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Functional Plant Biology

Supplementary Material

A meta-analysis of plant tissue O2 dynamics

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Supplementary materials

Literature search

A structured and systematic literature search was performed in the following steps. The search was performed using the Web of Science BIOSIS database. Search terms grouped into blocks were combined using Boolean operators OR, AND, NEAR and NOT since simply searching for the combination of plant tissues (Plant OR root OR leaf) with key words relating to internal O₂ status (oxygen, O₂, aeration, anoxia, hypoxia, etc.) resulted in a very high number of hits (> 50.000). Following multiple attempts and evaluation of the resulting hits, the following search string resulted in a broad but inclusive list of 2,136 studies:

TS= ((O2 OR O-2 OR OXYGEN) NEAR/2(TISSUE OR INTERNAL OR "PARTIAL PRESSURE" OR CONCENTRATION* OR LEVEL* OR GRADIENT* OR DYNAMIC* OR PROFILE* OR CONTENT* OR MEASUREMENT* OR KPA OR "INTERNAL GAS" OR MICROELECTRODE* OR ELECTRODE* OR MICROSENSOR*))

AND

TS=((O2 OR O-2 OR OXYGEN) NEAR/6(PLANT* OR ROOT* OR SEED* OR LEAF OR LEAVES OR GRASS OR SEAGRASS OR RHIZOME* OR MERISTEM* OR PETIOLE* OR BUD* OR STEM* OR NODE* OR INTERNOD* OR "LEAF BLADE*" OR SHOOT* OR "ADVENTITIOUS ROOT*" OR "CROWN ROOT*" OR "NODAL ROOT*" OR STELE OR CORTEX OR "SEMINAL ROOT*" OR NODULE* OR CUTTINGS)) NOT TS=*Algae

The Boolean operator NEAR/6 was chosen after carefully evaluating which papers were excluded in steps from NEAR/2 to NEAR/7. Changing NEAR/5 to NEAR/6 resulted in the retrieval of some relevant papers, while changing NEAR/6 to NEAR/7 resulted in retrieving additional non-relevant papers.

Prior to the above literature search, we had compiled a list of 59 studies already known by us to include data relevant for this review. These 59 studies were retrieved when cross-referencing with the 2,136 studies identified in the systematic literature search, demonstrating that the systematic literature search did in fact identify the relevant studies. Studying the abstract, title, and on some occasions figures and materials and methods sections, of the 2,136 studies allowed us to discard > 90% as non-relevant (no internal O_2 measurements conducted). When reviewing the remaining relevant studies, citations within some of these

studies led to the discovery of additional studies. Since the BIOSIS database (preferred since it allows for restricting results to plant studies) only encompasses studies published after 1969, the above search was repeated in Web of Science Core Selection for 1900–1969 which did not identify any additional studies. Finally, the above steps resulted in a final list of 129 studies used for this review.

Data conversions

The studies used for this review provide a wide range of ways to measure and report levels of plant tissue O₂. O₂ levels reported as mm Hg, concentrations (mg L⁻¹, µmol L⁻¹), % of air saturation or % O₂ was converted into kPa as detailed in the following.

Converting data reported as µmol O₂ L⁻¹ to kPa O₂ required retrieving the temperature prevailing during the experiment, in order to determine the relevant O₂ solubility. The reported O₂ in µmol L⁻¹ was then transformed by dividing by the O₂ solubility and multiplying with the pO₂ at air equilibrium (20.59 kPa assuming atmospheric pressure of 101,33 kPa and 3% water vapour inside plant tissues equalling 100% RH, which is a valid assumption inside hydrated tissues). O₂ values reported as mg L⁻¹ were converted in the same way following conversion from mg to µmol.

O₂ levels reported as % O₂ were converted into kPa O₂ by multiplying with the atmospheric pressure of 1 atmosphere (101,33 kPa) and dividing by 100. If O₂ levels were reported as % of air equilibrium, the reported % O₂ was divided by 100 and multiplied by 20.95 which is the percentage of O₂ present in the atmosphere. I.e., 50% of O₂ at air equilibrium corresponding to 10.6 kPa. Finally, mm Hg were converted into kPa using a conversion factor of 0.133 mm Hg kPa⁻¹.

Modelling

We evaluated the influence of environmental conditions, plant species and tissue type on tissue pO₂ using an information-theoretic model selection approach. The model selection was carried-out using R statistical software (R Core Team 2014) with the 'MuMIn' package (Barton and Barton 2022). Prior to modelling, we examined variables for variance inflation factor using the 'vif' function (Fox and Weisberg 2018). The Linear Mixed-effects Models (LMM) were applied using the "lme4" package (Pinheiro *et al.* 2022). We used LMMs with

maximum likelihood to estimate model parameters and their importance in defining plant O_2 status. The model included tissue pO_2 as response variable, flooding status, light status, and tissue type as factorial predictors. Flooding status was categorised into three levels (completely submerged, partial submerged or with entire shoot in air) based on descriptions of the experimental conditions. Results from studies where the environmental pO_2 conditions were manipulated (i.e., surrounding the shoot with N_2 gas) were excluded. Light status was categorised into two levels: dark or light, based on descriptions of the experimental conditions. We excluded studies with ambiguous light conditions. We categorised tissue types into root, stem, or leaf tissues. In addition, we included plant species as a random factor. We fitted the full model, compared all the possible factor and interaction combinations and selected the best model using the Akaike Information Criterion (AIC) (Burnham and Anderson 2004). Conditional and marginal R^2 values were obtained using the 'r.squaredGLMM' function. We verified model assumptions looking at diagnostic plot of the distribution of the residuals (Fig. S1). The response variable (tissue pO_2) was square root transformed to improve distribution of the residual.

