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Morphoanatomical Characteristics in Riparian Vegetation and Its Adaptative Value

Marina García and Damelis Jáuregui

Abstract

Riparian vegetation comprises plant communities that grow laterally to rivers and streams. They have multiple adaptations, which allows them to persist in these variable and dynamic habitats. This chapter focuses on the morphological and anatomical adaptations of vegetative organs, due to the fact that they are more vulnerable to environmental changes that occur in riparian ecosystems. We also discuss some dispersal mechanisms in riparian species exposed to flooding conditions. Most morphoanatomical adaptations in riparian plants reflect constraints imposed by long periods of waterlogging or complete submergence, as well as the high diversity of strategies that species have developed in order to cope with flooding. Furthermore, riparian ecosystems are being impacted by an increasing artificialization of rivers and banks with losses, or profound changes, in the natural riparian vegetation a problem that will increase with the ongoing climate change, and which must be contained. In order to reduce the vulnerability of these ecosystems, a deeper knowledge of the morphoanatomical attributes that make possible the successful adaptation of riparian flora is necessary so as to implement appropriate measures for the rehabilitation and sustainability of riparian ecosystems.

Keywords: riparian vegetation, morphoanatomy, vegetative organs, diaspores, plasticity

1. Introduction

Riparian ecosystems are diverse, dynamic and complex habitats. They are the interface between terrestrial and aquatic systems, encompassing different environmental gradients, communities and ecological processes [1]. Riparian vegetation has ecological functions of immense biological importance within these ecosystems, since it provides habitat and food for a wide variety of terrestrial organisms, as well as maintains its stability, by providing a buffer zone that filters sediments, controls nutrients and stabilizes river banks [2], increasing the biological diversity and productivity of their aquatic communities. In a broad context, the term riparian refers to the biotic communities and the environment adjacent to streams, rivers, ponds, lakes, and some wetlands [3]. Recently, riparian vegetation has been defined as the complex of plant communities growing in the riparian zone that is, in the transitional region between aquatic and terrestrial ecosystems [4].

Riparian vegetation is strongly affected by fluvial processes such as flooding and alluvial soil deposition forming a terrestrial flora that is distinctive in structure and function [2]. The plant diversity of riparian forests comprises a wide range of taxonomic groups and life forms with a variety of morphological, anatomical, physiological and reproductive adaptations which allows them to persist in these habitats [5]. It has been widely accepted that the main threat to the diversity and abundance of native flora of riparian ecosystems is related to anthropogenic activity [6]. This includes the conversion of natural lands into areas of varied anthropic use such as agricultural use, transformation into pastures, introduction of forest species and deforestation practices, among others [1, 7, 8]. This situation, coupled with climate change, has strongly reduced the number of native species in these ecosystems putting many of them at risk of extinction and it is predicted that the impact of climate change on the stressors of riparian communities will probably increase in the future [9].

In order to control the erosion of riparian vegetation, it is necessary to implement plans to promote the natural regeneration and restoration of disturbed areas [10]. This can be possible by knowing the plasticity of the species, that is, their ability to change their phenotype in response to variations in the environment [11]. From the ecological point of view, the plasticity can facilitate the adaptation of species that grow in riparian ecosystems [12], as it allows them to explore different habitats and expand their geographical distribution [13]. However, genetic adaptation is required for the persistence of these characters [14].

This chapter summarizes a wide range of literature regarding the main morphological and anatomical characteristics of vegetative organs, as well as dispersal mechanisms that allow riparian vegetation to adapt and survive in riparian ecosystems. The aim of it is to provide a deep and updated overview of these basic principles, which must be taken into account in order to undertake appropriate measures for the rehabilitation, adaptation and sustainability of riparian ecosystems.

2. Morphological and anatomical adaptations in riparian vegetation

Phenotypic plasticity has long been recognized as the property that allows species to face the heterogeneity of the environment, being of great importance from the adaptive point of view. Due to the fact that it can cause changes in attributes of ecological importance and in heterogeneous environments, species with greater phenotypic plasticity can form ecotypes [11] reducing their extinction risks. Likewise, modular plasticity is also important, since it can influence the activity of meristems and the morphological and anatomical characteristics of vegetative organs mainly stems and leaves more than of the whole plant [15].

Globally, natural and anthropogenic stressors cause multiple disturbances in all riparian environments affecting biological processes in riparian vegetation that reduces their resilience and genetic diversity [6] as summarized in **Figure 1**. One of the factors that most affects the development of riparian plants is being subject to dry soils during some time of the year and flooded soils during others. Another group of plants may be under stress from excessive water during great part of their life cycle because of permanent flooding. In both groups the sheets of water in the soil can cause severe hypoxia, and even anoxic conditions in the radical zone [16].

Riparian plants can cope with the physical disturbances of floods through traits that allow the survival of individuals or that facilitate their rapid growth in the population [17]. The following two main strategies for the adaptation of plants to immersion have been recognized: an escape strategy and a waiting-quiescence one.

