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Review

Ventilation Systems in Wetland Plant Species

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Abstract: Molecular oxygen and carbon dioxide may be limited for aquatic plants, but they have various mechanisms for acquiring these gases from the atmosphere, soil, or metabolic processes. The most common adaptations of aquatic plants involve various aerenchymatic structures, which occur in various organs, and enable the throughflow of gases. These gases can be transferred in emergent plants by molecular diffusion, pressurized gas flow, and Venturi-induced convection. In submerged species, the direct exchange of gases between submerged above-ground tissues and water occurs, as well as the transfer of gases via aerenchyma. Photosynthetic O_2 streams to the rhizosphere, while soil CO_2 streams towards leaves where it may be used for photosynthesis. In floating-leaved plants anchored in the anoxic sediment, two strategies have developed. In water lilies, air enters through the stomata of young leaves, and streams through channels towards rhizomes and roots, and back through older leaves, while in lotus, two-way flow in separate air canals in the petioles occurs. In *Nypa* Steck palm, aeration takes place via leaf bases with lenticels. Mangroves solve the problem of oxygen shortage with root structures such as pneumatophores, knee roots, and stilt roots. Some grasses have layers of air on hydrophobic leaf surfaces, which can improve the exchange of gases during submergence. Air spaces in wetland species also facilitate the release of greenhouse gases, with CH_4 and N_2O released from anoxic soil, which has important implications for global warming.

Keywords: metabolic gases; greenhouse gases; aerenchyma; anoxic soil

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 [21–24]. 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. In this review, we summarize the outcomes of research, and point out the similarity, diversity,

and functional features of ventilation systems in various functional groups of wetland plants, and point out their potential effects on the wider environment.

2. Ventilation Mechanisms in Various Wetland Plant Groups

2.1. Submerged Species

In submerged aquatic species, the ventilation system is especially important since these have no direct connection with the atmosphere [26]. Extensive aerenchyma in the stems of all submerged plants that may be lysigenous and schizogenous (Figure 1) enable buoyancy for their flexible stems in water; however, this may limit the distribution of aquatic vascular plants to the depth where hydrostatic pressure does not compress stems [27]. Gases in submerged species come from plant metabolism, water, and sediment. The aerenchyma function as a reservoir for metabolic gases. Hartman and Brown [28], studying gas dynamics in *Elodea canadensis* Michx. and *Ceratophyllum demersum* L., detect a lag between peak values for dissolved oxygen in the surrounding water, and oxygen in the internal atmosphere. This situation is also true of the representatives of the genus *Lobelia* L., *Lilaeopsis* Greene, and *Vallisneria* L., which obtain more than 75% of their CO_2 needs from the sediment [29,30]. However, photosynthesis is important for internal O_2 status and aeration of anoxic sediments [31–33]. Sand-Jensen et al. [34] show that submerged macrophytes release oxygen from their roots during illumination, and at lower rates during darkness. The amounts of oxygen released varies among species from 0.04 to 3.12 μg O_2/mgDM/h; the species *Lobelia dortmanna* is the most effective. This involvement of photosynthesis enables aerobic metabolism of roots, sediment oxygenation due to radial oxygen loss, and improves nutrient uptake from the sediment [26].
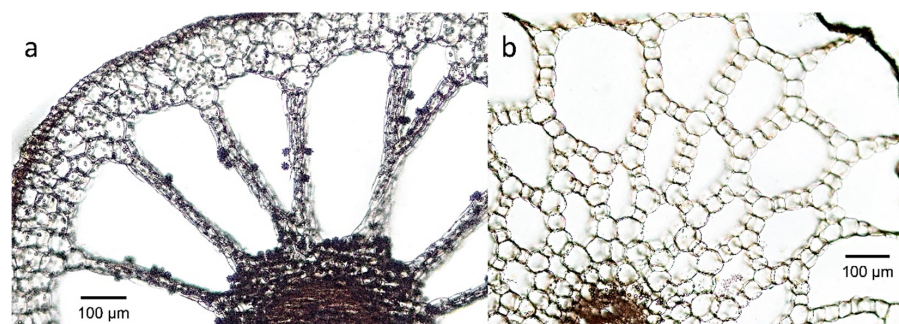

Figure 1. Transection of stems of two submerged species showing different types of aerenchyma; (**a**) lysigenous in *Myriophyllum spicatum* and (**b**) schizogenous in *Potamogeton crispus.* Photo: Matej Holcar.

A few outstanding representatives of submergent species include quillworts, *Isoëtes* L., which are the only surviving genus of a large plant group, distantly related to the clubmosses. This group emerged about 300 million years ago in ephemeral pools and oligotrophic lakes, and later radiated into terrestrial habitats [35]. Species in this group are well-adapted to cold environments, and limited light and carbon dioxide supply [36]. This genus represents the oldest lineage of plants with Crassulacean acid metabolism (CAM) [33].

At least some of species of the genus *Isoëtes* have air canals from the leaves through the periderm to the cortex aerenchyma in the stem [37]. Green [38] compares the air canals and aerenchyma in *Isoëtes* with the corresponding structures in Carboniferous–Permian arborescent lycopsids, such as *Lepidodendron* Stern. spp. The extinct lycopsid swamp trees called *Stigmaria* Stern. have similar air channels in their roots [39].

Most modern species of *Isoëtes* grow in wet environments, and use CAM to fix carbon. Due to the mineralization of organic matter, the CO_2 concentration in sediment is 10–250 times higher than atmospheric equilibrium [40]. Thus, these species uptake sedimentary CO_2 that is transferred via the large gas channels [38], which are present in various *Isoëtes* organs [41] (Figure 2). CO_2 leakage from gas spaces is prevented by the extremely high diffusional resistance of water. However, some *Isoëtes* species have an amphibious

character, and may develop leaves with stomata and switch to C_3 photosynthesis if plant parts emerge into the air from the water [35]. In addition, Pedersen et al. [42,43] show that various isoetids (small, aquatic plants with thick, stiff leaves or stems that form basal rosettes [42]), seagrasses, and rosette-bearing wetland species may have leaves buried in sediments, and their achlorophyllous bases may function as an exit for O_2 to the sediment, and entrance for CO_2 from the sediment [42,43]. This system may also affect the concentrations of gases in aerenchyma and photosynthesis [44].
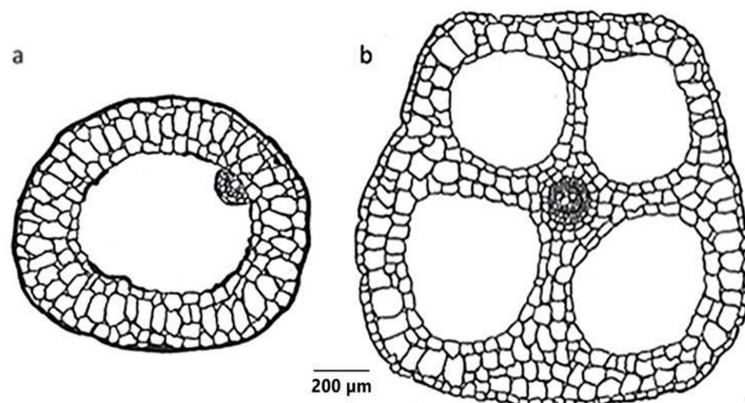

Figure 2. The root (**a**) and leaf (**b**) cross-section of *Isoëtes* L. sp. with large central air spaces. Drawings: Alenka Gaberščik.

2.2. Species with Natant Leaves

The advantage for these species is a direct connection with the atmosphere via natant leaves; however, since some of them grow in water as deep as 3 m [27,45], they need also effective aeration of the anoxic sediment.

Water lilies of the genus *Nymphaea* L. and *Nuphar* Sm. possess well-developed ventilation systems (Figure 3). Air enters through the stomata of young leaves that have just reached the water surface, streams through the channels of long petioles, through rhizomes and roots, and back to the external air through older leaves (Figure 4). This system accelerates O_2 flow from the atmosphere to the roots, and CO_2 and CH_4 flow from the roots to the atmosphere. This remarkable ventilation system has significant physiological and ecological consequences [46]. Laing [10] measures the daily dynamics of internal gas composition in various tissues of *Nuphar advena* (Aiton) W.T. Aiton, and finds a decrease in carbon dioxide and an increase in oxygen during the day, while the opposite is true at night. These findings show the important role of the metabolic process in influencing gas concentrations in various tissues.
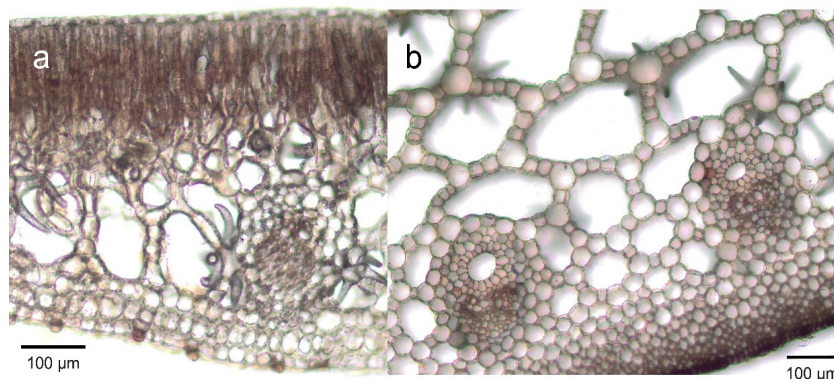

Figure 3. Transection of (**a**) natant leaf and (**b**) petiole of *Nuphar luteum*. Photo: Matej Holcar.

The ventilation is driven by the pressurization of the gas in air spaces of young natant leaves, due to thermo-osmosis of gases during cooling by transpiration [45,46]. Cooling

by transpiration of the upper leaf surface enables a steeper temperature gradient within the leaf, intensifying internal aeration [47]. The leaves are warmed by the sun during the day, and by water in the surrounding environment at night, which enables ventilation at night [48]. This process is also supported by specific morphological features that may differ among species [49]. One important feature is that gas transport through a small opening varies with the dimensions of the opening, depending on whether the gas transport takes place by diffusion or by mass flow. The rate of gas transport by diffusion is proportional to the diameter (or some other linear dimension if the opening or aperture is not circular), and to the difference in concentration of the gas on the two sides of the opening, with the slower movement of heavy vs. light gas molecules.

