

REVIEW

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# Functional traits: the pathways to riverine plant resistance in times of hydropeaking

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## Abstract

Hydropeaking, which refers to rising or falling discharges caused by the turning on or off of hydro-turbines to generate electricity, is a topic of growing interest due to its impact on fluvial ecosystems. To date, most hydropeaking studies have focused on the impact of peak fluctuations on invertebrate and fish communities, but little attention has been paid to its impact on riverine plants and how functional traits may make them resistant to hydropeaking. We performed a review to assess how a set of 32 plant functional traits can be expressed in riverine plant species, and found evidence of how such expression affects their capacity to cope with common sources of hydropeaking disturbance (i.e., inundation, fast water drawdown, and rapid water fluctuations linked to up-ramping and down-ramping hydropeaking operations). The information here presented can simplify the evaluation of impacts on riverine plant communities worldwide, as well as to detect suitable species to successfully restore rivers affected by hydro-power production.

**Keywords** Drought, Flooding, Waterlogging, Hydropeaking, Plant trait, Riverine vegetation

## Background

Hydropeaking (HP), which refers to repeated daily or sub-daily sudden water releases downstream of a hydropower plant in response to daily peaks of electricity demand (e.g., Cushman 1985; Morrison and Smokorowski 2000; Costa et al. 2019), is considered a flexible method of producing electricity because it can generate power within minutes. Unfortunately, it is also one of the most ecologically harmful modes of hydropower generation since the river ecosystem's downstream biotic and abiotic elements suffer from extreme flow events that deviate greatly from the free-flowing natural regime (Smokorowski 2022). The range of flow alterations resulting from HP depends highly on the operation scheme of the hydropower plant

(i.e., magnitude, rate of change, frequency, duration, and timing of HP operations; Harby and Noack 2013), but four distinct operational phases are commonly distinguished: baseflow discharge (no electricity production), increasing discharge or up-ramping (start of the turbines), continuous high peak discharge (peak energy demand), and decreasing discharge or down-ramping (shutdown of the turbines) (e.g., Bruder et al. 2016; Tonolla et al. 2017). The succession of multiple daily hydropeaks (with their respective operational phases) introduces a significant number of artificial flow events altering the ecological integrity of the river downstream of hydropower stations (e.g., Bunn and Arthington 2002).

Like other organisms, riverine plants in HP systems are exposed to frequent inundations, fast water draw-downs, and short-term fluctuations in water flow and water levels, but also extended periods of drought linked to periods of low energy supply and along bypassed river reaches (Stella et al. 2010; Bejarano et al. 2020; Baladrón et al. 2022). Novel hydrology caused by HP has no natural correspondence in freshwater systems, and hence few species have adaptations to all its aspects (Bejarano et al.

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2018). Although riverine plants have mechanisms and adaptations to cope with peak flows, drought periods, fast water currents, and rapid water-level changes (see Kawecki and Ebert 2004), the frequent and abrupt variations in hydraulic parameters imposed by HP may exceed plant tolerance (Bejarano et al. 2018), ultimately affecting germination, growth and long-term survival, inducing changes in plants' morphology and physiology (Baladrón et al. 2022), and modifying long-established patterns of local adaptation.

Climate change is putting pressure on governments to reduce reliance on fossil fuels. In this regard, hydropower can play a dual role in the transition toward a low-carbon energy future (Jager et al. 2022). First, it can support the grid when wind and solar are not available. In addition, hydropower has flexibility similar to that provided by natural gas and may constitute a key renewable source in the electricity portfolio (Shan et al. 2020). Therefore, given that HP is unavoidable (Smokorowski 2022), it is critical to understand the adaptive capacity of riverine plants to the various environmental stresses resulting from it to ensure proper river management. The study of plant functional traits can serve this purpose, as they are behind the mechanisms that determine whether species manage to adapt to environmental change and stress (Kearney et al. 2010; Pollock et al. 2012; Regos et al. 2019).

Functional traits are defined as morphological, anatomical, biochemical, physiological, and phenological features or mechanisms of resilience, with the capacity to impact fitness via their effects on growth, reproduction, and survival of individuals (McGill et al. 2006; Violle et al. 2007; Mouillot et al. 2013; Nock et al. 2016). The use of plant functional traits to investigate the effects of human disturbance at multiple field scales (from plant communities to ecosystem-level functions; e.g., Suding et al. 2008) is gaining momentum nowadays (e.g., Garnier et al. 2004; Miedema Brown and Anand 2022). The adaptive capacity of plants to the surrounding environment depends on functional trait expression (e.g., Pollock et al. 2012), meaning that only species adopting particular trait values or modalities have the opportunity to become abundant under certain environmental conditions (Tang et al. 2022). The values or modalities taken by each trait are called attributes (see Violle et al. 2007). Independently of their taxonomic identity, plants sharing identical attributes are expected to respond similarly to environmental stressors (Lavorel et al. 1997; Merritt et al. 2010; Stromberg and Merritt 2015) and will display similar degrees of tolerance to them (see Valladares et al. 2007). Environmental filters, such as fluvial disturbances, can exclude species lacking suitable attributes from entering