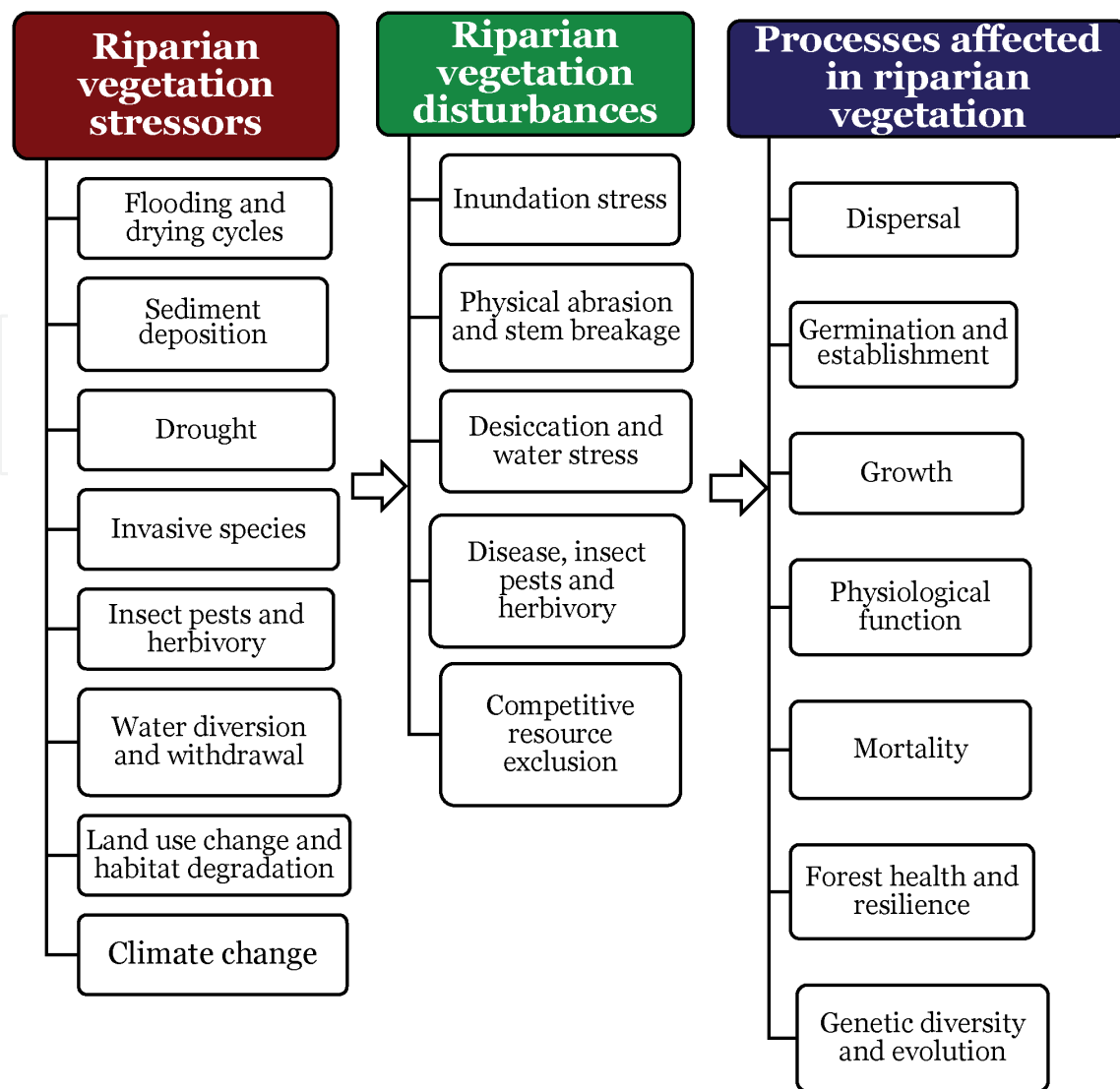


Figure 1.
 Main stressors, plant disturbances and processes affected in riparian vegetation.

The former involves the lengthening of shoots to restore the contact of leaves with the atmosphere which is beneficial when a flood is prolonged and superficial. The latter strategy is based on the conservation of energy to prolong survival during the submerging and allowing growth to resume after water backs off, which is beneficial in case of short duration floods and/or deep submersion [18].

The responses of plants to floods are morphoanatomical, physiological and biochemical. These traits vary among species due to their genetic characteristics the age of the plants and the duration and depth of the water sheet to which they are submitted. It has been suggested that morphoanatomical changes are likely involved with long-term acclimation [18].