The rate of mass flow follows Poiseuille's law. The flow rate is proportional to the total pressure gradient between younger and older leaves [5], and the diameter (or corresponding measure) is raised to the fourth power. Therefore, diffusion often dominates in plant parts with small openings, and mass flow when the openings are large [46]. The openings in young leaves are narrow. According to Grosse and Schröder [50], the important openings, in this case, are not the stomata ($\approx$5.6 µm × 2.4 µm), but narrow passages (intercellulars) ($\approx$1 µm) between cells inside the leaves. The oxygen concentration outside the leaves is higher than in the airspaces inside the leaves. This situation is partly because the air inside is diluted by water vapor, and is almost saturated in the intercellular spaces. Therefore, oxygen diffuses into the young leaves, and the total gas pressure there exceeds that of the external air. As the passages to the higher-oxygen external air are so narrow, little air escapes from the young leaves to the external atmosphere. It is easier for air to flow through the wider "pipes" in the petioles down to the rhizomes and roots, where oxygen is consumed by respiration. The rest of the air streams out to the atmosphere through the older leaves, where the passages are wider than in the younger leaves.

The streaming of air in the yellow water lily, *Nuphar luteum* (L.) Sm. is described not only by Schröder et al. [51], but also in a series of articles by John Dacey and coworkers, and the results are summarized by Dacey [46]. Richards et al. [45] perform similar studies on *Nymphaea odorata* Aiton. In the case of *N. luteum*, the network of internal gas spaces enables a pressurized flow-through system, that directs air rich with oxygen from young leaves to the underground organs, and with air rich in carbon dioxide back via the older emergent leaves to the atmosphere [46]. Konnerup et al. [52] compare pressure differences and convective gas flow in twenty species of tropical angiosperms (Table 1). The highest flow rates are found for *Nymphaea rubra* Roxb. and *Nelumbo nucifera* Gaertn.. Some species achieving large pressure differences have low flow rates. The two *Eleocharis* R. Br. species differ remarkably with respect to the pressure differences produced.

Table 1. Comparison of pressure differences and convective gas flow in twenty species of tropical angiosperms (adapted from Konnerup et al. [52]).

Plant	ΔP(Pa)	Air Flow (mL/min)	Plant	ΔP(Pa)	Air Flow (mL/min)
Monocotyledons			**Dicotyledons**		
Cyperaceae			*Nymphaeaceae*		
Cyperus compactus Retz.	20	0.60	*Nymphaea rubra* Roxb.	236	140
Cyperus digitatus Roxb.	14	1.29	*Nymphaea nouchali* Burm. f.	116	15.2
Eleocharis dulcis (Burm. f.) Trin. ex Hensch	628	11.9	*Nelumbonaceae*		
Eleocharis acutangula Schultes	15	0.10	*Nelumbo nucifera* Gaertn.	295	288
Scirpus grossus L. f.	3	0.22	*Menyanthaceae*		
Scirpus littoralis Shrad.	83	0.39	*Nymphoides indica* (L.) Kuntze	485	36
Scleria poaeformis Retz.	22	1.11	*Convolvulaceae*		
Poaceae			*Ipomoea aquatica* Forssk.	3	0.18
Phragmites vallatoria (L.) Veldkamp	482	1.59			
Urochloa mutica (Forsk T.Q. Nguyen	11	0.09			
Hymenachne acutigluma (Steud.) Gilliland	141	0.55			

Table 1. *Cont.*

Plant	ΔP(Pa)	Air Flow (mL/min)	Plant	ΔP(Pa)	Air Flow (mL/min)
Monocotyledons			**Dicotyledons**		
Oryza rufipogon Griff.	23	0.32			
Leersia hexandra Swartz.	62	0.15			
Pontederiaceae					
Eichhornia crassipes (Mart.) Solms	8	0.12			
Araceae					
Colocasia esculenta (L.) Schott	3	0.10			i
Limnocharitaceae					
Limnocharis flava (L.) Buchenau	6	0.81			

Lotus (*N. nucifera*) is not closely related to water lilies, but has a similar growth form, and ventilates its organs in oxygen-deficient sediment by streaming air. The thermo-osmotic gas transport depends on a temperature differential between the air in the aerenchyma of the leaves and the surrounding atmosphere [53]. Stomata located in the central parts of leaves have an important function in the active regulation of airflow [54]. These central stomata are three times larger than stomata of the other part of the leaf lamina, and control the gas release by opening and closing [55]. Lotus differs from other groups because each petiole has separate channels for descending and ascending air [53,56]. Air is, thus, transferred from leaves, down through petioles, rhizomes, and then back to the atmosphere through large stomata [54] (Figure 4).
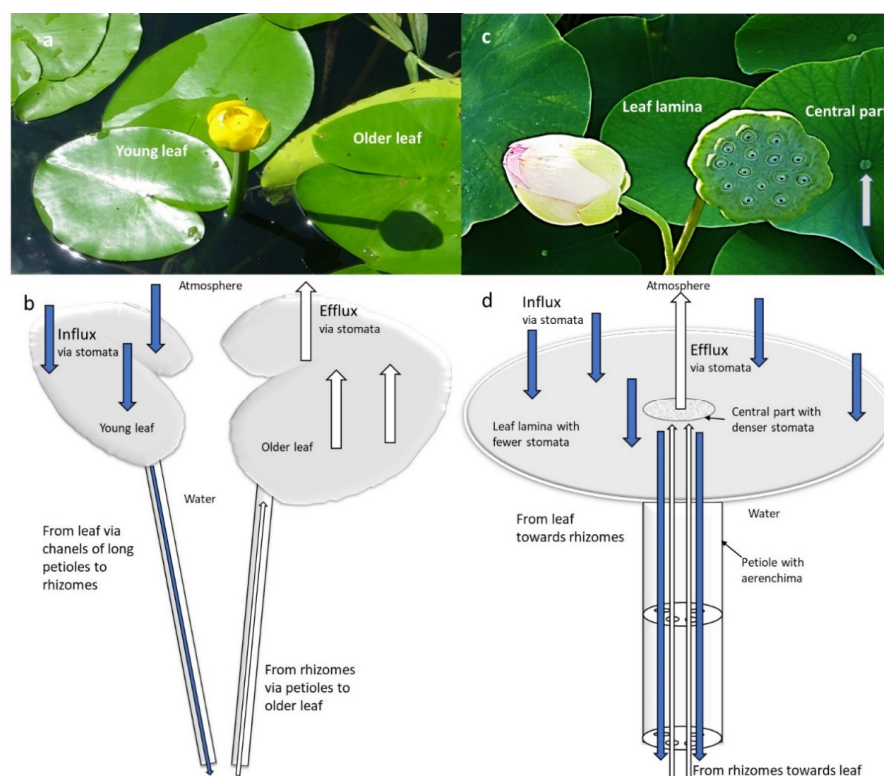

Figure 4. Ventilation system in *Nuphar luteum* (**a**,**b**) *Nelumbo nucifera* (**b**,**c**). (**a**) *N. luteum* young and older leaves; (**b**) the scheme of ventilation system where arrows shows that air from atmosphere enters via young leaves through stems with aerenchyma to rhizomes, and via older leaves back to the atmosphere; (**c**) *N. nucifera* leaves with visible central part with denser stomata; (**d**) the scheme of ventilation system with arrows indicating the direction of flow (blue—influx from atmosphere via stomata in leaf lamina through aerenchyma in leaf and petiole to aerenchyma in rhizomes; light grey—efflux from rhizomes through aerenchyma in petiole to the central part of the lamina, and finally to atmosphere). Photos and drawings: Alenka Gaberščik.

Polygonum amphibium L. is an amphibious plant with natant leaves. and thrives in water up to 2 m, with its hollow stems that enable the aeration of underground organs (Figure 5). However, gases trapped in the aerenchyma may also benefit the photosynthesis and lower photorespiration rate [57], due to changes in the ratio of internal CO_2/O_2 concentrations.
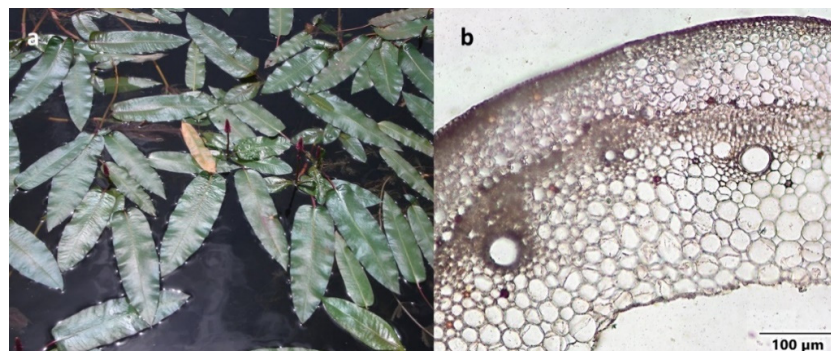

Figure 5. *Polygonum amphibium* L. f. natans; (**a**) natant leaves and (**b**) section of a hollow stem. Photo: Matej Holcar.

2.3. Helophytes

Helophytes live anchored in water-saturated sediment, while their above-ground organs are usually in air. Most of them have well-developed aerenchyma [1]. When leaves of different helophytes are submerged, they produce gas films at the leaf surface to improve photosynthesis. Colmer and Pedersen [58] show that *Phalaris arundinacea*, *Phragmites australis*, and *Typha latifolia* form gas films on both leaf sides, *Glyceria maxima* form gas films on the adaxial only, and *Acorus calamus* and *S. emersum* do not form gas films.

