Ventilation Systems in Wetland Plant Species

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Contributor: Lars Olof Björn , Beth A. Middleton , Mateja Germ , Alenka Gaberščik

Ventilation systems rely on a passive molecular diffusion process, on pressurized gas flow, or Venturi-induced convection.

metabolic gases greenhouse gases aerenchyma

1. Introduction

The aquatic environment holds special challenges for plant survival. The diffusion of gases in water is about 10^4-fold slower than in air, so that aquatic plants must perform photosynthesis in water, and maintain aerobic respiration in flooded conditions [1][2]. Herbaceous wetland plants differ significantly, according to the accessibility of gases for their metabolism regarding their position in the water column. Researchers define various functional groups, namely, (1) emergent macrophytes or helophytes that are rooted in water-saturated soil, with foliage extending into the air (e.g., *Typha latifolia*, *Phragmites australis*); (2) floating-leaved macrophytes that are living in water rooted in hypoxic or anoxic sediment, with leaves floating on the water surface (e.g., *Nuphar luteum*, *Nymphaea alba*); (3) submerged macrophytes that grow completely submerged under the water, with roots or rhizoids attached to the substrate (e.g., *Myriophyllum spicatum*, *Potamogeton crispus*); and (4) free-floating macrophytes that float on or under the water surface, and are usually not rooted in the sediment (e.g., *Ceratophyllum demersum*) [3]. In addition, wetlands also host many different woody plants that are permanently or occasionally rooted in water-saturated sediment [4]. These species, belonging to different groups, often possess adaptations to overcome oxygen and carbon dioxide deficiencies, in order to maintain optimal conditions for photosynthesis and respiration. Emergent and floating-leaved species have an advantage over submerged species because their above-ground parts are fully or partly exposed to air. Aerial leaves have stomata in their epidermis, which can be adjusted to optimize exposure of internal tissues to the atmosphere and the exchange of gases. Thus, aerial plant parts are well supplied with oxygen, but for roots and rhizomes anchored in water-saturated soils, oxygen for respiration can be limited. Therefore, efficient ventilation systems are crucial for their survival. Ventilation systems rely on a passive molecular diffusion process, on pressurized gas flow, or Venturi-induced convection [5]; however, in submerged plant tissue, the direct exchange of gases between these tissues and water also occurs [6]. In most aquatic species, ventilation is enabled by an extended system of air canals and intercellular spaces called aerenchyma, which develop in different plant organs from roots, to stems and leaves. [7][8]. Gases in aerenchyma can originate from the atmosphere, rhizosphere, or plant metabolism [9]. Laing [10] shows a strong relationship between the leaf area and the extent of changes of oxygen and carbon dioxide concentrations in aerenchyma during periods of illumination; thus, the contribution of metabolic gases may vary significantly among species.

Aquatic plants mainly form aerenchyma constitutively in different organs, namely, roots, leaves, and stems, while some amphibious and terrestrial plants produce aerenchyma in response to an oxygen shortage [7]. The presence of aerenchyma may differ among species. Independent of habitat, aerenchyma patterns are stable at the genus level, and the consistency of pattern is stronger in the roots than in the shoots [11]. In addition to the atmosphere, gases in aerenchyma can originate from the rhizosphere or plant metabolism [9]. The formation of aerenchyma may not depend on environmental conditions, or be induced by flooding [1]. Aerenchyma cells are formed lysigenously by programmed cell death, as is the case of rice roots; schizogenously by the expansion of intercellular spaces [11]; and expansigenously (secondary aerenchyma) by cell division or enlargement, without cell separation or death [12]. These enlarged spaces may develop either in primary tissues (primary aerenchyma), or in secondary tissues (secondary aerenchyma) [13]. According to Doležal et al. [14], lysigenous aerenchyma are mostly produced by submerged plants, schizogenous aerenchyma by terrestrial and perennial wetland plants, and expansigenous honeycomb aerenchyma by aquatic floating-leaved plants. The amount of intercellular spaces varies significantly among species. In aquatic species, these intercellular spaces contribute up to 60% of the leaf volume [15], while in mesophytes, their volumes range from 2–7% [16]. Thus, in non-tolerant species, flooding may result in the demise of the plant.

Beyond ventilation, aerenchyma cells have other important ecological functions, including acting to store gases and increasing their internal conductance to roots and shoots [7]. The transfer of oxygen to underground organs, via aerenchyma during soil flooding, may prevent the suffocation of plants. Oxygen can also be transferred from roots to the rhizosphere, via aerenchyma. This critically important oxygen to oxidize and detoxify toxic chemicals formed in sediments in environments with low redox potential [17][18], noting that a lack of oxygen is associated with reduced forms of sulfur, manganese, and iron that may reach toxic levels in the soil [6].

In wetland soils, gas concentrations of several gases, such as carbon dioxide and methane, exceed atmospheric concentrations. Thus, aerenchyma can also be a path for greenhouse gas emissions from the plant, as methane and nitrous dioxide are released via plants from waterlogged sediments to the atmosphere [19][20].

Some photosynthetic O_2 produced by submerged plants oxygenates the water column, while natant plants can prevent oxygen diffusion from the atmosphere to water [21][22][23][24]. Aerenchyma cells lend buoyancy and mechanical resistance to breakage, with a relatively small investment in biomass by aquatic plants [25].