Resistance strategies include flexibility of stems leaves and roots and the reduction of the size of the plant and brittle branches, among others. These strategies help plants face events that disturb their development [17, 19]. The appearance or modification of morphonatomical characters that enhance oxygen supply could be one of the causes of acclimation of a species under flood conditions [20]. Among the used strategies, the following stand out: the formation of adventitious roots, the development of aerenchyma in submerged roots and stems, the establishment of barriers to prevent the radial loss of oxygen in the roots, the formation of hypertrophic lenticels and cracked stems and the hypertrophy in the stem base [16, 17]. The morphological and anatomical adaptations in the root and shoot of riparian vegetation are summarized in **Figure 2**.

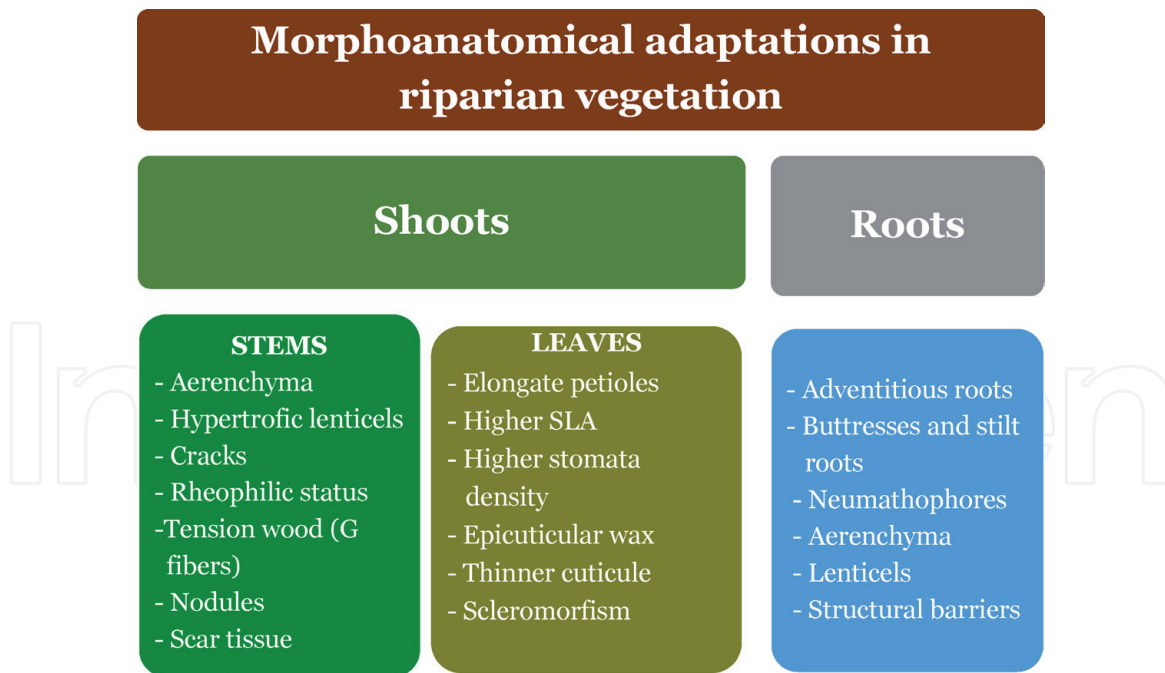


Figure 2.
Main morphoanatomical adaptations in riparian vegetation.

2.1 Morphoanatomical adaptations in the radical system

Flooded soils are low in oxygen, due to reduced exchange rates with the atmosphere. Hypoxia in the radical tissues induces anaerobic respiration and increased consumption of stored carbohydrates [19]. Lack of energy affects growth, cell maintenance, reduced nutrient absorption and even root death [21].

The primary root system of plants subject to flooding is strongly affected by reduction of their biomass, as well as by that of the length and diameter of the roots. This is due to cellular damage at the membrane level. In some species, roots can turn black and die when flooded. In mature trees the root system can break down during prolonged soil flooding, so the production of new roots is an important process [22].

The riparian plants can avoid (or “resist”) the effects of water deficit by developing either deep roots that extend to the water table, or resistant traits that allow rapid recolonization [17].

Among the adaptation strategies in the radical system to hypoxic conditions we can mention:

The formation of adventitious roots, which is an adaptive mechanism of ecological importance in riparian plants, since it allows to replace roots that have died or have been affected due to waterlogging. It is necessary to distinguish among different types of adventitious roots, as it has been proven that their formation is regulated differently. The adventitious roots are separated into two large groups: the first one includes those potentially established in the embryo such as those of the monocotyledons, the nodal roots of some eudicotyledons and the stilt roots; the second group is composed of the roots whose formation is induced by a stressor (in this case flooding) which may or may not be nodal [23].

In some species the primordia of adventitious roots are formed during normal development, but they emerge when plants are under a sheet of water (e.g. *Rumex palustris*). However, it has been suggested that in others taxa submergence induces root development (e.g. *Eucalyptus* species). The moment of emergence of adventitious roots induced by floods is specific to each species [22, 24] and depends on factors such as the stage of development of the plant, water temperature, and the depth and duration of the flood [25].