Rhizomes and stems of wetland representatives of horsetail (*Equisetum*) have large canals [59]. Internal ventilation systems differ among *Equisetum* species, and are best developed in the great horsetail, *E. telmateia* Ehrh. In this species, an airflow of 120 mL/min and a wind speed of 10 cm/s were measured [60], and this flow may be evaporation-driven. Air enters via stomata on branches, passes to substomatal cavities, and then via intercellulars to aerenchyma channels in branches, to the main stem, rhizome, and cortical intercellular spaces of roots [61].

Methane release from *E. fluviatile* L. stands suggests that this species lacks a pressurized ventilation system because no diurnal changes are detected [59]. In addition, no or very low airflow is measured in this species, even though it thrives in deep water [62]. The power for the airflow comes from the evaporation of water inside the plant. If the air surrounding the plant is saturated with water vapor, the flow stops, and it is sped up by wind that evaporates water vapor from the plant surface [61]. For example, *E. palustre* L. maintains an inner mass flow of up to 13 mL/min (Figure 6). No flow is found in *E. sylvaticum* L. or *E. arvense* L., perhaps because these species lack air channels in the branches [60]. These species only rely on diffusion for oxygen provision to their below-ground parts, which is facilitated in environments of well-aerated soil.

Figure 6. The cross-section of marsh horsetail (*Equisetum palustre* L.) stem. Photo Matej Holcar.

Common reed and other *Phragmites* species frequently grow in water-saturated anoxic soil. *Phragmites* are ventilated by "compressed air" in a similar way to water lilies and lotus [63,64], but additional aeration may be obtained by suction from old broken reeds when the wind is blowing over them, a Venturi-effect [65], and also by oxygen from photosynthesis. The oxygen pressure in the rhizomes rises rapidly in the morning, peaks near midday, and declines slowly to a minimum at 6 am [66]. Three factors probably contribute to the midday peak including light (photosynthesis), temperature, and the difference in water vapor pressure between the external air and the intercellulars. External humidity is at its lowest in the early afternoon, when humidity in leaf intercellulars (due to insolation) is highest. Oxygen from roots is released in the nearby rhizosphere, which is known as radial oxygen loss [67], and oxidizes different toxic substances produced in anoxic soils that can harm soil biocenosis. This situation is also the case in *Phragmites australis* (Cav.) Trin. ex Steud, where the aeration system increases rhizosphere oxygenation and lowers toxic sulfide concentrations [68]. Some species prevent excessive oxygen loss from roots by forming a barrier in their epidermis, exodermis, or subepidermal layers [69].

Konnerup et al. [52] also find convective ventilation in *P. vallatoria* (L.) Veldkamp, and eight other wetland plant species. The only other monocotyledon species for which a similar pressure difference is found is *Eleocharis dulcis* (Burm. f.) Trin. ex Hensch (*Cyperaceae*), but the flow rate is lower.

In *Scirpus lacustris* (L.), sediment-derived CO_2 in aerenchyma (Figure 7) presents an important source of inorganic carbon used for photosynthesis in submerged green stems, especially before they reach the water surface [70]. In this species, leaves are usually reduced, however, leaf blades up to 100 cm long can develop under water [71].
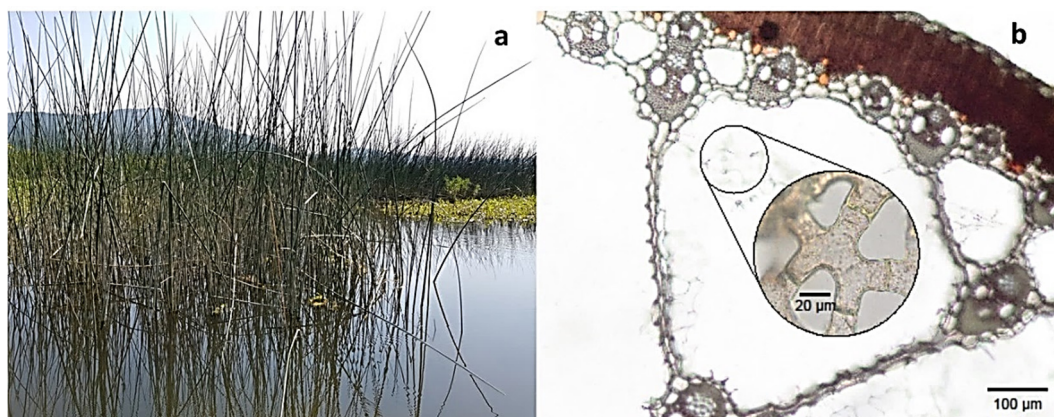

Figure 7. (**a**) Leafless *Schoenus lacustris* stems; (**b**) transection of stem with lacunae filled with thin-wall aerenchymal parenchyma. The magnification of parenchymatic cells is shown in the magnified circular insert. Photo: Matej Holcar.

In plants with reduced pressurized ventilation, the growth rate is diminished, possibly due to reduced mineral uptake and availability, a poorly developed root system, or impaired root function [63]. Studies in the USA reveal differences in function between native and non-native *P. australis* types. Ventilation efficiency is 300% higher per unit area for non-native types in comparison to native types, due to the increased oxidation of the rhizosphere [72].

The cattails (*Typha* L., Figure 8) are phylogenetically related to reeds. *Typhaceae* and reeds ventilate their below-ground parts in similar ways. An air stream of 8 mL/min per leaf is observed for *T. latifolia*, and 3.5 mL/min for *T. angustifolia* L. [73]; however, some leaves can function with influx or efflux in changing environments. A flux of 11 mL/min is observed, compared to a maximum of 60 mL/min through a water lily petiole [46]. Contrary to the situation in lotus, for *Typha*, the stomata constitute the pressure-generating pores [74]. The stomata are most effective for creating an inner pressure when they are partially closed, and provide almost no pressure when they are open to 0.3 μm wide. Air enters through middle-aged leaves, and exits through the oldest ones [73].

Figure 8. Cattail, *Typha* L. sp. Top left, shoots seen from below. Top right, a cross-section of a leaf with large air spaces, which are connected to air spaces throughout the plant. Bottom, rhizomes. Reproduced with permission from Bansal et al. [75].

Duarte et al. [76] claim that oxygen in the root area is not obtained exclusively from the atmosphere or photosynthesis in the leaves, but, in addition, oxygen in the root is supplemented by the decomposition of hydrogen peroxide by catalase. The study of Laing [10] reveals that the shading of *T. latifolia* has little effect on gas composition in air spaces of the submerged stolon; however, a slight decrease in oxygen concentration is observed in leaves. In hypoxic growth conditions, various *Typha* species behave in diverse ways; *T. angustifolia* increases its root porosity and root mass ratio, while *T. latifolia* increases its root diameter [77].

Rice (*Oryza sativa* L.) can grow in deep water ([78]). Under complete submergence, rice leaves and stems elongate significantly to reach the air–water interface; however, this may exhaust its energy reserves, and cause death if deep water persists for a long time [79]. Rice mitigates waterlogging stress by forming lysigenous aerenchyma and a barrier to prevent radial O_2 loss from roots, in order to supply O_2 to the root tip [80]. However, it differs from the species described above in the transport of air. Air is partly transported through a layer of air on the surface of the leaves. At least in the majority of rice cultivars, the leaves are water-repellent on both sides. A layer of air is formed on these leaves, up to 25 μm thick [81], and with a volume that is 44% of that of the leaf (Figure 9). Gas molecules in the thin layer are transported forward by diffusion at a greater pace than if they could move in all directions, but there may also be some mass flow. A layer of air at the leaf surface also contributes to the tolerance against submergence in the case of *Spartina anglica* C.E. Hubb. [44]. The floating leaves of the grass *Glyceria fluitans* (L.) R. Br. have a lower cuticle resistance for dark O_2 uptake on the wettable abaxial side, compared to the hydrophobic adaxial side [82].

Figure 9. Rice (*Oryza longistaminata* A. Chev. & Roehr.) leaves protrude through the water surface, covered below the water surface by a layer of air. Photo by Ole Pedersen, University of Copenhagen. Cf. the cover of Science Vol. 228, No. 4697, 19 April 1985.

Rice also has large air spaces inside both leaves and roots, while the transition between shoot and root provides greater resistance to flow [83]. In rice, aerenchyma forms constitutively under aerobic conditions, while their formation is further induced under oxygen-deficient conditions [84]. Aerenchyma formation is promoted by ethylene production in adventitious roots [8] and in internodes, and this aerenchyma formation is mediated by reactive oxygen species (ROS) [85]. Little is known about the signaling and molecular regulatory mechanisms of ROS during plant-programmed cell death [86]. In the case of the fast-elongating 'Arborio Precoce' variety, ethylene controls aerenchyma formation, while in the variety 'FR13A', ROS accumulation plays an important role [87]. The study shows that the SNORKEL1 and SNORKEL2 genes that promote internode elongation are exclusively present in the genomes of deep-water rice [88].

Under O_2 deficiency, the porosity of adventitious roots enhances O_2 diffusion towards the root tip [89]. Flow takes place because the respiring plant replaces oxygen with carbon dioxide, which at pH = 7 and 25 °C has a solubility in water that is 140 times that of oxygen [78]. The study of Colmer and Pedersen [90] reveals that the dynamics in pO_2 within shoots and roots of submerged plants are related to periods of darkness and light, which supports the connection of underwater photosynthesis and internal aeration.

In *Pontederia cordata* L., the innermost layer of ground meristem in adventitious roots forms the endodermis and aerenchymatous cortex [91]. The comparison of pO_2 in submerged roots of *Rumex palustris* Sm. (flood-tolerant) and *R. acetosa* L. (flood-intolerant) reveals that roots of the former remain oxic, while in the latter, root pO_2 drops significantly (to 4.6 and 0.8 kPa, respectively) [92].

2.4. Mangrove Forest

Ferns of the genus *Acrostichum* L. (closely related to *Ceratopteris*) live rooted in mangrove vegetation and other settings [93]. All parts of these plants have large air spaces, including the roots. Aerenchyma are found in the roots of *Acrostichum* fossils, which suggests a coastal paleoenvironment [94]. Fonini et al. [95] also report large aerenchyma in the leaves of species *A. danaeifolium* Langsd. & Fisch., which is a feature endemic to mangrove.

