FLOODED FORESTS

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Summary

Wetlands cover an estimated 6% of the planet's land surface and approximately half of this area is located in the tropics, particularly in South America that contains 1.5 million square kilometers out of the world's total of 5.7 million. Swamps and flooded forests account for the largest proportion of wetland areas, as compared to lakes, marshes, bogs and fens where vegetation is mostly composed of herbs. This is as true worldwide as it is to the tropics. Plants in wetlands are subjected to varying periods of oxygen shortage due to flooding and/or submersion. Although aerobic organisms, such as higher plants, need an adequate supply of oxygen for the performance of vital functions (e.g., cell division), they are often capable to survive under partial or total lack of oxygen, and there is a large inter-specific variation regarding the length of time they can do so. In the case of higher plants, survival under oxygen shortage can last from hours to years. Flooding induces oxygen shortage in the soil, which directly affects the roots of plants. Thus, in order to colonize a flood-prone habitat, plants must resort to biochemical, physiological and/or morpho-anatomic mechanisms to tolerate or avoid the deleterious

effects of oxygen deprivation. Even possessing such mechanisms, these individuals must overcome dispersal, germination and young age hazards. Swamps and flooded forests are curious in that they comprise many examples of trees that are capable to survive hypoxia and/or anoxia. Perhaps the most extreme example is that of the Amazon floodplains, in the Neotropics, where tall trees are often fully submerged for 6-8 months a year when rivers overflow. Their amazing set of life strategies to cope with such a regime range from cambial dormancy to fish dispersal of seeds. Swamp trees are subjected to root flooding only, which however may last a whole-year with water that is most times stagnant. High rates of destruction of flooded forests are a threat to this biodiversity and decrease also the fixation of atmospheric carbon. Thus, this chapter concludes by providing some examples of conservation and restoration efforts in flooded forests.

1. Introduction

Wetlands are defined by the "Convention on Wetlands of International Importance especially as Waterfowl Habitat" (or the Ramsar Convention) as "areas of marsh, fen, peatland or water, whether natural or artificial, permanent or temporary, with water that is static or flowing, fresh, brackish or salt, including areas of marine water the depth of which at low tides does not exceed six meters". Despite the apparent clarity of this definition, wetland classification remains problematic. There are up to thirty categories of natural wetland types and nine manmade ones.

They cover an estimated 6% of the planet's land surface and approximately half of this area is located in the tropics, particularly in South America that contains 1.5 million square kilometers out of the world's total of 5.7 million (Table 1). **Swamps** and flooded forests account for the largest proportion of wetland areas, as compared to lakes, **marshes**, **bogs** and **fens** where vegetation is mostly composed of herbs. This is as true worldwide as it is to the tropics (Table 2). Interestingly, although South America is the continent containing the largest area of wetlands, and Brazil is the country with the largest contribution to these figures, this habitat type accounts to no more than 2% of Brazil's vegetation cover, which predominantly consists of major forests (42%) and grass & shrubs (36%), according to WCMC (1992).

Region	**10^3 x km^2**
South America	1.524
Russia and northern Asia	1.512
Canada	1.268
All others	< 355
Total	5.691

Table 1. Land covered by wetlands in the world. Adapted from Aselmann and Crutzen (1989)

Vegetation type	**Area covered (10^3 x km^2)**		**%**
	South America	**World's total**	
Floodplains	543	823	66
Lakes	68	114	60

Marshes	62	274	23
Swamps	851	1130	75

Table 2. Major types of wetlands and their area cover in South America in relation to the world's total. Bogs and fens are not listed because they do not occur in South America. South America ranks first in the world among the continents for all other vegetation types in regard to area covered. Sources: Aselmann and Crutzen (1989) and WCMC (1992)

It is worth highlighting however that, due to the highly dynamic nature of wetlands, seasonal and long-term changes often pose difficulties to a precise definition of boundaries. Therefore, the figures presented in Tables 1 and 2 often vary between authors.

Global attention to wetlands have also implied in an increasing scientific output on the biology of such systems, including those in the tropics. This Chapter focuses on tropical flood-prone forests, which represent most of the world's wetlands. In addition to their relevance in ground cover, flooded forest are also richer in biomass than other types of wetlands due to the presence of tree species. Since South America has over a third of the world's wetlands, some case studies from that part of the world will be discussed in more detail. However, before discussing plant life in tropical flooded forests, we must first address the survival mechanisms found in plants that are subjected to oxygen stress caused by flooding.