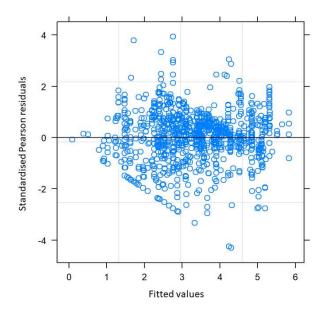


Fig. S1. Residual plot of the full linear mixed-effects model predicting tissue O₂ from 'light', 'tissue', 'submergence' and interactions, with 'species' as a random factor. Fitted square root transformed values vs. standardised Pearson residuals.

Studies used for data extractions

Aguilar, EA, Turner, DW, Gibbs, DJ, Armstrong, W, Sivasithamparam, K (2003) Oxygen distribution and movement, respiration and nutrient loading in banana roots (*Musa spp.* L.) subjected to aerated and oxygen-depleted environments. *Plant and Soil* **253**, 91-102.

Andersen, F, Kristensen, E (1988) Oxygen microgradients in the rhizosphere of the mangrove *Avicennia marina*. *Marine Ecology Progress Series* **44**, 201-204.

Andersen, T, Andersen, FO, Pedersen, O (2006) Increased CO₂ in the water around *Littorella* uniflora raises the sediment O₂ concentration. Aquatic Botany **84**, 294-300.

Armstrong, W, Cousins, D, Armstrong, J, Turner, DW, Beckett, PM (2000) Oxygen distribution in wetland plant roots and permeability barriers to gas-exchange with the rhizosphere: A microelectrode and modelling study with *Phragmites australis*. *Annals of Botany* **86**, 687-703.

Armstrong, W, Strange, ME, Cringle, S, Beckett, PM (1994) Microelectrode and modelling study of oxygen distribution in roots. *Annals of Botany* **74**, 287-299.

Armstrong, W, Webb, T, Darwent, M, Beckett, PM (2009) Measuring and interpreting respiratory critical oxygen pressures in roots. *Annals of Botany* **103**, 281-293.

Ayi, Q, Zeng, B, Liu, J, Li, S, van Bodegom, PM, Cornelissen, JHC (2016) Oxygen absorption by adventitious roots promotes the survival of completely submerged terrestrial plants. *Annals of Botany (London)* **118**, 675-683.

Binzer, T, Borum, J, Pedersen, O (2005) Flow velocity affects internal oxygen conditions in the seagrass *Cymodocea nodosa*. *Aquatic Botany* **83**, 239-247.