A species of palm, *Nypa fruticans* Wurmb. or "snorkeling palm" adapted to life in mangrove forests; usually only the leaves appear above the water surface. These leaves eventually abscise when aging, but the leaf bases remain, and function as air inlets by developing a network of lenticels covering the leaf base [96]. These lenticels are connected with expansigenous aerenchyma [96]. The lenticels allow gases through, but prevent the entry of fluid water. The air spaces of the lenticels are connected to air spaces via the underwater stem to the roots. The first- and second-order roots have a small central stele surrounded by a wide zone of cortex with very spacious air channels, which develop after the separation and dissolution of cells. The mature crown may contain 6 to 8 living leaves, and 12 to 15 bulbous leaf bases at a time [97]. These leaf bases can function for up to 4 years after leaf abscission [96].

The main constituent of mangrove forests includes various types of mangrove species, which are not all closely related. Various mangrove species developed a variety of unique adaptations [98]. Most species possess structures, such as pneumatophores, knee roots, or stilt roots, which provide ventilation during low tides [99]. Studies by Scholander et al. [100] reveal that high oxygen pressure in the roots of *Rhizophora* L. is maintained via ventilation through the lenticels of the stilt roots. The cortex of *Rhizophora* roots have interconnected schizogenous intercellular spaces, extending to within 150 μm of the tip [101].

Pneumatophores act as "snorkels" from the roots of *Sonneratia apetala* Banks (Figure 10). Pneumatophores have numerous lenticels connected with aerenchyma; however, the pneumatophore development phase significantly affects the volume of gas spaces, since young pneumatophores have a less-developed lacunose cortex, in comparison to mature pneumatophores [98]. In *S. alba* Sm., root porosity in different root types ranges from 0 to 60%. Cable roots and pneumatophores have the highest ratio of aerenchyma per area (50–60%) [101]. The changes in cortex cells with developing gas spaces suggests schizogenous and lyzogenous formation of aerenchyma [102].

Figure 10. Pneumatophores of the mangrove tree *Sonneratia apetala* Buch. Ham. From Zhang et al. [103]. Creative Attribution license.

Comparing mangrove species belonging to various orders, Cheng et al. [104,105] find that the more air spaces the roots possesses, the greater the flooding tolerance. Curran et al. [106] conclude that *Avicennia marina* (Forsk.) Vierh. does not need airflow because the diffusion of oxygen satisfies the oxygen requirement. Oxygen enters the pneumatophores of this species through lenticels and "horizontal structures" on the pneumatophores [107]. The volume of gas spaces determined in the roots of this species is 40–50% [108].

2.5. Other Wetland Species

Baldcypress (*Taxodium distichum* (L.) Rich) is a conifer in the south–east of the USA, which can grow under both very wet and dry conditions. Growing in water, *T. distichum* develops "knees" emerging from the roots, which may be involved in oxygen transfer (Figure 11) and carbohydrate storage [109]. Under root and knee submergence, internal O_2 concentrations are significantly higher than during drawdown [110]. The knees do not possess gas conduits, so Rogers [109] concludes that knees serve to aerate the phloem in the inner bark for the oxygen requirements of the phloem, and downward conduction of oxygen dissolved in the phloem sap. Wang and Cao [111] report that flooding in *T. distichum* increases the porosity of the roots, stems, and leaves and, consequently, enhances O_2 diffusion to roots.

Figure 11. "Knees" emerging from the roots of baldcypress, *Taxodium distichum* (L.) Rich. in Arkansas, USA. From Middleton [112]. CC BY 4.0 license.

Some tree species in wetlands develop adventitious roots from the trunk during the rainy season, as an adaptation to the flooded environment. In *Syzygium kunstleri* (King) Bahadur and R.C. Gaur that is native to Borneo and Malaya, oxygen transportation occurs through aerenchyma in the root tips, periderm near the root base, and secondary aerenchyma between layers of phellem [113].

The roots of species colonizing flood forests and riparian zones are often subjected to water-saturated soil. Schröder [51] and Grosse and Schröder [4,50] find a thermo-osmotically driven gas flow in *Alnus glutinosa* (L.) Gaertn. from the external air, through the stems to the roots. A temperature difference of up to 3.6 degrees exists in other *Alnus* Mill. species between the intercellular spaces and the external air [114]. As the temperature difference increases from 0.6 to 3.6 °C, due to increasing light (from 50 to 200 μmol m^{-2} s^{-1}), the pressure difference between the external air and the intercellular spaces in the stem increases from 5 to 17 Pa. An efficient thermo-osmosis process needs a narrow passage,

comparable in width to the mean free path lengths of the gas molecules (ca. 0.1 µm), between two compartments of different temperatures. However, some pressurization is possible with larger pores [115]. Details of thermo-osmosis of gases are provided by Denbigh [116], and Denbigh and Raumann [117]. In short, the pressures p1 and p2, which can develop in two compartments (designated 1 and 2), are determined by the equation:

$$\ln\left(\frac{p1}{p2}\right) = K_*\left(\frac{1}{T1} - \frac{1}{T2}\right)$$

where T1 and T2 are the absolute temperatures of the two compartments, and K a constant.

The constrictions in the pathway that are needed for the development of thermo-osmotic gas flow in alder are related to the lenticels in the bark of the stem [118,119]. Gas flows from the colder external atmosphere to the warmer intercellular spaces.

In contrast, Armstrong and Armstrong [120] use *A. glutinosa* as an experimental species, and find that the thermo-osmotic gas flow is incompatible with the species plant anatomy, and so claim that roots are supplied with oxygen produced by chlorophyll-containing stems. The apparent discrepancy in the results of Armstrong and Armstrong vs. Grosse's group may be due to a difference in the age of the plants used by the two research groups, or to differences in submergence times. But the experiments by Dittert et al. [119] offer another explanation. They find that under experimental conditions, when the temperature of the trunk is kept above the temperature of the air, thermo-osmotic gas transport takes place, while under natural conditions (in Germany), there is only transport by diffusion, at all times of the year. Batzli and Dawson [121] find that in *Alnus rubra* Bong., lenticels develop (in this case on roots and root nodules) after 50 days of flooding.

3. 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 2). 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 [122]. Bedoya and Madrinán [123], 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 [124]. *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 [125].

Table 2. 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	[38,44]
	Angiosperms	Water, metabolism, Sediment	Diffusion	Metabolic gasses trapped in aerenchyma	[29,31]

Table 2. *Cont.*

Plant Group	Taxonomic Group	Source of Gasses	Ventilation Principle	Special Features	Reference
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., [45,48,51]
	Nelumbo nucifera	Air, metabolism, Sediment	Pressurized ventilation, influx via laminal stomata of natant leaves through aerenchyma to rhizomes; back from rhizomes through aerenchyma in petiole through stomata in leaf central part	Leaf lamina with fewer and smaller stomata, leaf central part with larger and denser stomata, which actively regulate the airflow by opening and closing	[53–55]
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.	[60,61]
	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	[58,63–65,126]
	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	[58,73,74,76]
	Oryza sativa	Air films on leaves when submerged	Flow from above-ground parts via roots by diffusion, and possibly also by mass flow	Water-repellent leaf surface; air layer up to 25 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	[81,83,89]
Species of mangrove forest	*Acrostichum* spp.			All plant parts have large air spaces	[94,95]
	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	[96]
	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	[99]

Table 2. *Cont.*

Plant Group	Taxonomic Group	Source of Gasses	Ventilation Principle	Special Features	Reference
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	[4,51,120,127]
	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	[109]
	Syzygium kunstleri		Oxygen transportation occurs through aerenchyma in the root tips, periderm near the root base, and secondary aerenchyma between layers of phellem		[113]

Most species use aerenchyma as a ventilation path, and as a reservoir for gases originating from the atmosphere, soil, and metabolic processes (e.g., respiration, photorespiration, and photosynthesis). The differences among groups are related either to specific environmental conditions (e.g., emergence, submergence), to specific species anatomy, as is the case for the lotus, or to metabolic processes and properties related to their growth form (e.g., emergent, submerged, floating-leaved, rosette, woody plants).

4. Plant Role in Emission of Greenhouse Gases

Ventilation systems are also important in the emission of greenhouse gases. We concentrate on methane (CH_4), although nitrous oxide (N_2O) is also important. Although the global warming potential (GWP) of methane is much greater than that of nitrous oxide over brief time intervals, nitrous oxide has about twice the warming potential of methane at a time horizon of 100 years (IPPC 2013), because it persists longer in the atmosphere. This section focuses on the role of plants rooted in water-saturated soils in the emission of greenhouse gases. The production of CH_4 in wetlands depends on carbon availability, soil redox potential, availability of O_2, pH, and temperature, and it is released from wetland soils by ebullition, convection, diffusion, and ventilation [128,129]. Thus, CH_4 emissions depend on the plant species present, and their abundance [130–132].

A key role in greenhouse gas emission is also played by different growth forms of plants. On one hand, Kosten et al. [133] find that free-floating plants may reduce methane emissions. On the other hand, some floating-leaved species contribute significantly to methane emission, including *N. odorata* [20], *N. nucifera* [19], and *N. luteum* L. [20], and helophytes such as *Juncus effusus* L. [134], *Spartina anglica* and *P. australis* [135,136], *P. mauritianus* Kunth [137], *T. latifolia* [137], *Typha* spp. [20,130], and *Cyperus papyrus* L. [137,138]. In areas colonized by *P. australis* and *S. lacustris*, methane is emitted exclusively by plant-mediated transport, with the highest emission rates at daytime, and emission peaks following sunrise [139].

The effects of aquatic plants on methane emission are complex [140]. Their dead and decaying remains provide the raw material for methane production, and their aerenchyma and gas canals facilitate the transport of methane to the atmosphere. At the same time, the aeration of their rhizospheres, and their methane-oxidizing microorganisms, decrease the amount of methane that escapes into the atmosphere [141]. In rice, two mutants with decreased root aerenchyma cause 70% less methane emission to the atmosphere than the wild type, while the oxygen transport is only reduced by 50% [142]. However, it is unlikely that such mutants will be a practical solution to the very high contribution of rice paddies to the greenhouse gas budget.