Floods can promote the formation of roots from the hypocotyl, knots beneath the ground (crown), or above it (brace), as well as internodes. Adventitious roots facilitate gas flow, water transport, and nutrient absorption during and after floods ensuring plant survival [26]. Likewise, it has been pointed out that the formation of these roots in trees improves their internal aeration and promotes water absorption after the first floods as observed in a Mapire igapó [20].

The formation or increase in number of adventitious roots has been confirmed by various authors in different tropical riparian species, such as: *Polygonum ferrugineum* and *P. stelligerum* [27], *Senna reticulata* [28], *Tabebuia rosea* [29] and *Triplaris gardneriana* [30].

Another important adaptive trait of roots in riparian vegetation is the formation of abundant buttress roots and stilts [31]. Buttress roots are common in plants that grow on riverbanks and streams, as well as in trees that lack a deep root. They are closely related to the duration of the flood period and the dynamics of the habitat [32]. It has also been pointed out that buttresses roots are common in trees that develop on substrates where their anchorage is difficult, such as those with a thin layer of sediments (e.g. *Byrsonima amazonica*), while in areas with deep layers many stilt roots are formed, as occurs in *Alchornea castaneifolia* [31]. Buttress and arch roots are piles in sloping areas, providing stability. Its occurrence has been cited in *Aquilaria malaccensis* and *Drypetes* spp. [33].

In some riparian species pneumatophores are noticeable, which are specialized roots with negative geotropism that grow outside the water. These develop as ascending erect organs with lenticels along the surface and spongy tissue that allow the flow of oxygen and facilitates its diffusion throughout the plant. This type of roots has been observed in *Pithecellobium latifolium* and, experimentally, in some palms that grow at the headwaters of rivers and in swampy areas, for example, *Euterpe* and *Mauritia* [31].

Another root adaptation to flooding is the increase in its porosity generated by evenly distributed intercellular spaces, small lagoons or the formation of aerenchyma in the cortex [23, 34]. This tissue constitutes a low-resistance internal pathway for the movement of gases among the different parts of the plants thus improving oxygen supply to the roots [35]. The presence of this tissue prevents anaerobiosis in the root system, making it an efficient mechanism that contributes to the general adaptation of tree species to long-term floods [36].

It has been indicated that roots of plants in mesic environments have a porosity (percentage of air spaces) of 2 to 7% of their volume, while in flooded areas this porosity can reach values close to 60% [37]. The formation of aerenchyma may be less important for the longitudinal flow of oxygen in adult trees because lagoons are destroyed [38]. In this case, ATP production in radical cells is achieved by reducing the number of cells that consume oxygen in the cortex [39].

Species that normally grow in the Amazon were classified according to the presence and development of gas exchange and mobilization system: the first group with roots lacking spaces; the second group with pronounced intercellular spaces in roots, but which are not modified with hypoxia treatments; the third group with intercellular spaces in roots, which are partially modified when plants are subject to flooding; and the last group in which species produce a large quantity of adventitious roots with well-developed aerenchyma [34].

In herbaceous species or in seedlings of different biotypes primary aerenchyma of diverse origin occurs. However, when secondary growth has occurred secondary aerenchyma is formed, mainly from the phellogen [35, 40].

The presence of constitutive aerenchyma, or that induced by hypoxia in roots and stems of riparian plants, has been verified in various studies. The first occur in *Guazuma ulmifolia* [41] and in three shrub species of Melastomataceae that inhabit

areas with frequent flooding [42], and the last in *Eucalyptus camaldulensis subsp. refulgens* an Australian timber species which grows mainly on the river banks and their alluvial plains, but which can endure drought [22].

Likewise, in *Rumex palustris*, a species tolerant to flooding, has been indicated a greater development of the aerenchyma than in *R. acetosa*, the latter being an intolerant species to this condition [43]. In *Tabebuia rosea* seedlings, aeriferous parenchyma was evident in roots and stems, as well as in *Handroanthus chrysotrichus* stems in which aerenchymatous phellem was noticed [29].

The development of aeriferous parenchyma, lenticels and fissures or cracks allows the axial diffusion of gases especially oxygen between air space and the internal part of roots [34].

Deposition of hydrophobic compounds (suberin and lignin) can be found in the cortical region of the roots as barriers of thick-walled cells. Suberin deposits are able to prevent radial loss of oxygen from the root cortex to the rhizosphere [17, 34, 44]. Suberized walls are reported to diverse degrees, mainly in the exodermis of young roots of species typical of varzeas in Manaus, Brazil [39].

The hypoxic condition induced by floods promotes a greater diameter in roots due to a thicker cortex. Likewise, the area occupied by the stela is smaller which suggests that both features are variables to consider in the adaptability to waterlogging conditions [45]. However, this response may be the opposite, and a reduction in root diameter may occur [29, 46]. In *Guazuma ulmifolia* and *Genipa americana*, species with high plasticity adaptable to flooded soils, the reduction on these traits is associated with energy savings [41].