and remaining in a community, consequently shaping its structure (Venn et al. 2011). In this respect, the novel hydrology imposed by HP regimes may filter out species from functional groups without appropriate trait attributes to cope with flooding, frequent water-level fluctuations, and drought (i.e., intolerant plants). Conversely, species with attributes suitable to deal with the new fluvial environment (i.e., easily dispersed, flexible, flood-tolerant, and amphibious plants; Keddy 1992; Mouillot et al. 2013; Bejarano et al. 2018) may successfully germinate, grow, and persist.

Identifying functional trait attributes capable to confer plants advantages against common HP disturbances may help determine which riverine communities are vulnerable to HP and, conversely, which ones may reasonably withstand it without risk of suffering severe degradation (Baladrón et al. 2022). Additionally, analyzing the impact of HP on plant species from a trait-based perspective is more informative than predicting their response according to "ecological affinities" (i.e., data that describe the general response of a species to an environmental variable, habitat, or resource (e.g., drought or flooding tolerance, soil moisture); see Palmquist et al. 2017). Trait-based approaches facilitate the generalization of patterns and transfer across systems since traits may be shared among different floristic regions (Díaz et al. 1998; Bejarano et al. 2016), whereas "ecological affinities" approaches often integrate multiple traits, obscuring linkages among environmental variables and hampering efforts to avoid circularity in cause and effect (Verberk et al. 2013; Palmquist et al. 2017).

Previous trait database and website projects, including EcoFlora (Fitter and Peat 1994), BioFlor (Klotz et al. 2002), BIOPOP (Poschlod et al. 2003), LEDA (Kleyer et al. 2008), PLANTS (USDA 2010), SID (SER, INSR, RBGK 2023), GLOPNET (Reich et al. 2009), MARIWENN (Baralotto et al. 2011), BROT (Paula and Pausas 2013), FLOWBASE (Aguiar et al. 2013), TRY (Boenisch and Kattge 2014), and eHALOPH (Flowers et al. 2015), have gathered data on biological traits and ecological affinities of thousands of common plant species throughout the world (Bejarano et al. 2016; Palmquist et al. 2017). Likewise, there is an extensive literature published on how plants benefit from functional traits to withstand the effects of fluvial disturbances and water availability gradients in a variety of freshwater ecosystems (Tables 1, 2, 3).

However, to date, no specific studies have been conducted to compile information on traits capable of improving the fitness of riverine plant species exposed to common HP disturbances. The goal of this study is to synthesize and bring together information from published sources on functional plant traits scattered in the