Wetland trees contribute to methane emission, while rainforest trees may function as sinks [143], except when flooded [144,145]. In *Phragmites* spp. [136], pressurized gas flow is important in emission; in the case of these species, the population of methane-producing microbes in the rhizosphere may be the most crucial factor. The relative importance of these factors is discussed by Laanbroek [146].

5. Conclusions

Ventilation in different groups of wetland plants that thrive in oxygen-deficient soils is related to aerenchyma as a ventilation path; however, the mechanisms may differ significantly. This diversity is a consequence of (1) phylogeny, as waterlogging presents an environmental filter that excludes certain species; (2) specific environmental conditions in plant/species habitat; (3) specific morphological adaptations at plant/species level (as is the case for water lily and lotus); (4) growth form (e.g., emergent, submerged, floating-leaved, rosette, woody plants) is related to plant medium (air, water, or both); and (5) metabolic processes (photosynthesis, respiration, photorespiration) that may act as a source or a sink of gases. These diverse structures and processes are related to ventilation support, photosynthesis, and respiration processes. Along with plant ventilation, they contribute to the oxygenation of otherwise anoxic wetland soils by radial oxygen loss from roots to the rhizosphere, and, thus, its detoxification, and also facilitate the release of greenhouse gases from these soils, which sets off a cascade of environmental consequences.

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References

1. Jackson, M.B. Ethylene and Responses of Plants to Soil Waterlogging and Submergence. *Annu. Rev. Plant Physiol.* **1985**, *36*, 145–174. [CrossRef]
2. Voesenek, L.A.C.J.; Colmer, T.D.; Pierik, R.; Millenaar, F.F.; Peeters, A.J.M. How Plants Cope with Complete Submergence. *New Phytol.* **2006**, *170*, 213–226. [CrossRef] [PubMed]
3. Janauer, G.; Germ, M.; Kuhar, U.; Gaberščik, A. Ecology of Aquatic Macrophytes and Their Role in Running Waters. In *Macrophytes of the River Danube Basin*; Janauer, G., Gaberščik, A., Květ, J., Germ, M., Exler, N., Eds.; Academia, Živá Příroda: Prague, Czech Republic, 2018; pp. 13–33. ISBN 9788020027436.
4. Große, W.; Schröder, P. Oxygen Supply of Roots by Gas Transport in Alder-Trees. *Z. Für Nat. C* **1984**, *39*, 1186–1188. [CrossRef]
5. Colmer, T.D. Long-Distance Transport of Gases in Plants: A Perspective on Internal Aeration and Radial Oxygen Loss from Roots. *Plant Cell Environ.* **2003**, *26*, 17–36. [CrossRef]
6. Mitsch, W.J.; Gosselink, J.G. *Wetlands: Human History, Use, and Science*, 4th ed.; Wiley: Hoboken, NJ, USA, 2007; ISBN 9780471699675.
7. Jackson, M.B.; Armstrong, W. Formation of Aerenchyma and the Processes of Plant Ventilation in Relation to Soil Flooding and Submergence. *Plant Biol.* **1999**, *1*, 274–287. [CrossRef]
8. Justin, S.H.F.W.; Armstrong, W. The Anatomical Characteristics of Roots and Plant Response to Soil Flooding. *New Phytol.* **1987**, *106*, 465–495. [CrossRef]
9. Evans, D.E. Aerenchyma Formation. *New Phytol.* **2004**, *161*, 35–49. [CrossRef]
10. Laing, H.E. The Composition of the Internal Atmosphere of Nuphar Advenum and Other Water Plants. *Am. J. Bot.* **1940**, *27*, 861–868. [CrossRef]
11. Jung, J.; Lee, S.C.; Choi, H.-K. Anatomical Patterns of Aerenchyma in Aquatic and Wetland Plants. *J. Plant Biol.* **2008**, *51*, 428–439. [CrossRef]

12. Bailey-Serres, J.; Voesenek, L.A. Life in the Balance: A Signaling Network Controlling Survival of Flooding. *Curr. Opin. Plant Biol.* **2010**, *13*, 489–494. [CrossRef]

13. Takahashi, H.; Yamauchi, T.; Colmer, T.D.; Nakazono, M. Aerenchyma Formation in Plants. In *Plant Cell Monographs*; Springer: Berlin/Heidelberg, Germany, 2014; Volume 21, pp. 247–265.

14. Doležal, J.; Kučerová, A.; Jandová, V.; Klimeš, A.; Říha, P.; Adamec, L.; Schweingruber, F.H. Anatomical Adaptations in Aquatic and Wetland Dicot Plants: Disentangling the Environmental, Morphological and Evolutionary Signals. *Environ. Exp. Bot.* **2021**, *187*, 104495. [CrossRef]

15. Laan, P.; Berrevoets, M.J.; Lythe, S.; Armstrong, W.; Blom, C.W.P.M. Root Morphology and Aerenchyma Formation as Indicators of the Flood-Tolerance of Rumex Species. *J. Ecol.* **1989**, *77*, 693–703. [CrossRef]

16. Larcher, W. *Physiological Plant Ecology: Ecophysiology and Stress Physiology of Functional Groups*, 4th ed.; Springer: Berlin, Germany, 2003.

17. Jia, Y.; Huang, H.; Chen, Z.; Zhu, Y.-G. Arsenic Uptake by Rice Is Influenced by Microbe-Mediated Arsenic Redox Changes in the Rhizosphere. *Environ. Sci. Technol.* **2014**, *48*, 1001–1007. [CrossRef]

18. Smith, K.E.; Luna, T.O. Radial Oxygen Loss in Wetland Plants: Potential Impacts on Remediation of Contaminated Sediments. *J. Environ. Eng.* **2013**, *139*, 496–501. [CrossRef]

19. Riya, S.; Sun, H.; Furuhata, H.; Shimamura, M.; Nasu, H.; Imano, R.; Zhou, S.; Hosomi, M. Role of Leaves in Methane Emission from Sacred Lotus (*Nelumbo nucifera*). *Aquat. Bot.* **2020**, *163*, 103203. [CrossRef]

20. Villa, J.A.; Ju, Y.; Stephen, T.; Rey-Sanchez, C.; Wrighton, K.C.; Bohrer, G. Plant-mediated Methane Transport in Emergent and Floating-leaved Species of a Temperate Freshwater Mineral-soil Wetland. *Limnol. Oceanogr.* **2020**, *65*, 1635–1650. [CrossRef]

21. Caraco, N.F.; Cole, J.J. Contrasting Impacts of a Native and Alien Macrophyte on Dissolved Oxygen in a Large River. *Ecol. Appl.* **2002**, *12*, 1496. [CrossRef]

22. Carpenter, S.R.; Lodge, D.M. Effects of Submersed Macrophytes on Ecosystem Processes. *Aquat. Bot.* **1986**, *26*, 341–370. [CrossRef]

23. Goodwin, K.; Caraco, N.; Cole, J. Temporal Dynamics of Dissolved Oxygen in a Floatingleaved Macrophyte Bed. *Freshw. Biol.* **2008**, *53*, 1632–1641. [CrossRef]

24. Horvat, B.; Urbanc-Berčič, O.; Gaberščik, A. Water Quality and Macrophyte Community Changes in the Komarnik Accumulation Lake (Slovenia). In *Wastewater Treatment, Plant Dynamics and Management in Constructed and Natural Wetlands*; Springer: Dordrecht, The Netherlands, 2008; pp. 13–22.

25. Raven, J.A. Into the Voids: The Distribution, Function, Development and Maintenance of Gas Spaces in Plants. *Ann. Bot. Co.* **1996**, *78*, 137–142. [CrossRef]

26. Rascio, N. The Underwater Life of Secondarily Aquatic Plants: Some Problems and Solutions. *Crit. Rev. Plant Sci.* **2002**, *21*, 401–427. [CrossRef]

27. Sculthorpe, C.D. *The Biology of Aquatic Vascular Plants*; American Association for the Advancement of Science: London, UK, 1967.

28. Hartman, R.T.; Brown, D.L. Changes in Internal Atmosphere of Submersed Vascular Hydrophytes in Relation to Photosynthesis. *Ecology* **1967**, *48*, 252–258. [CrossRef]

29. Winkel, A.; Borum, J. Use of Sediment CO_2 by Submersed Rooted Plants. *Ann. Bot.* **2009**, *103*, 1015–1023. [CrossRef] [PubMed]

30. Madsen, T.v.; Olesen, B.; Bagger, J. Carbon Acquisition and Carbon Dynamics by Aquatic Isoetids. *Aquat. Bot.* **2002**, *73*, 351–371. [CrossRef]

31. Borum, J.; Pedersen, O.; Greve, T.M.; Frankovich, T.A.; Zieman, J.C.; Fourqurean, J.W.; Madden, C.J. The Potential Role of Plant Oxygen and Sulphide Dynamics in Die-off Events of the Tropical Seagrass, Thalassia Testudinum. *J. Ecol.* **2005**, *93*, 148–158. [CrossRef]

32. Sand-Jensen, K.; Pedersen, O.; Binzer, T.; Borum, J. Contrasting Oxygen Dynamics in the Freshwater Isoetid Lobelia Dortmanna and the Marine Seagrass Zostera Marina. *Ann. Bot.* **2005**, *96*, 613–623. [CrossRef]

33. Pedersen, O.; Rich, S.M.; Pulido, C.; Cawthray, G.R.; Colmer, T.D. Crassulacean Acid Metabolism Enhances Underwater Photosynthesis and Diminishes Photorespiration in the Aquatic Plant Isoetes Australis. *New Phytol.* **2011**, *190*, 332–339. [CrossRef]

34. Sand-Jensen, K.; Prahl, C.; Stokholm, H. Oxygen Release from Roots of Submerged Aquatic Macrophytes. *Oikos* **1982**, *38*, 349–354. [CrossRef]

35. Keeley, J.E. CAM Photosynthesis in Submerged Aquatic Plants. *Bot. Rev.* **1998**, *64*, 121–175. [CrossRef]

36. Břízová, E. Quillwort (Isoëtes), a Mysterious Plant from the Czech Republic. *Acta Mus. Nat. Pragae Ser. B Hist. Nat.* **2011**, *67*, 25–34.