Previous considerations correspond mainly to the adaptations observed in root system of herbaceous plants and seedlings of tree species, which could be associated to the difficulty of working with underground systems in trees. It is important to further study the roots traits of adult individuals since it is not certain that those obtained from seedlings could be extrapolated [20, 34].

2.2 Morphoanatomical adaptations in the shoots

Initially, the importance of some biotypes in riparian vegetation should be highlighted. Trees and shrubs play an important role by blocking wind and stabilizing terrain. Herbs contribute to the stabilization of soil and are valuable tools for the rehabilitation of degraded riparian environments [47]. It is important to know the mechanisms that each species has to tolerate or adapt to the conditions of each particular habitat in order to have tools to choose useful species to reforest when necessary.

The impact of hypoxia on stem tissues has not been widely studied. It was also pointed out that it occurs particularly at the meristem level, especially when flood water is muddy and makes it difficult for light to pass through [21].

2.2.1 Stems

Few details have been reported regarding the adaptive importance of rhizomes and stolons in plants from riparian environments. However, it is known that amphibian species can develop rhizomatous and stoloniferous stems with cortex made up of aerenchyma, which constitutes an adaptive trait. These types of stem have been observed in amphibian species such as *Cynodon dactylon* and *Paspalum distinum* [48].

Likewise, the shrubby species *Ficus squamosa* is able to grow stolon-like stems when it grows on banks of the Ping River in Thailand [49]. The development of these types of stems constitutes an adaptive advantage not only because the

presence of aerenchyma allows them to stay afloat, but also because they constitute diaspores of propagation of the species since these fragments can be part of a new individual [48].

Stem nodulation has been observed in several species of legumes that inhabit flooded, or likely to flood places. This phenomenon is an adaptation which allows legumes to fix nitrogen in these environments. Plant species that exhibit stem nodulation are typically tropical or subtropical and grow in wetlands, rivers or lake margins, and belong to *Aeschynomene*, *Sesbania*, *Neptunia* and *Discolobium* genera [50]. Along with the formation of nodules, some species develop a large number of parenchymal cells, which facilitates the entry of sufficient oxygen for different metabolic functions [51].

Stems do not have selective barriers (such as the exodermis and endodermis) but they can develop a cuticle, which due to its hydrophobic characteristics can perform the same function as the previously mentioned tissues [40]. However, it is possible that in riparian plants with stolons and rhizomes those tissues differ. Nonetheless, this assumption must be verified through further morphoanatomical studies.

Species adapted to prolonged flooding avoid anoxia by spreading out of the water [17]. The lengthening of seedlings shoots or epicormic is a response to flooding of various plant species. It ensures the restoration of contact with the atmosphere in order to maintain internal aeration [52]. This lengthening occurs mainly in internodes and petioles, which causes leaves to approach the surface achieving better lighting conditions. *Rumex palustris* [53] and *Chloris gayana* benefit from this strategy, which is considered an escape during prolonged periods of flooding [54].

Sometimes fissures or cracks are visible in the basal part of young stems of grasses and trees, which are the result of pressure exerted by the development of cells of the aerenchymatous phellem on the epidermis and on some other external cortical layer until it is broken exposing the internal tissue to the atmosphere [55]. In *Sesbania javanica* [56], *Tabebuia rosea* and *Myracrodruon urundeuva* [29], cracks were observed on the surface of the seedling stems, growing in flooded soils.

Many flood-tolerant riparian species develop hypertrophic lenticels on stems which penetrate the phellogen layer and allow gas exchange. Hypertrophic lenticels facilitate the absorption of oxygen by the plant, but they are also supposed to contribute to the release of carbon dioxide and volatile compounds, such as acetaldehyde and ethanol [57]. These structures were observed in the riparian species *Schinus terebinthifolius*, in which they appear as soft whitish masses in the basal portion of the stems [58]. They are also a response to flood in *Sesbania javanica* [52], *Tabebuia avellanedae*, a riparian species of the Paraná River-Brazil [59], and in *Guazuma ulmifolia* [41]. In *Genipa americana* they are still present under non-stressful conditions, thus they are considered constitutive. However, waterlogging stress causes an increase in its frequency and size [41].

Some species of riparian zones have characteristics in their woods that allow them to adapt to watercourses. Therefore, they constitute an alternative in the stabilization and protection of river slopes. Knowledge of the internal structure of wood is essential to understand its behavior in these habitats, particularly when it comes to structural features related to flexibility [60].

The set of adaptive characteristics of wood can, as a whole, be called “anatomical rheophilic syndrome”. It is characterized by: small and solitary vessels of 100 μm in diameter, multiple radial, with walls 2.5–5.0 μm thick; scarce or absent axial parenchyma; narrow rays; and the presence of gelatinous fibers [61]. These woods are constituted by: 10 to 30 percent of vessels, 0 to 5 percent of axial parenchyma, 10 to 20 percent of rays and 60 to 70 percent of fibers. Several of these characteristics have been observed in riparian species such as *Colliguaya brasiliensis* [60] and *Aspidosperma riedelii* [62].