**Table 1** Selected reviews/syntheses on functional traits that protect plants from the effects of fluvial disturbances

Paper topic	Fluvial disturbance	Functional traits referenced in the text	References
Plant responses to avoid the adverse effects of submergence	Submergence	Aerenchyma formation, shoot elongation, underwater photosynthesis, leaf cuticle thickness, specific leaf area, chloroplasts reorientation, gene regulatory networks aimed at sensing submergence	Voesenek et al. (2006)
Exploration of natural variation in strategies that improve O <sub>2</sub> and carbohydrate status for plants during flooding	Partial and complete submergence	Shoot elongation, aerenchyma formation, leaf cuticle thickness, chloroplast position, gene regulation to enhance anaerobic catabolism (e.g., fermentation capacity), carbohydrate consumption (i.e., intolerant species to flooding will up-regulate genes controlling carbohydrate consumption to promote shoot elongation and "escape" from submergence; in contrast, plant adopting a quiescence strategy to "resist" under the water, will downregulate carbohydrate consumption to save energy)	Bailey-Serres and Voesenek (2008)
Functional traits and their role in wetland plant adaptation and ecosystem functioning	Waterlogging and submergence	Adventitious roots, aerenchyma formation and ventilation systems (e.g., convective flow of gases through shoot organs and along rhizomes of some wetland species), radial O <sub>2</sub> loss barrier, anaerobic energy production, carbohydrate conservation (i.e., downregulation of ATP consumption), prevention of reactive oxygen species (ROS), antioxidant mechanisms, nastic movements, shoot elongation, aquatic leaf traits, leaf gas films	Colmer and Voesenek (2009)
Mechanisms of tolerance to anoxia in plant tissue exposed to lack of O <sub>2</sub> as a consequence of waterlogging and submergence	Soil waterlogging and submergence	Metabolic acclimations: regulation of anaerobic catabolism (e.g., synthesis of anaerobic proteins such as starch-degrading enzymes, and other enzymes involved in sugar catabolism under anoxia), carbohydrate conservation, coleoptile elongation, aerenchyma formation, root detipping ("controlled" root tip death), nucleotide regeneration (i.e., recovery of oxidized nucleotides reduced during glycolysis, from NO <sub>3</sub> <sup>-</sup> to NH <sub>4</sub> <sup>+</sup> )	Gibbs and Greenway (2003)
Mechanisms of tolerance to anoxia in plants exposed to lack of O <sub>2</sub> due to waterlogging and submergence	Soil waterlogging and submergence	Metabolic acclimations: carbohydrate conservation, gene regulation to enhance anaerobic catabolism (e.g., transcription of genes involved in the alcoholic and lactic fermentation pathways) and to repress the transcription of enzymes involved in protein degradation (i.e., allows protein turnover to be decreased, thereby conserving ATP)	Geigenberger (2003)
Review of structural and metabolic features that participate in antioxidant protection under anoxia	Soil waterlogging and submergence	Antioxidant mechanisms	Blokhina et al. (2003)
Review on how aerenchyma and radial O <sub>2</sub> loss barriers favor O <sub>2</sub> diffusion into the plant rhizosphere, which enhances root penetration into anaerobic substrates	Partial or total submergence, waterlogged soils	Aerenchyma formation and ventilation systems (e.g., convective flow of gases through shoot organs and along rhizomes of some wetland species), radial O <sub>2</sub> loss barrier	Colmer (2003)
Evidence implicating ethylene as the principal factor initiating fast underwater elongation by leaves or stems is evaluated comprehensively, along with its interactions with other hormones and gases	Partial or total submergence, waterlogged soils	Ethylene-mediated underwater elongation	Jackson (2008)

Studies listed in this table refer to any freshwater ecosystem (i.e., rivers, streams, wetlands, lakes and ponds)

**Table 2** Selected reviews/syntheses on functional traits that protect plants from the effects of fluvial disturbances

Paper topic	Fluvial disturbance	Functional traits referenced in the text	References
Database of traits underlying responses of woody riparian species in Sweden to different hydrological and hydraulic conditions	Flooding, drawdown, fast water fluctuations	Plant growth form, shoot growth-form, size at maturity, woodiness, leaf length, leaf width, leaf area, leaf consistency, leaf anatomy, leaf persistence, rooting depth, root morphology, active growth period, bloom period, seed dispersal period, germination, seed/spore bank longevity, age of first flowering, reproduction type, resprouting ability, diaspore type, diaspore length, diaspore width, diaspore weight, pollen vector, dispersal vector, numbers of seeds, life-span, plant growth rate, tolerance to drought, tolerance to prolonged submergence or soil waterlogging, tolerance to salty conditions, tolerance to frost, light requirements, fertility requirements, germination requirements, substrate type preferences, substrate pH preferences, bank-slope preferences, strategy type	Bejarano et al. (2016)
Hydropeaking effects on riverine plants	Flooding, drawdown, fast water fluctuations, water quality changes	Shoot elongation, hyponastic growth, presence of suberin barriers in root epidermis, adventitious roots, aerenchyma formation, leaf cuticle thickness, leaf size, leaf shape, leaf consistency, leaf anatomy, leaf persistence, leaf mass per leaf area, stomata closure, chloroplasts in epidermis, woodiness, CO <sub>2</sub> concentrating mechanisms, regulation of anaerobic catabolism, antioxidant generation, perennial life cycles (i.e., particularly sensitive life stages such as seed germination do not have to face fluvial disturbance every year), plant growth-form, plant height, plant flexibility/shape reconfiguration, resprouting ability, below-ground organs and mass allocation	Bejarano et al. (2018)
Key processes enabling forest trees to cope with extreme drought	Drought	Hydraulic conductivity, stomatal conductance, stomatal control (i.e., opening/closing), water storage capacity in the sapwood, xylem conduit dimensions, biomass allocation, leaf venation network	Breda et al. (2006)
A review on trait-driven responses shown by trees of the Amazonian floodplains to extreme changes of hydric conditions in the annual cycle	Waterlogging, submergence, drought, rapid changes of water levels	Accumulation of carbohydrate reserves, underwater photosynthesis, plant height, aerenchyma formation and ventilation systems (i.e., pressurized gas transport), root suberization, adventitious roots, presence of pneumatophores, knees and pneumatodes, plank-buttresses and stilt roots, nitrogen fixation via stem-nodulation and nodulated adventitious roots, leaf structure, leaf persistence, leaf cuticle thickness, leaf size, leaf chlorophyll content, specific leaf mass, leaf xeromorphism, leaf nitrogen content, presence of sunken stomata, parenchyma structure, resprouting ability, dormancy of seeds, fruit maturation and seed release, timing of germination	Parolin et al. (2004)