37. Green, W.A. The Parichnos Problem and the Function of Aerenchyma in the Lycopsida. *Bull. Peabody Mus. Nat. Hist.* **2014**, *55*, 191–200. [CrossRef]

38. Green, W.A. The Function of the Aerenchyma in Arborescent Lycopsids: Evidence of an Unfamiliar Metabolic Strategy. *Proc. R. Soc. B Biol. Sci.* **2010**, *277*, 2257–2267. [CrossRef] [PubMed]

39. Breecker, D.O.; Royer, D.L. The Pedogenic Formation of Coal Balls by CO_2 Degassing through the Rootlets of Arborescent Lycopsids. *Am. J. Sci.* **2019**, *319*, 529–548. [CrossRef]

40. Pedersen, O.; Sand-Jensen, K.; Revsbech, N.P. Diel Pulses of O_2 and CO_2 in Sandy Lake Sediments Inhabited by Lobelia Dortmanna. *Ecology* **1995**, *76*, 1536–1545. [CrossRef]

41. Smits, A.J.M.; Laan, P.; Thier, R.H.; van der Velde, G. Root Aerenchyma, Oxygen Leakage Patterns and Alcoholic Fermentation Ability of the Roots of Some Nymphaeid and Isoetid Macrophytes in Relation to the Sediment Type of Their Habitat. *Aquat. Bot.* **1990**, *38*, 3–17. [CrossRef]

42. Smolders, A.J.P.; Lucassen, E.C.H.E.T.; Roelofs, J.G.M. The Isoetid Environment: Biogeochemistry and Threats. *Aquat. Bot.* **2002**, *73*, 325–350. [CrossRef]

43. Pedersen, O.; Pulido, C.; Rich, S.M.; Colmer, T.D. In Situ O_2 Dynamics in Submerged Isoetes Australis: Varied Leaf Gas Permeability Influences Underwater Photosynthesis and Internal O_2. *J. Exp. Bot.* **2011**, *62*, 4691–4700. [CrossRef] [PubMed]

44. Winkel, A.; Colmer, T.D.; Pedersen, O. Leaf Gas Films of Spartina Anglica Enhance Rhizome and Root Oxygen during Tidal Submergence. *Plant Cell Environ.* **2011**, *34*, 2083–2092. [CrossRef]

45. Richards, J.H.; Kuhn, D.N.; Bishop, K. Interrelationships of Petiolar Air Canal Architecture, Water Depth, and Convective Air Flow in Nymphaea Odorata (*Nymphaeaceae*). *Am. J. Bot.* **2012**, *99*, 1903–1909. [CrossRef]

46. Dacey, J.W.H. Internal Winds in Water Lilies: An Adaptation for Life in Anaerobic Sediments. *Science* **1980**, *210*, 1017–1019. [CrossRef]

47. Grosse, W.; Bernhard Büchel, H.; Tiebel, H. Pressurized Ventilation in Wetland Plants. *Aquat. Bot.* **1991**, *39*, 89–98. [CrossRef]

48. Dacey, J.W.H.; Klug, M.J. Ventilation by Floating Leaves in Nuphar. *Am. J. Bot.* **1982**, *69*, 999. [CrossRef]

49. Grosse, W.; Jovy, K.; Tiebel, H. Influence of Plants on Redox Potential and Methane Production in Water-Saturated Soil. In *Management and Ecology of Freshwater Plants*; Springer: Dordrecht, The Netherlands, 1996; pp. 93–99.

50. Grosse, W.; Schröder, P. Pflanzenleben Unter Anaeroben Umweltbedingungen, Die Physikalischen Grundlagen Und Anatomischen Voraussetzungen. *Ber. Der Dtsch. Bot. Ges.* **1986**, *99*, 367–381. [CrossRef]

51. Schröder, P. Characterization of a Thermo-Osmotic Gas Transport Mechanism in *Alnus glutinosa* (L.) Gaertn. *Trees* **1989**, *3*, 38–44. [CrossRef]

52. Konnerup, D.; Sorrell, B.K.; Brix, H. Do Tropical Wetland Plants Possess Convective Gas Flow Mechanisms? *New Phytol.* **2011**, *190*, 379–386. [CrossRef]

53. Mevi-Scutz, J.; Grosse, W. A Two-Way Gas Transport System in *Nelumbo nucifera*. *Plant Cell Environ.* **1988**, *11*, 27–34. [CrossRef]

54. Matthews, P.G.D.; Seymour, R.S. Stomata Actively Regulate Internal Aeration of the Sacred Lotus *Nelumbo Nucifera*. *Plant Cell Environ.* **2014**, *37*, 402–413. [CrossRef]

55. Vogel, S. Contributions to the Functional Anatomy and Biology of Nelumbo Nucifera (*Nelumbonaceae*) I. Pathways of Air Circulation. *Plant Syst. Evol.* **2004**, *249*, 9–25. [CrossRef]

56. Matthews, P.G.D.; Seymour, R.S. Anatomy of the Gas Canal System of *Nelumbo nucifera*. *Aquat. Bot.* **2006**, *85*, 147–154. [CrossRef]

57. Gaberščik, A. Measurements of Apparent CO_2 Flux in Amphibious Plant *Polygonum amphibium* L. Growing over Environmental Gradient. *Photosynthetica* **1993**, *29*, 473–476.

58. Colmer, T.D.; Pedersen, O. Underwater Photosynthesis and Respiration in Leaves of Submerged Wetland Plants: Gas Films Improve CO_2 and O_2 Exchange. *New Phytol.* **2008**, *177*, 918–926. [CrossRef] [PubMed]

59. Hyvönen, T.; Ojala, A.; Kankaala, P.; Martikainen, P.J. Methane Release from Stands of Water Horsetail (*Equisetum Fluviatile*) in a Boreal Lake. *Freshw. Biol.* **1998**, *40*, 275–284. [CrossRef]

60. Armstrong, J.; Armstrong, W. Reasons for the Presence or Absence of Convective (Pressurized) Ventilation in the Genus *Equisetum*. *New Phytol.* **2011**, *190*, 387–397. [CrossRef] [PubMed]

61. Armstrong, J.; Armstrong, W. Record Rates of Pressurized Gas-flow in the Great Horsetail, Equisetum Telmateia. Were Carboniferous Calamites Similarly Aerated? *New Phytol.* **2009**, *184*, 202–215. [CrossRef]

62. Strand, V.V. The Influence of Ventilation Systems on Water Depth Penetration of Emergent Macrophytes. *Freshw. Biol.* **2002**, *47*, 1097–1105. [CrossRef]

63. Vretare Strand, V.; Weisner, S.E.B. Interactive Effects of Pressurized Ventilation, Water Depth and Substrate Conditions on Phragmites Australis. *Oecologia* **2002**, *131*, 490–497. [CrossRef]

64. Vretare, V.; Weisner, S.E.B. Influence of Pressurized Ventilation on Performance of an Emergent Macrophyte (*Phragmites australis*). *J. Ecol.* **2000**, *88*, 978–987. [CrossRef]

65. Armstrong, J.; Armstrong, W.; Beckett, P.M. Phragmites Australis: Venturi- and Humidity-Induced Pressure Flows Enhance Rhizome Aeration and Rhizosphere Oxidation. *New Phytol.* **1992**, *120*, 197–207. [CrossRef]

66. Faußer, A.C.; Dušek, J.; Čížková, H.; Kazda, M. Diurnal Dynamics of Oxygen and Carbon Dioxide Concentrations in Shoots and Rhizomes of a Perennial in a Constructed Wetland Indicate Down-Regulation of below Ground Oxygen Consumption. *AoB Plants* **2016**, *8*, plw025. [CrossRef]

67. Kludze, H.K.; DeLaune, R.D.; Patrick, W.H. Aerenchyma Formation and Methane and Oxygen Exchange in Rice. *Soil Sci. Soc. Am. J.* **1993**, *57*, 386–391. [CrossRef]

68. Bart, D.; Hartman, J.M. Environmental Determinants of Phragmites Australis Expansion in a New Jersey Salt Marsh: An Experimental Approach. *Oikos* **2000**, *89*, 59–69. [CrossRef]

69. Visser, E.J.W.; Colmer, T.D.; Blom, C.W.P.M.; Voesenek, L.A.C.J. Changes in Growth, Porosity, and Radial Oxygen Loss from Adventitious Roots of Selected Mono- and Dicotyledonous Wetland Species with Contrasting Types of Aerenchyma. *Plant Cell Environ.* **2000**, *23*, 1237–1245. [CrossRef]

70. Singer, A.; Eshel, A.; Agami, M.; Beer, S. The Contribution of Aerenchymal CO_2 to the Photosynthesis of Emergent and Submerged Culms of Scirpus Lacustris and Cyperus Papyrus. *Aquat. Bot.* **1994**, *49*, 107–116. [CrossRef]

71. Jermy, A.C.; Anthony, C.; Simpson, D.; Oswald, P.H. Botanical Society of the British Isles. "*Schoenoplectus lacustris* (L.) Palla". In *Sedges of the British Isles. BSBI Handbook*, 3rd ed.; Botanical Society of the British Isles: London, UK, 2007; Volume 1, pp. 105–107. ISBN 9780901158352.