In riparian environments trees can be inclined or crooked, which is the result of the so-called tension wood, characterized anatomically by the lack or scarce lignification in cell walls of the fibers, as well as by the presence of an internal gelatinous layer in them (so-called G fibers). These cells support high stresses in mature organs, allowing their movement, or reinforcing their structure and stability [63]. G fibers have been observed in *Sebastiania commersoniana* [64] and *Ludwigia* species [65] when these grow in flooded soils.

Likewise, the presence of macules in the wood has been highlighted. These structures are parenchymal cells with thicker walls than those of the adjacent cells with starch and phenolic compounds, which facilitate anaerobic survival. These structures were observed in *Sebastiania commersoniana* [64] and in *Eugenia inundata* [66].

2.2.2 Leaves

Leaves are the most plastic plant organ. Therefore, their morphology and anatomy are usually closely linked to the environment in which plants grow [67]. Several foliar parameters have been considered important for the adaptation to specific riparian microenvironments among them size and mass, water content, and anatomical characteristics of the leaf surface and mesophyll.

A common foliar adaptation in riparian species subject to waterlogging conditions is the elongation of the petioles of submerged leaves which allows them to emerge, thus avoiding the low luminosity to which they are exposed during flood periods [52]. In the Amazonian floodplain, many tree species shed their leaves in the first week to months of waterlogging or submergence and produce new ones near the end of the flood period [68]. However, in these ecosystems there are also evergreen trees that keep their leaves throughout the waterlogging period, even when completely submerged. These leaves are generally xeromorphic [20, 69, 70].

In trees of a seasonally flooded forest of the Mapire River in Venezuela, it has been found that both submerged and non-submerged leaves have xeromorphic characteristics such as: thick cuticle, large epidermal cells, bifacial mesophyll and abundance of sclerenchyma. These traits remaining practically unchanged regardless of the phase of the flood cycle [70]. It is believed that these trees experience a water deficit during the waterlogging phase similar to that faced by plants from dry habitats, due to a decrease in water absorption by roots. Therefore, these xeromorphic leaves allow trees to cope with the drought during the non-waterlogging phase [69]. In riparian species that are not periodically flooded both mesomorphic and xeromorphic adaptations may occur [71].

The riparian species *Guazuma ulmifolia* and *Sapium glandulosum* have contrasting histological characteristics in the leaf blade [71] and also in the midrib and petiole (**Figure 3**). *G. ulmifolia* shows higher density of xylem vessels (narrow diameter) and a greater development of sclerenchyma (**Figure 3A, B**) than *S. glandulosum* (**Figure 3C, D**) on both midrib and petiole. These traits are associated with xeromorphic leaves [72, 73] because they can maximize the efficiency of water transport into the leaf and prevent foliar collapse under drought conditions [74]. These anatomical differences can help explain the environments in which they grow: *S. glandulosum* frequently inhabits floodplains and swampy areas [75, 76] whilst *G. ulmifolia* has been reported in both floodplains [77, 78] and dry and inter-vened areas [71, 79]. Furthermore, the secretory cavities in the midrib and petiole of *G. ulmifolia* (**Figure 3A, B**) accumulate a mucilage that can retain water [41] and has also been associated with a defense mechanism against biotic stressors [80].

The specific leaf area (SLA, $\text{cm}^2 \text{g}^{-1}$) is related to the photosynthetic capacity, nitrogen content, longevity of the leaf and foliar architecture [81]. It is usually lower in species growing in arid environments [82] and higher in wetland habitats [83],