Table 2 (continued)

Paper topic	Fluvial disturbance	Functional traits referenced in the text	References
Relationships between ecological-response traits (i.e., those describing how a plant will respond to abiotic stressors) and morphological-effect traits (i.e., those determining how a plant alters the flow of water and transport of sediment)	Dry conditions; high-flow conditions, mechanical disturbance from floods	Specific leaf area, carbon isotope ratio, stem-tissue density, plant height, biomass, volume, wood density, root depth, seed mass, seed size, seed dormancy, plant frontal area, basal diameter, root frontal area, root architecture, stem flexibility, leaf shape, resprouting ability, leaf buoyancy, branching	Diehl et al. (2017)
A trait-based data compilation to analyze riparian vegetation change in response to dam operations and climate change in the Grand Canyon	Waterlogging, submergence, rapid changes of water levels	Specific leaf area, relative growth rate, maximum salinity tolerated, seed weight, maximum rooting depth, average height at maturity, anaerobic tolerance, drought tolerance, fire tolerance, moisture use, salinity tolerance, shade tolerance, growth rate, lifespan, ability to reproduce sexually, ability to reproduce vegetatively, spread rate, resprouting ability, bloom period, seeding period	Palmquist et al. (2017)

Studies listed in this table refer to rivers and riparian corridors

**Table 3** Selected reviews/syntheses on functional traits that protect plants from the effects of fluvial disturbances

Paper topic	Fluvial disturbance	Functional traits referenced in the text	References
Ventilation mechanisms in plant groups that thrive in oxygen-deficient environments	Saturated soils, partial or total submergence	Aerenchyma formation, pressurized ventilation, thermo-osmotic gas transport, humidity-induced diffusion mechanisms, radial oxygen loss barriers, water-repellent leaf surface, leaf buoyancy, leaf shape, special structures (i.e., pneumatophores, knee roots and stilt roots), hypertrophied lenticels, "knees" emerging from the roots to the surface of the water	Björn et al. (2022)
Functional traits and their role in wetland plant adaptation and ecosystem functioning	Water table fluctuations, drought, flooding, soil saturation	Physiological down-regulation, leaf dimorphism, aerenchyma formation, rapid shoot elongation, adventitious roots, radial oxygen loss barriers, hypertrophied lenticels, water-conserving mechanisms (such as temporary stomatal closure or lower stomatal pore area), hydraulic conductance, wood density, specific leaf area, photosynthetic capacity, leaf cuticle thickness, root porosity, root mechanical strength, root depth, plant growth rate, below-ground biomass allocation, leaf dry matter content, stem flexibility, leaf mechanical resistance, sclerophylly, clonal reproduction	Moor et al. (2017)
Study on several angiosperm plant species of wetlands that aerate their submerged organs by thermo-osmotic transport of gas, a special adaptation of the wetland plants to the anoxic environment	Partial or total submergence, waterlogged soils	Ventilation systems (i.e., thermo-osmotic transport of gas to submerged organs)	Grosse et al. (1991)
A review of mechanisms that underlie short- and long-term tolerance to external anaerobic conditions (i.e., soil inundation and submergence)	Soil inundation and submergence	Regulation of anaerobic energy metabolism (e.g., control of the expression of anaerobic proteins genes under anoxia), avoidance of self poisoning (i.e., controlling levels of with ethanol derived from fermentation), regulation of cytoplasmic acidosis, root elongation, root regeneration, aerenchyma formation, adventitious roots, presence of large carbohydrate stocks, plant quasi-dormant state (i.e., to survive under seasonal anoxia and avoid energy starvation), detoxification of free radicals (antioxidant mechanisms)	Vartapetian and Jackson (1997)
A systematic review of the peer-reviewed literature (published 2000 to 2020) addressing plant functional traits in wetland restoration	Soil inundation, submergence, rapid water fluctuations	Due to the extensive list of traits reported, the reader is invited to revise it here: <a href="https://doi.org/https://doi.org/10.1007/s13157-023-01741-z">https://doi.org/https://doi.org/10.1007/s13157-023-01741-z</a>	Sloey et al. (2023)

Studies listed in this table refer to wetland ecosystems



**Table 4** Main consequences resulting from HP affecting plant performance (Baladrón et al. 2023; adapted from Bejarano et al. 2018)