- Borum, J, Pedersen, O, Greve, TM, Frankovich, TA, Zieman, JC, Fourqurean, JW, Madden, CJ (2005) The potential role of plant oxygen and sulphide dynamics in die-off events of the tropical seagrass, *Thalassia testudinum. Journal of Ecology* **93**, 148-158.
- Borum, J, Pedersen, O, Kotula, L, Fraser, MW, Statton, J, Colmer, TD, Kendrick, GA (2016) Photosynthetic response to globally increasing CO₂ of co-occurring temperate seagrass species. *Plant, Cell & Environment* **39**, 1240-1250.
- Bowling, DJF (1973) Measurement of a gradient of oxygen partial pressure across the intact root. *Planta (Heidelberg)* **111**, 323-328.
- Brodersen, KE, Hammer, KJ, Schrameyer, V, Floytrup, A, Rasheed, MA, Ralph, PJ, Kuhl, M, Pedersen, O (2017) Sediment resuspension and deposition on seagrass leaves impedes internal plant aeration and promotes phytotoxic H₂S intrusion. *Frontiers in Plant Science* **8**, 657.
- Canini, A, Caiola, MG (1993) Characterization of gonidial zone of *Cycas revoluta* coralloid roots by means of microelectrodes. *FEMS (Federation of European Microbiological Societies) Microbiology Letters* **109**, 75-79.
- Chung, H, Kim, S, Kim, K-T, Hwang, B-G, Kim, H-J, Lee, S-J, Lee, Y-H (2019) A novel approach to investigate hypoxic microenvironment during rice colonization by *Magnaporthe oryzae*. *Environmental Microbiology* **21**, 1151-1169.
- Colmer, TD, Pedersen, O (2008) Oxygen dynamics in submerged rice (*Oryza sativa*). New *Phytologist* **178**, 326-334.
- Colmer, TD, Pedersen, O, Wetson, AM, Flowers, TJ (2013) Oxygen dynamics in a salt-marsh soil and in *Suaeda maritima* during tidal submergence. *Environmental and Experimental Botany* **92**, 73-82.
- Colmer, TD, Winkel, A, Kotula, L, Armstrong, W, Revsbech, NP, Pedersen, O (2019) Root O₂ consumption, CO₂ production and tissue concentration profiles in chickpea, as influenced by environmental hypoxia. *New Phytologist* **226**, 373-384.
- Darwent, M, Armstrong, W, Armstrong, J, Beckett, PM (2003) Exploring the radial and longitudinal aeration of primary maize roots by means of Clark-type oxygen microelectrodes. *Russian Journal of Plant Physiology* **50**, 722-732.
- De Simone, O, Haase, K, Mueller, E, Junk, WJ, Gonsior, G, Schmidt, W (2002) Impact of root morphology on metabolism and oxygen distribution in roots and rhizosphere from two Central Amazon floodplain tree species. *Functional Plant Biology* **29**, 1025-1035.
- De Simone, O, Haase, K, Mueller, E, Junk, WJ, Hartmann, K, Schreiber, L, Schmidt, W (2003) Apoplasmic barriers and oxygen transport properties of hypodermal cell walls in roots from four Amazonian tree species. *Plant Physiology (Rockville)* **132**, 206-217
- del Hierro, AM, Kronberger, W, Hietz, P, Offenthaler, I, Richter, H (2002) A new method to determine the oxygen concentration inside the sapwood of trees. *Journal of Experimental Botany* **53**, 559-563.
- Eklund, L (1990) Endogenous levels of oxygen, carbon dioxide and ethylene in stems of Norway spruce trees during one growing season. *Trees (Berlin)* **4**, 150-154.
- Eklund, L (2000) Internal oxygen levels decrease during the growing season and with increasing stem height. *Trees (Berlin)* **14**, 177-180.
- Fausser, AC, Dusek, J, Cizkova, H, Kazda, M (2016) 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* **8**, plw025.

- Gan, L, Zhang, W, Fang, F, Yang, L (2020) Evidence of a trade-off between root aeration and architecture in *Vallisneria natans* in the presence of *Pseudomonas putida* KT2440. *Aquatic Botany* **162**, 103189.
- Gansert, D, Burgdorf, M, Loesch, R (2001) A novel approach to the in situ measurement of oxygen concentrations in the sapwood of woody plants. *Plant Cell and Environment* **24**, 1055-1064.
- Geigenberger, P, Fernie, AR, Gibon, Y, Christ, M, Stitt, M (2000) Metabolic activity decreases as an adaptive response to low internal oxygen in growing potato tubers. *Biological Chemistry* **381**, 723-740.
- Gibbs, J, Greenway, H (2003) Mechanisms of anoxia tolerance in plants. I. Growth, survival and anaerobic catabolism. *Functional Plant Biology* **30**, 1-47.
- Gibbs, J, Turner, DW, Armstrong, W, Darwent, MJ, Greenway, H (1998) Response to oxygen deficiency in primary maize roots. I. Development of oxygen deficiency in the stele reduces radial solute transport to the xylem. *Australian Journal of Plant Physiology* **25**, 745-758.
- Greve, TM, Borum, J, Pedersen, O (2003) Meristematic oxygen variability in eelgrass (*Zostera marina*). *Limnology and Oceanography* **48**, 210-216.
- Hammer, KJ, Borum, J, Hasler-Sheetal, H, Shields, EC, Sand-Jensen, K, Moore, KA (2018) High temperatures cause reduced growth, plant death and metabolic changes in eelgrass *Zostera marina*. *Marine Ecology Progress Series* **604**, 121-132.
- Herzog, M, Pedersen, O (2014) Partial versus complete submergence: snorkelling aids root aeration in *Rumex palustris* but not in *R. acetosa. Plant, Cell & Environment* 37, 2381-2390.
- Holmer, M, Pedersen, O, Krause-Jensen, D, Olesen, B, Petersen, MH, Schopmeyer, S, Koch, M, Lomstein, BA, Jensen, HS (2009) Sulfide intrusion in the tropical seagrasses Thalassia testudinum and Syringodium filiforme. Estuarine Coastal and Shelf Science 85, 319-326.
- Hook, DD, McKevlin, MR (1988) Use of oxygen microelectrodes to measure aeration in the roots of intact tree seedlings. In 'The ecology and management of wetlands.' pp. 467-476. (Springer:
- Haase, K, De Simone, O, Junk, WJ, Schmidt, W (2003) Internal oxygen transport in cuttings from flood-adapted varzea tree species. *Tree physiology* **23**, 1069-1076.
- Johnson, CR, Koch, MS, Pedersen, O, Madden, CJ (2018) Hypersalinity as a trigger of seagrass die off events in Florida Bay: Evidence based on meristem O₂ and H₂S dynamics. *Journal of Experimental Marine Biology and Ecology* **504**, 47-52.
- Johnson, CR, Koch, MS, Pedersen, O, Madden, CJ (2020) Hypersalinity affects leaf and meristem O₂ dynamics exposing meristems to H₂S in the dominant tropical seagrass *Thalassia testudinum. Journal of Experimental Marine Biology and Ecology* **533**, 151458.
- Kitaya, Y, Yabuki, K, Kiyota, M, Tani, A, Hirano, T, Aiga, I (2002) Gas exchange and oxygen concentration in pneumatophores and prop roots of four mangrove species. *Trees (Berlin)* **16**, 155-158.
- Koch, MS, Erskine, JM (2001) Sulfide as a phytotoxin to the tropical seagrass *Thalassia* testudinum: Interactions with light, salinity and temperature. *Journal of Experimental Marine Biology and Ecology* **266**, 81-95.
- Koch, MS, Johnson, CR, Madden, CJ, Pedersen, O (2022) Irradiance, water column O₂, and tide drive internal O₂ dynamics and meristem H₂S detection in the dominant caribbean-tropical atlantic seagrass, *Thalassia testudinum*. *Estuaries and Coasts*