72. Tulbure, M.G.; Ghioca-Robrecht, D.M.; Johnston, C.A.; Whigham, D.F. Inventory and Ventilation Efficiency of Nonnative and Native Phragmites Australis (Common Reed) in Tidal Wetlands of the Chesapeake Bay. *Estuaries Coasts* **2012**, *35*, 1353–1359. [CrossRef]

73. Tornberg, T.; Bendix, M.; Brix, H. Internal Gas Transport in *Typha latifolia* L. and *Typha angustifolia* L. 2. Convective Throughflow Pathways and Ecological Significance. *Aquat. Bot.* **1994**, *49*, 91–105. [CrossRef]

74. White, S.D.; Ganf, G.G. Influence of Stomatal Conductance on the Efficiency of Internal Pressurisation in Typha Domingensis. *Aquat. Bot.* **2000**, *67*, 1–11. [CrossRef]

75. Bansal, S.; Lishawa, S.C.; Newman, S.; Tangen, B.A.; Wilcox, D.; Albert, D.; Anteau, M.J.; Chimney, M.J.; Cressey, R.L.; DeKeyser, E.; et al. Typha (*Cattail*) Invasion in North American Wetlands: Biology, Regional Problems, Impacts, Ecosystem Services, and Management. *Wetlands* **2019**, *39*, 645–684. [CrossRef]

76. Duarte, V.P.; Pereira, M.P.; Corrêa, F.F.; de Castro, E.M.; Pereira, F.J. Aerenchyma, Gas Diffusion, and Catalase Activity in Typha Domingensis: A Complementary Model for Radial Oxygen Loss. *Protoplasma* **2021**, *258*, 765–777. [CrossRef]

77. Matsui, T.; Tsuchiya, T. Root Aerobic Respiration and Growth Characteristics of Three Typha Species in Response to Hypoxia. *Ecol. Res.* **2006**, *21*, 470–475. [CrossRef]

78. Raskin, I.; Kende, H. Mechanism of Aeration in Rice. *Science* **1985**, *228*, 327–329. [CrossRef]

79. Bailey-Serres, J.; Fukao, T.; Ronald, P.; Ismail, A.; Heuer, S.; Mackill, D. Submergence Tolerant Rice: SUB1's Journey from Landrace to Modern Cultivar. *Rice* **2010**, *3*, 138–147. [CrossRef]

80. Nishiuchi, S.; Yamauchi, T.; Takahashi, H.; Kotula, L.; Nakazono, M. Mechanisms for Coping with Submergence and Waterlogging in Rice. *Rice* **2012**, *5*, 2. [CrossRef] [PubMed]

81. Herzog, M.; Konnerup, D.; Pedersen, O.; Winkel, A.; Colmer, T.D. Leaf Gas Films Contribute to Rice (*Oryza Sativa*) Submergence Tolerance during Saline Floods. *Plant Cell Environ.* **2018**, *41*, 885–897. [CrossRef] [PubMed]

82. Konnerup, D.; Pedersen, O. Flood Tolerance of Glyceria Fluitans: The Importance of Cuticle Hydrophobicity, Permeability and Leaf Gas Films for Underwater Gas Exchange. *Ann. Bot.* **2017**, *120*, 521–528. [CrossRef]

83. Groot, T.T.; van Bodegom, P.M.; Meijer, H.A.J.; Harren, F.J.M. Gas Transport through the Root–Shoot Transition Zone of Rice Tillers. *Plant Soil* **2005**, *277*, 107–116. [CrossRef]

84. Yamauchi, T.; Tanaka, A.; Mori, H.; Takamure, I.; Kato, K.; Nakazono, M. Ethylene-Dependent Aerenchyma Formation in Adventitious Roots Is Regulated Differently in Rice and Maize. *Plant Cell Environ.* **2016**, *39*, 2145–2157. [CrossRef]

85. Steffens, B.; Geske, T.; Sauter, M. Aerenchyma Formation in the Rice Stem and Its Promotion by H_2O_2. *New Phytol.* **2011**, *190*, 369–378. [CrossRef]

86. Ni, X.-L.; Gui, M.-Y.; Tan, L.-L.; Zhu, Q.; Liu, W.-Z.; Li, C.-X. Programmed Cell Death and Aerenchyma Formation in Water-Logged Sunflower Stems and Its Promotion by Ethylene and ROS. *Front. Plant Sci.* **2019**, *9*, 1928. [CrossRef]

87. Parlanti, S.; Kudahettige, N.P.; Lombardi, L.; Mensuali-Sodi, A.; Alpi, A.; Perata, P.; Pucciariello, C. Distinct Mechanisms for Aerenchyma Formation in Leaf Sheaths of Rice Genotypes Displaying a Quiescence or Escape Strategy for Flooding Tolerance. *Ann. Bot.* **2011**, *107*, 1335–1343. [CrossRef]

88. Nagai, K.; Kurokawa, Y.; Mori, Y.; Minami, A.; Reuscher, S.; Wu, J.; Matsumoto, T.; Ashikari, M. SNORKEL Genes Relating to Flood Tolerance Were Pseudogenized in Normal Cultivated Rice. *Plants* **2022**, *11*, 376. [CrossRef]

89. Colmer, T.D.; Cox, M.C.H.; Voesenek, L.A.C.J. Root Aeration in Rice (*Oryza sativa*): Evaluation of Oxygen, Carbon Dioxide, and Ethylene as Possible Regulators of Root Acclimatizations. *New Phytol.* **2006**, *170*, 767–778. [CrossRef]

90. Colmer, T.D.; Pedersen, O. Oxygen Dynamics in Submerged Rice (*Oryza sativa*). *New Phytol.* **2008**, *178*, 326–334. [CrossRef] [PubMed]

91. Seago, J.L.; Peterson, C.A.; Enstone, D.E. Cortical Development in Roots of the Aquatic Plant Pontederia Cordata (*Pontederiaceae*). *Am. J. Bot.* **2000**, *87*, 1116–1127. [CrossRef] [PubMed]

92. Herzog, M.; Pedersen, O. Partial versus Complete Submergence: Snorkelling Aids Root Aeration in R Umex Palustris but Not in *R. Acetosa*. *Plant Cell Environ.* **2014**, *37*, 2381–2390. [CrossRef] [PubMed]

93. Ting, T.M.; Poulsen, A.D. Understorey Vegetation at Two Mud Volcanoes in North-East Borneo. *J. Trop. For. Sci.* **2009**, *21*, 198–209.

94. Bonde, S.D.; Kumaran, K.P.N. A Permineralized Species of Mangrove Fern *Acrostichum* L. from Deccan Intertrappean Beds of India. *Rev. Palaeobot. Palynol.* **2002**, *120*, 285–299. [CrossRef]

95. Fonini, A.M.; Barufi, J.B.; Schmidt, É.C.; Rodrigues, A.C.; Randi, Á.M. Leaf Anatomy and Photosynthetic Efficiency of Acrostichum Danaeifolium after UV Radiation. *Photosynthetica* **2017**, *55*, 401–410. [CrossRef]

96. Chomicki, G.; Bidel, L.P.R.; Baker, W.J.; Jay-Allemand, C. Palm Snorkelling: Leaf Bases as Aeration Structures in the Mangrove Palm (*Nypa fruticans*). *Bot. J. Linn. Soc.* **2014**, *174*, 257–270. [CrossRef]

97. Rozainah, M.Z.; Aslezaeim, N. A Demographic Study of a Mangrove Palm, Nypa Fruticans. *Sci. Res. Essays* **2010**, *5*, 3896–3902.

98. Srikanth, S.; Lum, S.K.Y.; Chen, Z. Mangrove Root: Adaptations and Ecological Importance. *Trees* **2016**, *30*, 451–465. [CrossRef]

99. McKee, K.L. Soil Physicochemical Patterns and Mangrove Species Distribution-Reciprocal Effects? *J. Ecol.* **1993**, *81*, 477–487. [CrossRef]

100. Scholander, P.F.; van Dam, L.; Scholander, S.I. Gas Exchange in the Roots of Mangroves. *Am. J. Bot.* **1955**, *42*, 92. [CrossRef]

101. Purnobasuki, H.; Suzuki, M. Aerenchyma Formation and Porosity in Root of a Mangrove Plant, Sonneratia Alba (*Lythraceae*). *J. Plant Res.* **2004**, *117*, 465–472. [CrossRef]

102. Purnobasuk, H. Primary Structure and Intercellular Space Formation of Feeding Root in *Sonneratia alba* J. Smith. *Int. J. Bot.* **2012**, *9*, 44–49. [CrossRef]

103. Zhang, Y.; Ding, Y.; Wang, W.; Li, Y.; Wang, M. Distribution of Fish among Avicennia and Sonneratia Microhabitats in a Tropical Mangrove Ecosystem in South China. *Ecosphere* **2019**, *10*, e02759. [CrossRef]

104. Cheng, H.; Wu, M.-L.; Li, C.-D.; Sun, F.-L.; Sun, C.-C.; Wang, Y.-S. Dynamics of Radial Oxygen Loss in Mangroves Subjected to Waterlogging. *Ecotoxicology* **2020**, *29*, 684–690. [CrossRef] [PubMed]

105. Cheng, H.; Wang, Y.-S.; Fei, J.; Jiang, Z.-Y.; Ye, Z.-H. Differences in Root Aeration, Iron Plaque Formation and Waterlogging Tolerance in Six Mangroves along a Continues Tidal Gradient. *Ecotoxicology* **2015**, *24*, 1659–1667. [CrossRef]

106. Curran, M.; Cole, M.; Allaway, W.G. Root Aeration and Respiration in Young Mangrove Plants (*Avicennia marina* (Forsk.) Vierh.). *J. Exp. Bot.* **1986**, *37*, 1225–1233. [CrossRef]

107. Hovenden, M. Horizontal Structures on Pneumatophores of *Avicennia marina* (Forsk.) Vierh.—A New Site of Oxygen Conductance. *Ann. Bot.* **1994**, *73*, 377–383. [CrossRef]

108. Curran, M.; James, P.; Allaway, W.G. The Measurement of Gas Spaces in the Roots of Aquatic Plants—Archimedes Revisited. *Aquat. Bot.* **1996**, *54*, 255–261. [CrossRef]

109. Rogers, G.K. Bald Cypress Knees, Taxodium Distichum (Cupressaceae): An Anatomical Study, with Functional Implications. *Flora* **2021**, *278*, 151788. [CrossRef]

110. Martin, C.E.; Francke, S.K. Root Aeration Function of Baldcypress Knees (*Taxodium distichum*). *Int. J. Plant Sci.* **2015**, *176*, 170–173. [CrossRef]