Hydrological alterations	Changes triggered in the river environment	Consequences for vegetation
Flooding	Rapid light attenuation	Reduced biomass production, difficulties to regenerate plant organs (e.g., leaves and absorbing roots)
Flooding	Slow gas diffusion	Photosynthesis and respiration impairment, inhibition of root formation and branching, limited growth of existing roots and mycorrhizae
Flooding	Anoxia	Cell acidification, reactive oxygen species (ROS) generation, low ATP production (oxidative phosphorylation disruption), depletion of plant carbohydrate reserves, impairment of plant functions (e.g., stomatal opening, photosynthesis, water and mineral uptake, hormonal balance)
Flooding	Accumulation of toxic compounds	Impaired physiological and plant biochemical reactions, breakdown of cell membranes
Water drawdown	Soil moisture deficits and water shortage	Reduced growth and vigor, wilting, inhibition of seed germination
Water fluctuations	Increase in drag and lift mechanical forces	Physical injury, biomass loss, breakage and uprooting of plants, limited seed germination
Water fluctuations	Erosion during up-ramping and peak flow stages	Loss of riparian substrate, plant uprooting, biomass loss due to impact of river substrate materials (sand, gravel, pebbles)
Water fluctuations	Sediment deposition during receding discharge	Plants coated in silt or buried, soil surface clogging, limited seedling establishment and survival

literature which, if well selected and analyzed from an HP perspective, can help to advance science and management in the field of HP.

### Selection of relevant traits in the HP context

#### Common HP disturbances affecting riverine vegetation

We selected the most relevant hydrological alterations linked to HP (i.e., inundation, water drawdown and water fluctuations) likely impairing plants' performance (e.g., germination, plant survival and growth). The main consequences of HP on plant performance were retrieved from Bejarano et al. (2018) and summarized in Table 4.

#### Functional trait selection

We selected a list of 32 functional traits (19 morpho-anatomical and 13 physiological) which, directly or indirectly, have been extensively documented as capable to adapt plants to the stress imposed by submergence, soil waterlogging, mechanical forces exerted by large flow discharges, and drought. The selected pool of traits is therefore important with respect to the hydrological alterations and derived changes in the river environment (Table 4) resulting from HP.

A review of the TRY database (Kattge et al. 2011; Boenisch and Kattge 2014) and of multiple published papers in the field of plant traits was performed to find functional traits of interest in the field of HP. Consulted papers showed a wide variety of attribute descriptions, and focused on particular or several traits. Deciding on the number of functional traits to include in the study was a back-and-forth process in which multiple considerations were made. Some trait-based approaches rely on the smallest number of traits to explain plants' responses

to environmental conditions (principle of parsimony, e.g., Bernhardt-Römermann et al. 2008), whereas other approaches encourage to consider as many traits as possible in the analysis (e.g., Cornelissen et al. 2003). We chose to include multiple traits a priori intercorrelated and functionally redundant (i.e., traits syndrome; e.g., Bontemps et al. 2017). For instance, thick leaves, woody stems, and the presence of trichomes in plants' surfaces appear together as coordinated suites of traits to help plants prevent excessive evapotranspiration (Crang et al. 2018) during dry periods. Since these traits are functionally correlated, we could select one of them and disregard the other two. However, recent studies have highlighted that simplifying trait dimensionality can obscure overall patterns of plant adaptation because individual traits often contribute in a combined way to plant tolerance in different environments (Bruehlheide et al. 2018; Yin et al. 2018). Given that HP creates complex and substantially different environments in the river within short-time scales (i.e., inundation and desiccation may occur within periods of a few hours or days), it is possible that some traits framed within a given trait syndrome may provide resistance only against a specific HP component. For instance, thick leaves, woody stems, and trichomes protect plants against drought, but not against the mechanical forces that occur during up-ramping HP stages, or against the inundation events resulting from water storage. Therefore, we believe it is key to incorporate multiple traits presumably relevant from an HP standpoint, even those functionally redundant.

Additionally, trait selection is constrained by the amount of information available in the literature (Gayraud et al. 2003). Traits may be soft or hard. A variety of soft traits

(i.e., morphological traits; e.g., plant and shoot growth-form, presence of woody tissues, leaf cuticle thickness, leaf mass per leaf area) and hard traits (i.e., physiological traits; e.g., CO<sub>2</sub> concentrating mechanisms, antioxidants generation, stomatal control aperture) provide plants different abilities to live in a range of magnitudes, frequencies, and durations of extreme flow events (Bejarano et al. 2016), including those imposed by peaking hydropower plants. Soft traits are relatively easy and quick to quantify, but also less directly related to a given plant function (Hodgson et al. 1999; Cornelissen et al. 2003). Conversely, hard traits usually are more accurate indicators of plant responses (e.g., Lavorel and Garnier 2002; Cornelissen et al. 2003) than soft traits, but also time-consuming and difficult to measure. As a result, the amount of information available on soft traits was significantly higher than that published on hard traits, explaining the higher number of morphological traits included in our study.