- Koch, MS, Johnson, CR, Madden, CJ, Pedersen, O (2022) Low irradiance disrupts the internal O₂ dynamics of seagrass (*Thalassia testudinum*) leading to shoot meristem H₂S intrusion. *Aquatic Botany* **181**, 103532.
- Koch, MS, Johnson, CR, Travis, L, Pedersen, O, Madden, CJ (2022) Hypersalinity effects on O₂ flux across the diffusive boundary layer of leaves in the tropical seagrass *Thalassia testudinum*. *Journal of Experimental Marine Biology and Ecology* **555**, 151780.
- Konnerup, D, Moir-Barnetson, L, Pedersen, O, Veneklaas, EJ, Colmer, TD (2015)

 Contrasting submergence tolerance in two species of stem-succulent halophytes is not determined by differences in stem internal oxygen dynamics. *Annals of Botany* (London) 115, 409-418.
- Konnerup, D, Pedersen, O (2017) Flood tolerance of *Glyceria fluitans*: the importance of cuticle hydrophobicity, permeability and leaf gas films for underwater gas exchange. *Annals of Botany* **120**, 521-528.
- Konnerup, D, Toro, G, Pedersen, O, Colmer, TD (2018) Waterlogging tolerance, tissue nitrogen and oxygen transport in the forage legume *Melilotus siculus*: a comparison of nodulated and nitrate-fed plants. *Annals of Botany (London)* **121**, 699-709.
- Kotula, L, Clode, PL, Striker, GG, Pedersen, O, Laeuchli, A, Shabala, S, Colmer, TD (2015) Oxygen deficiency and salinity affect cell-specific ion concentrations in adventitious roots of barley (*Hordeum vulgare*). New Phytologist **208**, 1114-1125.
- Kumari, A, Gupta, KJ (2017) Visisens technique to measure internal oxygen and respiration in barley roots. In 'Plant Respiration and Internal Oxygen: Methods and Protocols.' (Ed. KJ Gupta.) Vol. 1670 pp. 39-45.
- Kumari, A, Preston, GM, Gupta, KJ (2017) Measurement of oxygen status in arabidopsis leaves undergoing the hypersensitive response during pseudomonas infection. In 'Plant Respiration and Internal Oxygen: Methods and Protocols.' (Ed. KJ Gupta.) Vol. 1670 pp. 71-76.
- Kuzma, MM, Hunt, S, Layzell, DB (1993) Role of oxygen in the limitation and inhibition of nitrogenase activity and respiration rate in individual soybean nodules. *Plant Physiology (Rockville)* **101**, 161-169.
- Laing, HE (1940) The composition of the internal atmosphere of *Nuphar advenum* and other water plants. *American Journal of Botany* **27**, 861-868.
- Lee, SC, Mustroph, A, Sasidharan, R, Vashisht, D, Pedersen, O, Oosumi, T, Voesenek, LACJ, Bailey-Serres, J (2011) Molecular characterization of the submergence response of the *Arabidopsis thaliana* ecotype Columbia. *New Phytologist* **190**, 457-471.
- Li, M, Jones, MB (1995) CO₂ and O₂ transport in the aerenchyma of *Cyperus papyrus* L. *Aquatic Botany* **52**, 93-106.
- Li, Y, Wang, X (2013) Root-induced changes in radial oxygen loss, rhizosphere oxygen profile, and nitrification of two rice cultivars in Chinese red soil regions. *Plant and Soil* **365**, 115-126.
- Licausi, F, Giorgi, FM, Schmälzlin, E, Usadel, B, Perata, P, Van Dongen, JT, Geigenberger, P (2011) Hre-type genes are regulated by growth-related changes in internal oxygen concentrations during the normal development of potato (*Solanum tuberosum*) tubers. *Plant and Cell Physiology* **52**, 1957-1972.
- Lin, C, Ogorek, LLP, Pedersen, O, Sauter, M (2021) Oxygen in the air and oxygen dissolved in the floodwater both sustain growth of aquatic adventitious roots in rice. *Journal of Experimental Botany* **72**, 1879-1890.
- Masepohl, B, Witty, JF, Riedel, KU, Klipp, W, Puehler, A (1993) *Rhizobium meliloti* mutants defective in symbiotic nitrogen fixation affect the oxygen gradient in alfalfa (*Medicago sativa*) root nodules. *Journal of Experimental Botany* **44**, 419-426.