2. Plant Survival under Oxygen Stress

2.1 Overview

Wetland plants are subjected to various types of flooding regimes. Flooding is a phenomenon of limited but uncertain duration and continuous flooding is fatal to most aerobic organisms such as higher plants. This is because flooding is one of the main triggers of reduction in oxygen availability. Aerobic organisms require an adequate supply of oxygen to perform vital functions, such as cell division. Although total oxygen deprivation (anoxia) often implies in the death of tissues of aerobic organisms, this condition is less common in nature than partial oxygen deprivation (hypoxia). Total or partial anaerobiosis, therefore, is a major hurdle faced by plants in flood-prone habitats. However, both plants and animals are capable to endure oxygen deprivation for varying periods of time and there is considerable inter-specific variation in this respect. For higher plants, survival under oxygen deprivation may last from a few hours to years. This suggests that there might be different primary causes of death that demand different strategies to circumvent this limitation. Indeed, a myriad of plant responses to flooding and anoxia are reported in the literature that might even evidence opposite behavior patterns. For instance, a given tolerant plant might reduce or increase transpiration, and aerenchyma formation, replacement of dead roots and accumulation of products of anaerobiosis might take place or not. In addition to the absence of general patterns in this respect, it is also difficult to determine the extent to which such responses are adaptive and advantageous or mere symptoms of injury.

The advent of the controversial theory of metabolic adaptations to anoxia by Robert Crawford in the early seventies was an important attempt of providing a generalization, but established a dichotomy. For some authors, plant survival to anoxia/hypoxia depended on biochemical or physiological adjustments, while for others morpho-anatomy and root-shoot communication mediated by hormones were the decisive factors. Carlos Joly, a Brazilian scientist, proposed however that, for tropical plants, the mechanisms of hypoxia/anoxia tolerance are more complex than for temperate plants and that frequently one can find a combination of metabolic and morpho-physiological adaptations. However, the number of studied species in the tropics remains insufficient to allow the detection of general patterns. Irrespective of this debate, fact is that flooding implies in the accumulation of a variety of toxic compounds in the soil and in a sequential change in plant metabolism and physiology, such as: (1) reduced water absorption and stomatal closure leading to a lowered rate of photosynthesis; (2) decreased permeability of roots; (3) reduced mineral uptake; (4) alterations in growth hormone balance; (5) leaf epinasty, chlorosis and abscission; and (6) arrested vegetation and reproductive growth.

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. Many species rated as flood-tolerant may be quite sensitive in the seed or seedling stage. Thus, from an ecological viewpoint, plant colonization of tropical wetlands is a matter that still demands a lot of research effort.

Thus, the next three sections cover these distinct types of mechanisms related to plant survival to flooding and oxygen shortage: metabolic mechanisms, morpho-physiological mechanisms and ecological mechanisms.

2.2 Metabolic Mechanisms

Oxygen deprivation prevents respiratory chain phosphorilation and, in consequence, stops the mechanism whereby plant tissue makes the vast majority of its ATP. ATP produced under anoxia as a result from fermentation implies in two problems: (1) fermentation yields a maximum of 3 moles of ATP per mole of hexose equivalent, whereas respiration gives a maximum of 39; thus, much more substrate has to be consumed to produce a given amount of ATP in anoxia than in air; (2) fermentative pathways use their own intermediates as hydrogen acceptors (e.g., pyruvate in glycolysis), in a way that breakdown of substrate is incomplete; products of fermentation include organic compounds (e.g., ethanol, lactate) that are potentially toxic, and multicellular organisms are much less able to dispose of the products of fermentation than of CO_2, which is a product of respiration. In conclusion, lack of ATP is the major hazard of anoxia, followed by inefficient use of the substrate and poisoning by fermentation products.

Despite some controversy, Robert Crawford’s viewpoint is predominant and proposes that flood-tolerant plants share four common features, which are possibly the background for tolerance: (1) control of metabolic rate; (2) diversification of end products of glycolysis; (3) provision of adequate carbohydrate supplies; and (4) coupling of metabolic pathways. In case (1), tolerant species have lower rates of respiration, minimum Pasteur Effect (see Glossary) and partial replacement of ethanol by lactate as the end product of glycolysis. In case (2), tolerant species diversify the end products of glycolysis, by producing for instance malate (more commonly in seeds) or shikimic acid (e.g., tuberous roots) or aminoacids and, as a result, potentially toxic compounds do not accumulate to toxic levels. In case (3), large carbohydrate reserves in the underground storage organs of plants prevent the starvation effect that takes place if all reserves are depleted during anoxia, and often grant success when growth is resumed after flooding recedes and aerobic conditions re-establish. Finally, in case (4), the coupling of metabolic pathways can yield significant increase in ATP production, since most biochemical synthesis involves an excess of oxidations over reductions and, therefore, if a tissue is to perform any anabolic activities under anaerobiosis, additional forms of proton disposal are necessary.

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Biographical Sketch

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