After having a definitive list of relevant traits, we defined modalities (i.e., trait attributes under which plant species can be grouped; Violle et al. 2007). Subsequently, we evaluated the degree of protection that each trait attribute may offer against HP disturbances. Generally, an attribute that confers an advantage against one disturbance triggered by HP may at the same time confer a disadvantage against a contrasting HP disturbance. For instance, deep-rooting systems in plants may contribute to capture water during dry conditions associated to HP drawdown (e.g., Bielak et al. 2014), but they will not be of help to avoid root hypoxia (e.g., Kaelke and Dawson 2003) in waterlogged soils resulting from frequent flow rise. Following this rationale, trait attributes were reclassified into three HP categories: "resistant", "partially resistant" and "vulnerable" (see Baladrón et al. 2023). We used the term "resistant" for attributes that may help plants to either avoid or tolerate HP disturbances (i.e., avoidance refers to traits that help plants to prevent the deleterious effects of adverse conditions, whereas tolerance consists in traits that enable plants to endure adverse conditions; Fitter and Hay 2002; Puijalon et al. 2011). On the contrary, the term "vulnerable" refers to attributes that may not offer plants the capacity to successfully avoid neither tolerate the negative effects of HP (Baladrón et al. 2023).

Traits were of binary nature when a functional property was present or absent (e.g., presence of chloroplasts in epidermis can adopt the categories "yes" or "no"), or adopted a set of categorical values e.g., stomatal control adopted three categories: (1) non-efficient control of stomatal aperture, (2) moderately efficient control, and (3) highly efficient control. The final list of selected traits, as well as the attributes adopted by each trait, is summarized in Table 5.

### Riverine vegetation-hydropeaking response traits

Trait–disturbance interactions, as well as the degree of resistance (or vulnerability) that trait attributes may confer against HP are described from Sects. "Plant growth-form (PGF)" to "Mycorrhizal symbioses (MS)", and summarized in Table 6.

#### Plant growth-form (PGF)

Plants can be grouped into life form or growth-form classes based on similarities in structure. PGF describes the plant form based on the place of the plant's growth-point (bud) during seasons with adverse (cold or dry) conditions (Raunkiaer 1934). Plant growth-forms can be divided into nine categories: (1) nano-phanerophyte; (2) micro-phanerophyte; (3) meso-phanerophyte; (4) macro-phanerophyte; (5) chamaephytes; (6) hemicryptophytes and cryptophytes; (7) hydrophytes; (8) helophytes; and (9) geophytes. Hydrophytes can live in water or on substrates at least periodically anaerobic due to excess water (Raunkiaer 1934), but will not tolerate exposure to drought. Helophytes can root in mud and waterlogged soils, but are less specialized to water than hydrophytes (Raunkiaer 1934). This suggests that helophytes may withstand sedimentation of fine materials during down-ramping stages and frequent soil moisture disturbances derived from HP rapid water fluctuations, but will not cope with long-lasting submergence as hydrophytes may do. Geophytes can protect buds under the soil from desiccation and the mechanical stress induced by drag and lift forces derived from rapid water fluctuations (Raunkiaer 1934). Phanerophytes (i.e., large shrubs and trees) present overwintering (perennating) structures (i.e., buds, meristems, and leaves) located high above the ground, and therefore can avoid a flood from reaching them (Raunkiaer 1934). Chamaephytes, hemicryptophytes, some cryptophytes and small phanerophytes may minimize the risk of breakage by flow mechanical forces by reducing plant frontal area (Puijalon et al. 2011) but, as opposed to tall plants (i.e., phanerophytes), their structures will be close to the ground, and therefore affected even by hydropeaks of reduced water release. Geophytes have buds positioned deep in the soil (Lubbe and Henry 2020), and this may confer an advantage to desiccation periods associated to low flow release.

#### Shoot growth-form (SGF)

This trait describes the canopy structure of shoots (Kleyer 1995). Shoot growth-forms can be (1) submerged, attached to the substrate; (2) free-floating plants; (3) floating leaves, attached to the substrate; (4) emergent, attached to the substrate (amphibious); (5) stem prostrate; (6) stem ascending to prostrate; and (7) stem erect.