111. Wang, G.-B.; Cao, F.-L. Formation and Function of Aerenchyma in Baldcypress (*Taxodium distichum* (L.) Rich.) and Chinese Tallow Tree (*Sapium Sebiferum* (L.) Roxb.) under Flooding. *S. Afr. J. Bot.* **2012**, *81*, 71–78. [CrossRef]

112. Middleton, B. Carbon Stock Trends of Baldcypress Knees along Climate Gradients of the Mississippi River Alluvial Valley Using Allometric Methods. *For. Ecol. Manag.* **2020**, *461*, 117969. [CrossRef]

113. Sou, H.-D.; Masumori, M.; Kurokochi, H.; Tange, T. Histological Observation of Primary and Secondary Aerenchyma Formation in Adventitious Roots of *Syzygium kunstleri* (King) Bahadur and *R.C.Gaur Grown* in Hypoxic Medium. *Forests* **2019**, *10*, 137. [CrossRef]

114. Grosse, W.; Schulte, A.; Fujita, H. Pressurized Gas Transport in Two Japanese Alder Species in Relation to Their Natural Habitats. *Ecol. Res.* **1993**, *8*, 151–158. [CrossRef]

115. Takaishi, T.; Sensui, Y. Thermal Transpiration Effect of Hydrogen, Rare Gases and Methane. *Trans. Faraday Soc.* **1963**, *59*, 2503–2514. [CrossRef]

116. Denbigh, K.G. Thermo-Osmosis of Gases through a Membrane. *Nature* **1949**, *163*, 60. [CrossRef]

117. Denbigh, K.G.; Raumann, G. The Thermo-Osmosis of Gases through a Membrane. I. Theoretical. *Proc. R. Soc. London Ser. A Math. Phys. Sci.* **1952**, *210*, 377–387.

118. Buchel, H.B.; Grosse, W. Localization of the Porous Partition Responsible for Pressurized Gas Transport in *Alnus glutinosa* (L.) Gaertn. *Tree Physiol.* **1990**, *6*, 247–256. [CrossRef]

119. Dittert, K.; Wätzel, J.; Sattelmacher, B. Responses of Alnus Glutinosa to Anaerobic Conditions-Mechanisms and Rate of Oxygen Flux into the Roots. *Plant Biol.* **2006**, *8*, 212–223. [CrossRef] [PubMed]

120. Armstrong, W.; Armstrong, J. Stem Photosynthesis Not Pressurized Ventilation Is Responsible for Light-Enhanced Oxygen Supply to Submerged Roots of Alder (*Alnus glutinosa*). *Ann. Bot.* **2005**, *96*, 591–612. [CrossRef] [PubMed]

121. Batzli, J.M.; Dawson, J.O. Development of Flood-Induced Lenticels in Red Alder Nodules Prior to the Restoration of Nitrogenase Activity. *Can. J. Bot.* **1999**, *77*, 1373–1377. [CrossRef]

122. Huber, M.; Linder, H.P. The Evolutionary Loss of Aerenchyma Limits Both Realized and Fundamental Ecohydrological Niches in the Cape Reeds (*Restionaceae*). *J. Ecol.* **2012**, *100*, 1338–1348. [CrossRef]

123. Bedoya, A.M.; Madriñán, S. Evolution of the Aquatic Habit in Ludwigia (*Onagraceae*): Morpho-Anatomical Adaptive Strategies in the Neotropics. *Aquat. Bot.* **2015**, *120*, 352–362. [CrossRef]

124. Hoffmann, M.H. To the Roots of Carex: Unexpected Anatomical and Functional Diversity. *Syst. Bot.* **2019**, *44*, 26–31. [CrossRef]

125. Visser, E.J.W.; Bogemann, G.M.; van de Steeg, H.M.; Pierik, R.; Blom, C.W.P.M. Flooding Tolerance of Carex Species in Relation to Field Distribution and Aerenchyma Formation. *New Phytol.* **2000**, *148*, 93–103. [CrossRef]

126. Armstrong, W.; Armstrong, J. Plant Internal Oxygen Transport (Diffusion and Convection) and Measuring and Modelling Oxygen Gradients. In *Low-Oxygen Stress in Plants*; Springer: Berlin, Germany, 2014; Volume 21, pp. 267–297.

127. Schröder, P.; Grosse, W.; Woermann, D. Localization of Thermo-Osmotically Active Partitions in Young Leaves of Nuphar Lutea. *J. Exp. Bot.* **1986**, *37*, 1450–1461. [CrossRef]

128. Bazhin, N.M. Influence of Plants on the Methane Emission from Sediments. *Chemosphere* **2004**, *54*, 209–215. [CrossRef]

129. Bridgham, S.D.; Cadillo-Quiroz, H.; Keller, J.K.; Zhuang, Q. Methane Emissions from Wetlands: Biogeochemical, Microbial, and Modeling Perspectives from Local to Global Scales. *Glob. Chang. Biol.* **2013**, *19*, 1325–1346. [CrossRef]

130. Bansal, S.; Johnson, O.F.; Meier, J.; Zhu, X. Vegetation Affects Timing and Location of Wetland Methane Emissions. *J. Geophys. Res. Biogeosci.* **2020**, *125*, e2020JG005777. [CrossRef]

131. Bhullar, G.S.; Iravani, M.; Edwards, P.J.; Olde Venterink, H. Methane Transport and Emissions from Soil as Affected by Water Table and Vascular Plants. *BMC Ecol.* **2013**, *13*, 32. [CrossRef] [PubMed]
132. Turetsky, M.R.; Kotowska, A.; Bubier, J.; Dise, N.B.; Crill, P.; Hornibrook, E.R.C.; Minkkinen, K.; Moore, T.R.; Myers-Smith, I.H.; Nykänen, H.; et al. A Synthesis of Methane Emissions from 71 Northern, Temperate, and Subtropical Wetlands. *Glob. Chang. Biol.* **2014**, *20*, 2183–2197. [CrossRef]
133. Kosten, S.; Piñeiro, M.; de Goede, E.; de Klein, J.; Lamers, L.P.M.; Ettwig, K. Fate of Methane in Aquatic Systems Dominated by Free-Floating Plants. *Water Res.* **2016**, *104*, 200–207. [CrossRef] [PubMed]
134. Henneberg, A.; Sorrell, B.K.; Brix, H. Internal Methane Transport through *Juncus effusus*: Experimental Manipulation of Morphological Barriers to Test Above- and Below-ground Diffusion Limitation. *New Phytol.* **2012**, *196*, 799–806. [CrossRef] [PubMed]
135. Kim, J.; Lee, J.; Yun, J.; Yang, Y.; Ding, W.; Yuan, J.; Kang, H. Mechanisms of Enhanced Methane Emission Due to Introduction of *Spartina anglica* and *Phragmites australis* in a Temperate Tidal Salt Marsh. *Ecol. Eng.* **2020**, *153*, 105905. [CrossRef]
136. van den Berg, M.; van den Elzen, E.; Ingwersen, J.; Kosten, S.; Lamers, L.P.M.; Streck, T. Contribution of Plant-Induced Pressurized Flow to CH4 Emission from a Phragmites Fen. *Sci. Rep.* **2020**, *10*, 12304. [CrossRef]
137. Were, D.; Kansiime, F.; Fetahi, T.; Hein, T. Carbon Dioxide and Methane Fluxes from Various Vegetation Communities of a Natural Tropical Freshwater Wetland in Different Seasons. *Environ. Processes* **2021**, *8*, 553–571. [CrossRef]
138. Jones, M.B. Methane Production and Emission from Papyrus-Dominated Wetlands. *SIL Proc.* **2000**, *27*, 1406–1409. [CrossRef]
139. Van der Nat, F.J.W.A.; Middelburg, J.J.; van Meteren, D.; Wielemakers, A. Diel Methane Emission Patterns from *Scirpus lacustris* and *Phragmites australis*. *Biogeochemistry* **1998**, *41*, 1–22. [CrossRef]
140. Sebacher, D.I.; Harriss, R.C.; Bartlett, K.B. Methane Emissions to the Atmosphere Through Aquatic Plants. *J. Environ. Qual.* **1985**, *14*, 40–46. [CrossRef]
141. Inubushi, K.; Sugii, H.; Nishino, S.; Nishino, E. Effect of Aquatic Weeds on Methane Emission from Submerged Paddy Soil. *Am. J. Bot.* **2001**, *88*, 975–979. [CrossRef] [PubMed]
142. Iqbal, M.F.; Liu, S.; Zhu, J.; Zhao, L.; Qi, T.; Liang, J.; Luo, J.; Xiao, X.; Fan, X. Limited Aerenchyma Reduces Oxygen Diffusion and Methane Emission in Paddy. *J. Environ. Manag.* **2021**, *279*, 111583. [CrossRef] [PubMed]
143. Machacova, K.; Borak, L.; Agyei, T.; Schindler, T.; Soosaar, K.; Mander, Ü.; Ah-Peng, C. Trees as Net Sinks for Methane (CH_4) and Nitrous Oxide (N_2O) in the Lowland Tropical Rain Forest on Volcanic Réunion Island. *New Phytol.* **2021**, *229*, 1983–1994. [CrossRef] [PubMed]
144. Pangala, S.R.; Enrich-Prast, A.; Basso, L.S.; Peixoto, R.B.; Bastviken, D.; Hornibrook, E.R.C.; Gatti, L.v.; Marotta, H.; Calazans, L.S.B.; Sakuragui, C.M.; et al. Large Emissions from Floodplain Trees Close the Amazon Methane Budget. *Nature* **2017**, *552*, 230–234. [CrossRef] [PubMed]
145. Pangala, S.R.; Moore, S.; Hornibrook, E.R.C.; Gauci, V. Trees Are Major Conduits for Methane Egress from Tropical Forested Wetlands. *New Phytol.* **2013**, *197*, 524–531. [CrossRef]
146. Laanbroek, H.J. Methane Emission from Natural Wetlands: Interplay between Emergent Macrophytes and Soil Microbial Processes. A Mini-Review. *Ann. Bot.* **2010**, *105*, 141–153. [CrossRef]