- McKee, KL (1996) Growth and physiological responses of neotropical mangrove seedlings to root zone hypoxia. *Tree physiology* **16**, 883-889.
- McKee, KL, Mendelssohn, IA (1987) Root metabolism in the black mangrove (*Avicennia germinans* (L.) L) repsponse to hypoxia. *Environmental and Experimental Botany* 27, 147-156.
- Meitha, K, Agudelo-Romero, P, Signorelli, S, Gibbs, DJ, Considine, JA, Foyer, CH, Considine, MJ (2018) Developmental control of hypoxia during bud burst in grapevine. *Plant, Cell & Environment* **41**, 1154-1170.
- Meitha, K, Konnerup, D, Colmer, TD, Considine, JA, Foyer, CH, Considine, MJ (2015) Spatio-temporal relief from hypoxia and production of reactive oxygen species during bud burst in grapevine (*Vitis vinifera*). *Annals of Botany (London)* **116**, 703-711.
- Mignolli, F, Todaro, JS, Vidoz, ML (2020) Internal aeration and respiration of submerged tomato hypocotyls are enhanced by ethylene-mediated aerenchyma formation and hypertrophy. *Physiologia Plantarum* **169**,
- Mommer, L, Pedersen, O, Visser, EJW (2004) Acclimation of a terrestrial plant to submergence facilitates gas exchange under water. *Plant, Cell & Environment* 27, 1281-1287.
- Mommer, L, Wolters-Arts, M, Andersen, C, Visser, EJW, Pedersen, O (2007) Submergence-induced leaf acclimation in terrestrial species varying in flooding tolerance. *New Phytologist* **176**, 337-345.
- Mori, Y, Kurokawa, Y, Koike, M, Malik, AI, Colmer, TD, Ashikari, M, Pedersen, O, Nagai, K (2019) Diel O₂ dynamics in partially and completely submerged deepwater rice: Leaf gas films enhance internodal O₂ status, influence gene expression and accelerate stem elongation for 'snorkelling' during submergence. *Plant and Cell Physiology* **60**, 973-985.
- Müller, JT, van Veen, H, Bartylla, MM, Akman, M, Pedersen, O, Sun, P, Schuurink, RC, Takeuchi, J, Todoroki, Y, Weig, AR, Sasidharan, R, Mustroph, A (2019) Keeping the shoot above water submergence triggers antithetical growth responses in stems and petioles of watercress (*Nasturtium officinale*). *New Phytologist submitted*.
- Møller, CL, Sand-Jensen, K (2008) Iron plaques improve the oxygen supply to root meristems of the freshwater plant, *Lobelia dortmanna*. *New Phytologist* **179**, 848-856.
- Møller, CL, Sand-Jensen, K (2011) High sensitivity of *Lobelia dortmanna* to sediment oxygen depletion following organic enrichment. *New Phytologist* **190**, 320-331.
- Møller, CL, Sand-Jensen, K (2012) Rapid oxygen exchange across the leaves of *Littorella uniflora* provides tolerance to sediment anoxia. *Freshwater Biology* **57**, 1875-1883.
- Ober, ES, Sharp, RE (1996) A microsensor for direct measurement of O₂ partial pressure within plant tissues. *Journal of Experimental Botany* **47**, 447-454.
- Olsen, YS, Fraser, MW, Martin, B, Pomeroy, A, Lowe, RJ, Pedersen, O, Kendrick, GA (2018) *In situ* oxygen dynamics in rhizomes of *Posidonia sinuosa* impact of light, water column oxygen, current speed and wave velocity. *Marine Ecology Progress Series* **590**, 67-77.
- Pedersen, O, Binzer, T, Borum, J (2004) Sulphide intrusion in eelgrass (*Zostera marina* L.). *Plant Cell and Environment* **27**, 595-602.
- Pedersen, O, Borum, J, Duarte, CM, Fortes, MD (1998) Oxygen dynamics in the rhizosphere of *Cymodocea rotundata*. *Marine Ecology-Progress Series* **169**, 283-288.
- Pedersen, O, Colmer, TD, Borum, J, Zavala-Perez, A, Kendrick, GA (2016) Heat stress of two tropical seagrass species during low tides impact on underwater net photosynthesis, dark respiration and diel *in situ* internal aeration. *New Phytologist* **210**, 1207-1218.