**Table 5** Trait names, sections where they are described, and attributes corresponding to each trait

Trait name	Section	Trait categories (attributes)
Plant growth-form (PGF)	Plant growth-form (PGF)	(1) Nano-phanerophytes; (2) micro-phanerophytes; (3) meso-phanerophytes; (4) macro-phanerophytes; (5) chamaephytes; (6) hemicryptophytes (7) cryptophytes (hydrophytes); (8) cryptophytes (helophytes); (9) cryptophytes (geophytes)
Shoot growth-form (SGF)	Shoot growth-form (SGF)	(1) Submerged, attached to the substrate; (2) free-floating plants; (3) floating leaves, attached to the substrate; (4) emergent, attached to the substrate (amphibious); (5) stem prostrate; (6) stem ascending to prostrate; (7) stem erect
Woodiness (WD)	Woodiness (WD)	(1) Non-woody; (2) semi-woody; (3) woody
Leaf cuticle thickness (LCT)	Leaf cuticle thickness (LCT)	(1) Thin leaves; (2) thick leaves
Leaf shape (LSH)	Leaf shape (LSH)	(1) Dissected leaves; (2) leaves finely divided into cylindrical pinnae; (3) finger-like leaves; (4) needle-like leaves (5) simple leaves, different than those described from 1 to 4 (e.g., egg-shaped, oblong, elliptical, obovate)
Leaf size (LSI)	Leaf size (LSI)	(1) Large; (2) medium; (3) small
Leaf consistency (LCON)	Leaf consistency (LCON)	(1) Succulent; (2) papery (malacophyllous); (3) between papery and coriaceous; (4) coriaceous
Leaf anatomy (LAN)	Leaf anatomy (LAN)	(1) Helomorphic (with well-developed aeration tissue as adaptation to oxygen deficiency in swampy soils (e.g., aerenchyma); (2) hygromorphic; (3) mesomorphic; (4) xeromorphic; (5) Kranz leaf anatomy
Leaf mass per leaf area (LMA)	Leaf mass per leaf area (LMA)	LMA to increase from (1) aquatic plants; (2) ferns; (3) herbs/grasses; (4) deciduous shrubs and trees; (5) evergreen shrubs and trees and (6) succulents
Rooting depth (RDE)	Rooting depth (RDE)	(1) Shallow-rooted; (2) moderately deep-rooted; (3) deep-rooted
Root morphology (RMO)	Root morphology (RMO)	(1) Lateral/fibrous systems; (2) lateral and taproot; (3) taproot
Shape reconfiguration (SHRE)	Shape reconfiguration (SHRE)	(1) Flexible, streamlined leaves and/or flapping leaves, elastic deformation of stems; (2) elastic deformation of stems likely occur, but leaves are not streamlined, absence of flapping leaves; (3) strong and rigid stems and/or leaves, plastic deformation of stems
Suberin barriers (SB)	Suberin barriers (SB)	(1) Strong barrier; (2) partial barrier; (3) no barrier
Below-ground organs and root mass allocation (BGOs)	Below-ground organs (BGOs) and root mass allocation	(1) Perennial herbs and shrubs adopting multi-stemmed growth forms, plants capable of clonal multiplication and lateral spreading, presence of rhizomes, tubers, stolons, roots with adventitious roots, buds and bulbs; plants capable to allocate mass in roots; (2) plants presenting at least one characteristic described in (1); (3) plants without any of the characteristics described in (1)
Plant height (PHE)	Plant height (PHE)	(1) Trees; (2) shrubs; (3) grasses/ forbs
Leaf venation network (LVN)	Leaf venation network (LVN)	(1) Vulnerable to HP; (2) partially resistant to HP; (3) resistant to HP
Presence of chloroplasts in epidermis (PCHE)	Presence of chloroplasts in epidermis (PCHE)	(1) Present (hydrophytes, floating plants with thin leaves); (2) absent (terrestrial/riparian plants)

