investigate different aspects of the regeneration process from seed germination to seedling recruitment and tolerance.

It is quite clear from these and other papers mentioned in this review, that an integrated approach to the matter, linking ecophysiology, population and community ecology is needed to provide practical answers to questions regarding conservation and plant cultivation in Brazilian flood-prone habitats.

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