- Pedersen, O, Colmer, TD, Garcia-Robledo, E, Revsbech, NP (2018) CO₂ and O₂ dynamics in leaves of plants with contrasting photosynthetic pathways (C₃ or CAM) application of a novel CO₂ microsensor. *Annals of Botany (London)* 10.1093/aob/mcy095.
- Pedersen, O, Malik, AI, Colmer, TD (2010) Submergence tolerance in *Hordeum marinum*: dissolved CO₂ determines underwater photosynthesis and growth. *Functional Plant Biology* **37**, 524-531.
- Pedersen, O, Pulido, C, Rich, SM, Colmer, TD (2011) *In situ* O₂ dynamics in submerged *Isoetes australis*: varied leaf gas permeability influences underwater photosynthesis and internal O₂. *Journal of Experimental Botany* **62**, 4691-4700.
- Pedersen, O, Rich, SM, Colmer, TD (2009) Surviving floods: leaf gas films improve O₂ and CO₂ exchange, root aeration, and growth of completely submerged rice. *The Plant Journal* **58**, 147-156.
- Pedersen, O, Vos, H, Colmer, TD (2006) Oxygen dynamics during submergence in the halophytic stem succulent *Halosarcia pergranulata*. *Plant Cell and Environment* **29**, 1388-99.
- Pellegrini, E, Konnerup, D, Winkel, A, Casolo, V, Pedersen, O (2017) Contrasting oxygen dynamics in *Limonium narbonense* and *Sarcocornia fruticosa* during partial and complete submergence. *Functional Plant Biology* **44**, 867-876.
- Peralta Ogorek, LL, Pellegrini, E, Pedersen, O (2021) Novel functions of the root barrier to radial oxygen loss radial diffusion resistance to H₂ and water vapour. *New Phytologist* **231**, 1365-1376.
- Porterfield, DM, Kuang, A, Smith, PJS, Crispi, ML, Musgrave, ME (1999) Oxygen-depleted zones inside reproductive structures of Brassicaceae: Implications for oxygen control of seed development. *Canadian Journal of Botany* 77, 1439-1446.
- Raetsch, G, Haase, K (2007) Anatomic prerequisites for internal root aeration of three tree species of the Amazonian inundation forest. *Amazoniana* **19**, 185-197.
- Raskin, I, Kende, H (1984) Regulation of growth in stem sections of deep water rice. *Planta* (*Heidelberg*) **160**, 66-72.
- Raun, AL, Borum, J (2013) Combined impact of water column oxygen and temperature on internal oxygen status and growth of *Zostera marina* seedlings and adult shoots *Journal of Experimental Marine Biology and Ecology* **441**, 16-22.
- Revsbech, NP, Pedersen, O, Reichardt, W, Briones, A (1999) Microsensor analysis of oxygen and pH in the rice rhizosphere under field and laboratory conditions. *Biology and Fertility of Soils* **29**, 379-385.
- Rich, SM, Ludwig, M, Pedersen, O, Colmer, TD (2011) Aquatic adventitious roots of the wetland plant *Meionectes brownii* can photosynthesize: implications for root function during flooding. *New Phytologist* **190**, 311-319.
- Rich, SM, Pedersen, O, Ludwig, M, Colmer, TD (2013) Shoot atmospheric contact is of little importance to aeration of deeper portions of the wetland plant *Meionectes brownii*; submerged organs mainly acquire O₂ from the water column or produce it endogenously in underwater photosynthesis. *Plant, Cell & Environment* 36, 213-23.
- Rijnders, JGHM, Armstrong, W, Darwent, MJ, Blom, CWPM, Voesenek, LACJ (2000) The role of oxygen in submergence-induced petiole elongation in *Rumex palustris*: In situ measurements of oxygen in petioles of intact plants using micro-electrodes. *New Phytologist* **147**, 497-504.
- Robe, WE, Griffiths, H (1990) Photosynthesis of *Littorella uniflora* grown under two par regimes c-3 and cam gas exchange and the regulation of internal carbon dioxide and oxygen concentrations. *Oecologia (Berlin)* **85**, 128-136.
- Romanov, VI, Gordon, AJ, Minchin, FR, Witty, JD, Skot, L, James, CL, Borisov, AY, Tikhonovich, IA (1995) Anatomy, physiology and biochemistry of root nodules of