The ventilation in wetland plants takes place via various plant structures, and is enabled by the presence of aerenchyma in these structures. The source of gases and influx and efflux locations may differ significantly among different species and plant groups.

2. Diversity of Ventilation Systems

Similar physical processes of ventilation occur in different taxonomical and functional plant groups that thrive in oxygen-deficient sediment; however, their morphological adaptations differ significantly (**Table 1**). Functional traits of these plants are not only the species' response to specific environmental conditions, but they also depend on their phylogeny. Jung et al. [11] find specific trends of aerenchyma patterns in several taxa of higher plants, and show that these patterns partially coincide with their phylogeny. The study of Cape reeds reveals that the presence of aerenchyma correlates with the eco-hydrological niche at the population and species level, indicating that waterlogging presents an environmental filter that excludes species without aerenchyma [26]. Bedoya and Madrinán [27], studying the evolution of the aquatic habit in genus *Ludwigia* L., find a convergence towards the absence of secondary growth in roots, smaller proportion of lignified tissue area in underground organs, and the presence of primary aerenchyma. However, there are also studies that are not consistent with these results. For example, the study of different *Carex* L. species in a phylogenetic context, with an even sampling across the different clades, shows that the size of the aerenchyma has only a weak relation to soil moisture [28]. *Carex* species with poorly developed aerenchyma have low performance in flooded soil, while partial submergence may even affect species with a larger amount of root aerenchyma [29].

Table 1. Ventilation mechanisms in different taxonomical and functional plant groups that thrive in oxygen-deficient sediment.

Plant Group	Taxonomic Group	Source of Gasses	Ventilation Principle	Special Features	Reference
Submerged	Isoetids	Water, metabolism, Sediment	Diffusion, aeration of rhizosphere via buried leaves	Aerenchyma, CAM	[30][31]
	Angiosperms	Water, metabolism, Sediment	Diffusion	Metabolic gasses trapped in aerenchyma	[32][33]
Floating	*Nuphar* spp., *Nymphaea* spp.	Air, metabolism, Sediment	Pressurized ventilation, thermo-osmotic gas transport,	‘Heat pump’ drives gasses from the atmosphere via young natant leaves, petioles to roots and back, via older leaves to the atmosphere	e.g., [34][35][36]
	Nelumbo nucifera	Air, metabolism, Sediment	Pressurized ventilation, influx via laminal stomata of natant leaves through aerenchyma to rhizomes; back from	Leaf lamina with fewer and smaller stomata, leaf central part with larger and denser stomata, which actively regulate the airflow by	[37][38][39]

Plant Group	Taxonomic Group	Source of Gasses	Ventilation Principle	Special Features	Reference
			rhizomes through aerenchyma in petiole through stomata in leaf central part	opening and closing	
Helophytes	*Equisetum* spp.—4 out of 9 have through-flow convection	Air, possibly also metabolism, sediment	Pressurized ventilation, humidity-induced diffusion,	Air moves through stomata through branches, via interconnecting aerenchyma channels in stem and rhizomes, with venting through the previous year's stubble or damaged shoot.	[40][41]
	Phragmites spp.	Air, possibly also metabolism, sediment	Pressurized ventilation, suction via old broken stems (Venturi-effect), air films on leaves when submerged	Via leaves, stems to root system, partly to sediment (ROL), and back to stems, leaves, and atmosphere	[42][43][44][45][46]
	Typha spp.	Air, sediment, possibly metabolism, oxygen in the rhizosphere may be obtained from the decomposition of hydrogen peroxide by catalase	Pressurized ventilation, leaf stomata create inner pressure, air films on leaves when submerged	Air enters through middle-aged leaves, and exits through the oldest ones	[42][47][48][49]
	Oryza sativa	Air films on leaves when submerged	Flow from above-ground parts	Water-repellent leaf surface; air layer up to 25	[50][51][52]

Plant Group	Taxonomic Group	Source of Gasses	Ventilation Principle	Special Features	Reference
			via roots by diffusion, and possibly also by mass flow	µm, large air spaces inside leaves and roots, the porosity of adventitious roots, a barrier in roots to prevent radial O_2 loss from roots	
Species of mangrove forest	*Acrostichum* spp.			All plant parts have large air spaces	[53][54]
	Nypa fruticans		Bases of abscised leaves function as air inlets, by developing a network of lenticels covering the leaf base connected to aerenchyma	“snorkeling palm” leaf bases function up to 4 years after leaf abscission	[55]
	Mangroves		High oxygen pressure in the roots is maintained via ventilation through the lenticels on different root structures connected with aerenchyma	Special structures, i.e., pneumatophores, knee roots, stilt roots, or plant roots, provide ventilation during low tides	[56]
Other wetland species	*Alnus* spp.	Thermo-osmotically driven gas flow	In *Alnus glutinosa,* the flow is from the external atmosphere through the stems to the roots	Thermo-osmotic flow in alder is related to the lenticels in the bark of the stem, stem photosynthesis	[4][36][57][58]

Plant Group	Taxonomic Group	Source of Gasses	Ventilation Principle	Special Features	Reference
	Taxodium distichum		“knees” emerging from the roots to the surface of the water, flooding increases the porosity of roots, stems, and leaves, and enhanced O_2 diffusion to roots.	Snorkeling	[59]
	Syzygium kunstleri		Oxygen transportation occurs through aerenchyma in the root tips, periderm near the root base, and secondary aerenchyma between layers of phellem		[60]

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