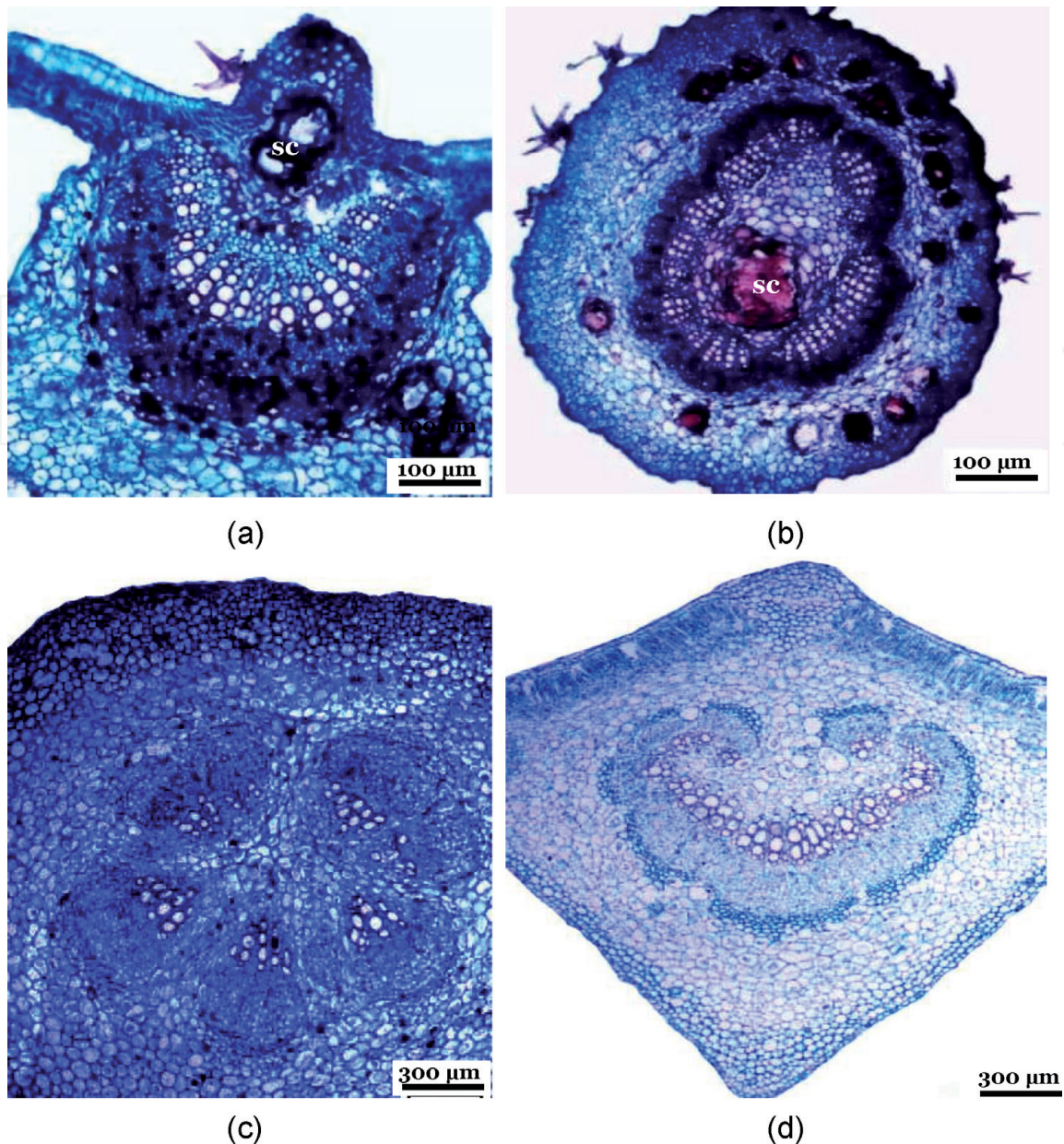


Figure 3. View of the midrib and petiole cross section in *Guazuma ulmifolia* and *Sapium glandulosum*. A-B: *G. ulmifolia*, midrib (A) and petiole (B); C-D: *S. glandulosum*, midrib (C) and petiole (D). sc: secretory cavity.

as it can promote gas exchange in plants whose leaves must withstand waterlogging conditions. However, in trees from a igapó of the Venezuelan Amazon, a decrease in SLA with flooding has been observed in both emerged and submerged leaves [70]. This seems to be associated with an acclimation process that can promote an increase in CO₂ conductance in the foliar mesophyll under waterlogging conditions [20].

In riparian ecosystems from Europe, the black poplar (*Populus nigra*) is one of the most studied species due to disturbances caused by the degradation of its natural habitat. A morphometric analysis on leaves across 17 native populations of *P. nigra* from the banks of six rivers in Croatia and Bosnia and Herzegovina including the hairy type (*P. nigra* subsp. *caudina*) of sub-Mediterranean climate, and the typical poplar type of continental riparian forests showed that the best features to differentiate these two types of populations were the distance between the broadest portion and the base of the blade together with the length of the petiole [84].

In genotypes of poplar species *P. deltoides*, *P. balsamifera*, *P. angustifolia* and hybrids between them it has been found that all of them have a high density of small stomata [85]. This can be associated with a high stomatal conductance and a lower

water use efficiency [86] consistent with their behavior as ecological pioneers that grow rapidly in low fertility areas after floods or other disturbances [87]. Likewise, all species had abundant cuticular wax which would reduce transpiration in poplars growing in dry riparian regions [88]. In native populations of *P. nigra* of the Serbian alluvial zone, no differences were found in stomatal characteristics which could indicate that each of them has a similar combination of genotypes [89].

Invasive exotic plants have a negative impact on native riparian species, mainly because they affect the flow of energy and the cycling of matter, as well as by their excessive use of resources. A study on *Echinocystis lobata* and *Parthenocissus quinquefolia* (invasive climbing species) growing on *Salix caprea* and *S. fragilis*, respectively, showed that in both willow species the leaf cuticle became thinner relative to that of plants that grew without these vines [90]. This is a disadvantage since the cuticle contributes to the mitigation of the adverse impact caused by both biotic and abiotic stressors.