- Sprint-2 Fix-, a symbiotically defective mutant of pea (*Pisum sativum L.*). *Journal of Experimental Botany* **46**, 1809-1816.
- Sand-Jensen, K, Pedersen, O, Binzer, T, Borum, J (2005) Contrasting oxygen dynamics in the freshwater isoetid *Lobelia dortmanna* and the marine seagrass *Zostera marina*. *Annals of Botany (London)* **96**, 613-623.
- Sand-Jensen, K, Prahl, C (1982) Oxygen exchange with the lacunae and across leaves and roots of the submerged vascular macrophyte *Lobelia dortmanna*. *New Phytologist* **91**, 103-120.
- Scholander, PF, van Dam, L, Scholander, SI (1955) Gas exchange in the roots of mangroves. *American Journal of Botany* **42**, 92-98.
- Schuette, JL (1996) Lacunar pressures in *Myriophyllum heterophyllum*: Manometric measurement and diurnal gas dynamics in field populations. *Aquatic Botany* **54**, 321-336
- Shimamura, S, Yamamoto, R, Nakamura, T, Shimada, S, Komatsu, S (2010) Stem hypertrophic lenticels and secondary aerenchyma enable oxygen transport to roots of soybean in flooded soil. *Annals of Botany (London)* **106**, 277-284.
- Skelton, NJ, Allaway, WG (1996) Oxygen and pressure changes measured in situ during flooding in roots of the grey mangrove *Avicennia marina* (Forssk.) Vierh. *Aquatic Botany* **54**, 165-175.
- Sorrell, BK, Tanner, CC (2000) Convective gas flow and internal aeration in *Eleocharis* sphacelata in relation to water depth. *Journal of Ecology* **88**, 778-789.
- Sorz, J, Hietz, P (2008) Is oxygen involved in beech (*Fagus sylvatica*) red heartwood formation? *Trees (Berlin)* **22**, 175-185.
- Sou, H-D, Masumori, M, Ezaki, G, Tange, T (2020) Source of oxygen fed to adventitious roots of *Syzygium kunstleri* (King) Bahadur and R.C. Gaur grown in hypoxic conditions. *Plants-Basel* **9**, 1433.
- Sou, H-D, Masumori, M, Yamanoshita, T, Tange, T (2021) Primary and secondary aerenchyma oxygen transportation pathways of *Syzygium kunstleri* (King) Bahadur & R. C. Gaur adventitious roots in hypoxic conditions. *Scientific Reports* 11, 4520.
- Soukup, A, Armstrong, W, Schreiber, L, Franke, R, Votrubová, O (2007) Apoplastic barriers to radial oxygen loss and solute penetration: a chemical and functional comparison of the exodermis of two wetland species, *Phragmites australis* and *Glyceria maxima*. *New Phytologist* **173**, 264-278.
- Spalding, MH, Stumpf, DK, Ku, MSB, Burris, RH, Edwards, GE (1979) Crassulacean acid metabolism and diurnal variations of internal CO₂ and O₂ concentrations in *Sedum praealtum* DC. *Functional Plant Biology* **6**, 557-567.
- Spicer, R, Holbrook, NM (2005) Within-stem oxygen concentration and sap flow in four temperate tree species: does long-lived xylem parenchyma experience hypoxia? *Plant Cell and Environment* **28**, 192-201.
- Steinmann, F, Braendle, R (1981) Flooding tolerance in bulrush *Schoenoplectus lacustris* relations between oxygen supply and adenylate energy charge of the rhizomes depending on the environmental oxygen concentrations. *Flora (Jena)* **171**, 307-314.
- Stiles, W (1960) The composition of the atmosphere (oxygen content of air, soil, intercellular spaces, diffusion, carbon dioxide and oxygen tension). In 'Encyclopedia of Plant Physiology, Plant respiration inclusive fermentations and acid metabolism.' (Ed. e W. Ruhland.) Vol. Vol. XII (Part 2) pp. 114 148. (Springer Verlag: Heidelberg, Germany)
- Studer, C, Braendle, R (1984) Oxygen consumption and availability in the rhizomes of *Acorus calamus, Glyceria maxima, Menyanthes trifoliata, Phalaris arundinacea, Phragmites communis* and *Typha latifolia*. *Botanica Helvetica* **94**, 23-32.

- Stuenzi, JT, Kende, H (1989) Gas composition in the internal air spaces of deepwater rice in relation to growth induced by submergence. *Plant and Cell Physiology* **30**, 49-56.
- Takaoki, T (1983) Accumulation of oxygen gas in excised maize root on aging in water and water uptake by the root. *Plant and Cell Physiology* **24**, 1175-1182.
- Teakle, NL, Colmer, TD, Pedersen, O (2014) Leaf gas films delay salt entry and enhance underwater photosynthesis and internal aeration of *Melilotus siculus* submerged in saline water. *Plant, Cell & Environment* 37, 2339-2349.
- Valeri, MC, Novi, G, Weits, DA, Mensuali, A, Perata, P, Loreti, E (2021) *Botrytis cinereainduces* local hypoxia in Arabidopsis leaves. *New Phytologist* **229**,
- van Dongen, JT, Schurr, U, Pfister, M, Geigenberger, P (2003) Phloem metabolism and function have to cope with low internal oxygen. *Plant Physiology (Rockville)* **131**, 1529-1543.
- van Veen, H, Mustroph, A, Barding, GA, Vergeer-van Eijk, M, Welschen-Evertman, RAM, Pedersen, O, Visser, EJW, Larive, CK, Pierik, R, Bailey-Serres, J, Voesenek, LACJ, Sasidharan, R (2013) Two *Rumex* species from contrasting hydrological niches regulate flooding tolerance through distinct mechanisms. *The Plant Cell* **25**, 4691-4707.
- Vashisht, D, Hesselink, A, Pierik, R, Ammerlaan, JMH, Bailey-Serres, J, Visser, EJW, Pedersen, O, van Zanten, M, Vreugdenhil, D, Jamar, DCL, Voesenek, LACJ, Sasidharan, R (2011) Natural variation of submergence tolerance among *Arabidopsis thaliana* accessions. *New Phytologist* **190**, 299-310.
- Verboven, P, Pedersen, O, Herremans, E, Ho, QT, Nicolaï, BM, Colmer, TD, Teakle, N (2012) Root aeration via aerenchymatous phellem: three-dimensional micro-imaging and radial O₂ profiles in *Melilotus siculus*. *New Phytologist* **193**, 420-431.
- Verboven, P, Pedersen, O, Ho, QT, Nicolai, BM, Colmer, TD (2014) The mechanism of improved aeration due to gas films on leaves of submerged rice. *Plant, Cell & Environment* 37, 2433-2452.
- Verslues, PE, Ober, ES, Sharp, RE (1998) Root growth and oxygen relations at low water potentials: Impact of oxygen availability in polyethylene glycol solutions. *Plant Physiology (Rockville)* **116**, 1403-1412.
- Voesenek, LACJ, Armstrong, W, Bogemann, GM, McDonald, MP, Colmer, TD (1999) A lack of aerenchyma and high rates of radial oxygen loss from the root base contribute to the waterlogging intolerance of *Brassica napus*. *Australian Journal of Plant Physiology* **26**, 87-93.
- Wang, W, Han, R, Wan, Y, Liu, B, Tang, X, Liang, B, Wang, G (2014) Spatio-temporal patterns in rhizosphere oxygen profiles in the emergent plant species *Acorus calamus*. *PLoS ONE* **9**, e98457.
- Weisner, SEB, Graneli, W (1989) Influence of substrate conditions on the growth of *Phragmites australis* after a reduction in oxygen transport to below-ground parts. *Aquatic Botany* **35**, 71-80.
- Weits, DA, Kunkowska, AB, Kamps, NCW, Portz, KMS, Packbier, NK, Nemec Venza, Z, Gaillochet, C, Lohmann, JU, Pedersen, O, van Dongen, JT, Licausi, F (2019) An apical hypoxic niche sets the pace of shoot meristem activity. *Nature* **569**, 714-717.
- Winkel, A, Colmer, TD, Ismail, AM, Pedersen, O (2013) Internal aeration of paddy field rice (*Oryza sativa*) during complete submergence importance of light and floodwater O₂. *New Phytologist* **197**, 1193-1203.
- Winkel, A, Colmer, TD, Pedersen, O (2011) Leaf gas films of *Spartina anglica* enhance rhizome and root oxygen during tidal submergence. *Plant, Cell & Environment* **34**, 2083-2092.

- Wittmann, C, Pfanz, H (2014) Bark and woody tissue photosynthesis: a means to avoid hypoxia or anoxia in developing stem tissues. *Functional Plant Biology* **41**, 940-953.
- Wittmann, C, Pfanz, H (2018) More than just CO₂-recycling: corticular photosynthesis as a mechanism to reduce the risk of an energy crisis induced by low oxygen. *New Phytologist* **219**, 551-564.
- Yabuki, K, Kitaya, Y, Sugi, J (1990) Studies on the function of mangrove pneumatophores 2. *Environment Control in Biology* **28**, 99-102.
- Yamasaki, S (1984) Role of plant aeration in zonation of *Zizania latifolia* and *Phragmites australis*. *Aquatic Botany* **18**, 287-298.
- Yamasaki, S (1987) Oxygen demand and supply in *Zizania latifolia* and *Phragmites australis*. *Aquatic Botany* **29**, 205-216.
- Yamasaki, S, Saeki, T (1979) The effects of the oxygen supply from the shoot on *Sizania latifolia* growth. *Japanese Journal of Ecology* **29**, 249-256.
- Zabalza, A, Van Dongen, JT, Froehlich, A, Oliver, SN, Faix, B, Gupta, KJ, Schmalzlin, E, Igal, M, Orcaray, L, Royuela, M, Geigenberger, P (2009) Regulation of respiration and fermentation to control the plant internal oxygen concentration. *Plant Physiology (Rockville)* **149**, 1087-1098.

Bibliography of Supplementary Materials

- Barton, K, Barton, MK (2022) 'Package 'MuMln', 1.47.1: Multi-Model Inference, version 1.47.1. 2022.' Available at https://cran.r-project.org/web/packages/MuMln/MuMln.pdf [Accessed October 1st 2022].
- Burnham, KP, Anderson, DR (2004) Multimodel inference: understanding AIC and BIC in model selection. *Sociological methods & research* **33**, 261-304.
- Fox, J, Weisberg, S (2018) 'An R companion to applied regression.' (Sage publications: Los Angeles, London, New Delhi, Singapore, Washington DC, Melbourne)
- Pinheiro, J, Bates, D, DebRoy, S, Sarkar, D, Heisterkamp, S, Van Willigen, B (2022) 'Package 'nlme': Linear and nonlinear mixed effects models, version 3.1.' Available at https://cran.r-project.org/package=nlme [Accessed October 1st 2022].
- R Core Team (2014) 'R: A language and environment for statistical computing.' (R Foundation for Statistical Computing: Vienna, Austria)