2.3 Dispersion units

The dispersal of plants in riparian environments is affected by the hydrogeomorphic characteristics of each place. Riparian species can be dispersed by various vectors, including wind (anemochoria), animals (zoocoria), and water (hydrochoria). However, the proportion in which these mechanisms occur is not quantified [17]. Hydrochoria is highlighted as a dominant dispersal vector in riparian habitats [17, 91, 92]. Both vegetative and generative propagules can be dispersed by water [92]. In these environments, the formation of a seed bank is not feasible [19].

Ichthyocoria is very common in tropical riparian environments. Diaspores dispersed by fish are highly variable in shape, texture, color and taste [92]. The intact seeds excreted by fish are small with high nutrient content in the pericarp of the fruits, as occurs in *Pouteria glomerata* [92]. Frugivorous fish can be effective dispersers of large, non-floating seeds, thus contributing to dispersal over long distances as well as upstream [93].

In several species hydrochoria is a secondary dispersal mechanism, as propagules often fall to the ground before being carried away by the water current. Other species drop them directly into the stream (*Disa uniflora*). Diaspores that lack buoyancy can be transported by water by adhering to floating objects such as logs, branches and litter [92].

In riparian plants hydrochoria offers several advantages: 1. Floating hydrochorous can disperse long distances compared to other dispersal vectors. 2. The dispersal distance of floating hydrochorous is largely independent of their mass consequently, they tend to be heavier than those dispersed by wind and heavier seeds produce taller seedlings (with the advantages that this implies). 3. Immersion in water prevents desiccation, thereby increasing the longevity of vegetative propagules. 4. It increases the odds that propagules will be deposited in suitable sites for germination and growth [17].

Small seeds can occupy a greater number of available microsites, while large ones allow a higher rate of seedling development since they have more endosperm or cotyledons with more accumulated substances that favor embryo development [91].

Floating propagules have cork or some spongy tissue and epidermis with waxes or thick cuticle which prevents the imbibition and collapse of them. The seeds of riparian species such as *Annona montana* and *Hevea spruceana* have aeriferous tissue in variable proportions [91]. *Manicaria saccifera* and *Crudia acuminata* have a hollow endosperm, while *Carapa guianensis* and *Pachira aquatica* have sparse endosperms which allow them to float [94]. *E. tenuifolia* has corky tissue and develops spongy tissue in the seed coat. *Tabebuia* species have their coat seed suberous and hydrophobic [95]. Many of these diaspores go through a long period of floating without losing their viability [91].

The presence of spikes, hooks, and other appendages on the surface of diaspores can reduce water surface tension. These structures allow them to attach to leaves, branches, and other surfaces [92]. They also catch air bubbles and, consequently, increase buoyancy [95]. The diaspores can have a hard cover, which gives them greater tolerance to anoxic conditions, resistance to abrasion and tolerance to burial allowing the seed to be transported with sediment and garbage, thus increasing its longevity in the soil [17].

In the Amazon, after fruits ripen which generally occurs when there are high levels of water [95] seeds fall into the water and can float and/or submerge for several weeks without losing their viability (quiescence). Seed germination begins only when the flood recedes, although in some species the radicle may protrude or even the entire seedling may be produced, while floating, as occurs in *Carapa guianensis* [96].

Vegetative fragments can detach and disperse during disturbance events, improving recolonization capacity. These fragments usually float and help the dispersion. Furthermore, they can remain viable for weeks after separation. They can begin to produce roots shortly after detachment, which facilitates their establishment by being immobilized somewhere [97]. *Salix martiana* shows intense vegetative propagation through parts of broken stems. In the case of *Eugenia inundata*, colonizing species of igapó areas in Brazil, lower branches take root [98] so vegetative fragments contribute to the fast and effective establishment in periods when soil lacks water.

3. Conclusions

Riparian areas have been substantially degraded mainly due to anthropogenic factors which have caused erosion of the riparian vegetation. This situation will become more serious in coming years due to events associated with climate change. In this chapter, we have discussed the main morphoanatomical adaptations of the vegetative organs and dispersal propagules of riparian species which determine their ability to survive in such variable and dynamic habitats. In species that face prolonged flooding periods, these adaptations help overcome the anoxia imposed by waterlogging. However, in arboreal species typical features of xeromorphism may be present especially in leaves, which not only allows them to face the water deficit caused by the decrease in absorption of water by roots due to waterlogging, but also drought conditions during the non-waterlogging period. In riparian species from drier areas, both mesomorphic and xeromorphic adaptations may occur. From an ecological point of view, more plastic morphoanatomical adaptations can reduce the risk of extinction of riparian species since this allows them to explore different habitats and thus, expand their geographic distribution. Understanding the scientific principles that support the adaptation of species to riparian habitats is crucial for the decision making process by landscapers and government entities that are responsible to promote the protection and conservation of these ecosystems. In order for this to be achieved, the contribution of different disciplines is required, since interdisciplinary teams are the ones that have the greatest possibility to successfully handle this challenge.

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