**Table 5** (continued)

Trait name	Section	Trait categories (attributes)
Location of stomata (LSTO)	Location of stomata (LSTO)	(1) Epistomatic (stomata on adaxial position); (2) hypostomatic (abaxial position); (3) amphistomatic (stomata on both sides of the leaf)
Presence of trichomes (PTRI)	Presence of trichomes (PTRI)	(1) Lack of hairs or trichomes (2) moderate trichome density; (3) high trichome density
Leaf persistence (LPER)	Leaf persistence (LPER)	(1) Deciduous hibernial; (2) vernal and/or aestival; (3) evergreen
Resprouting ability (RA)	Resprouting ability (RA)	(1) Resprouters; (2) relative potential to resprout; (3) non-resprouters
CO <sub>2</sub> concentrating mechanisms (CO <sub>2</sub> -CMs)	CO <sub>2</sub> concentrating mechanisms (CO <sub>2</sub> -CMs)	(1) Absence of traits to concentrate CO <sub>2</sub> ; (2) presence of a "soft" CO <sub>2</sub> -CM; (3) more than one "soft" CO <sub>2</sub> -CM is present; (4) presence of "hard" CO <sub>2</sub> -CMs
Antioxidant mechanisms (AM)	Antioxidant mechanisms (AM)	(1) Enzymatic antioxidant generationsystem; (2) non-enzymatic antioxidant generation system; (3) transportation of toxic products and excretion; (4) presence of enzymatic, non-enzymatic or excretion systems, but of limited efficacy to remove ROS; (5) Absence of AMs
Presence of coleoptile (PCOL)	Presence of coleoptile (PCOL)	(1) Present (e.g., monocotyledon species); (2) absent
Seed germination (SG)	Seed germination (SG)	(1) Annuals with long exposure to light to germinate; (2) annuals with short exposure to germinate; (3) biennials; (4) perennials
Stomatal control (STOC)	Stomatal control (STOC)	(1) Type I (non-efficient control); (2) type II (moderately efficient control); (3) type III (highly efficient control)
Non-structural carbohydrates and flooding acclimation responses (NSC)	Non-structural carbohydrates and flooding acclimation responses (NSC)	(1) Plants using carbohydrates to enable a quiescence strategy and with large carbohydrate reserves; (2) plants adopting a quiescence strategy with limited carbohydrate reserves; (3) plants adopting an escape strategy and with large carbohydrate reserves; (4) plants without the capacity to adopt flooding-induced acclimation responses
Plant ventilation systems (PVS)	Plant ventilation systems (PVS)	(1) Presence of aerenchymatous structures; (2) alternative ventilation systems; (3) reduced production of aerenchymatous structures and absence of alternative ventilation systems
Presence of adventitious roots (ADV)	Presence of adventitious roots (ADV)	(1) Well-developed; (2) poorly developed
Chloroplasts movement under changing light intensities (CHMOV)	Chloroplasts movement under changing light intensities (CHMOV)	(1) Shade-grown plants (strong chloroplast movement); (2) sun-grown plants (weak chloroplast movement)
Cortical photosynthesis (COPH)	Cortical photosynthesis (COPH)	(1) Present; (2) absent
Mycorrhizal symbioses (MS)	Mycorrhizal symbioses (MS)	Presence of (1) arbuscular mycorrhizas (AMs); (2) ericoid mycorrhizas (ERs); (3) ectomycorrhizas (ECMs); (4) absence of mycorrhizal symbioses

**Table 6** Summary of resistance (green), partial-resistance (orange) and vulnerability (red) conferred by each trait category described in Table 5 to flooding (F), water stress (WS) and water fluctuations (WF)

FUNCTIONAL TRAIT	1			2			3			4			5			6			7			8			9		
	F	WS	WF	F	WS	WF	F	WS	WF	F	WS	WF	F	WS	WF	F	WS	WF	F	WS	WF	F	WS	WF	F	WS	WF
Plant growth-form (PGF)																											
Shoot growth-form (SGF)																											
Woodiness (WD)																											
Leaf cuticle thickness (LCT)																											
Leaf shape (LSH)																											
Leaf size (LSI)																											
Leaf consistency (LCON)																											
Leaf anatomy (LAN)																											
Leaf mass per leaf area (LMA)																											
Rooting depth (RDE)																											
Root morphology (RMO)																											
Shape reconfiguration (SHRE)																											
Suberin barriers (SB)																											
Below-ground organs and root mass allocation (BGOs)																											
Plant height (PHE)																											
Leaf venation network (LVN)																											
Presence of chloroplasts in epidermis (PCHE)																											
Location of stomata (LSTO)																											
Presence of trichomes (PTRI)																											
Leaf persistence (LPER)																											
Resprouting ability (RA)																											
CO <sub>2</sub> concentrating mechanisms (CO <sub>2</sub> -CM)																											
Antioxidant mechanisms (AM)																											
Presence of coleoptile (PCOL)																											
Seed germination (SG)																											
Stomatal control (STOC)																											
Non-structural carbohydrates and flooding acclimation responses (NSC)																											
Plant ventilation systems (PVS)																											
Presence of adventitious roots (ADV)																											
Chloroplasts movement under changing light intensities (CHMOV)																											
Cortical photosynthesis (COPH)																											
Mycorrhizal symbioses (MS)																											

The blue color indicates that further research is needed to determine resistance against HP. The brown color indicate a shifting behavior (partial resistance or vulnerability) depending on the timing of HP operations

The diffusion of gases in water is about 10<sup>4</sup>-fold slower than in air and, therefore, plant submergence during HP events may difficult the access to gases (i.e., oxygen and carbon dioxide) for their metabolism (Voesenek et al. 2006). Aquatic plants efficiently maintain photosynthesis rates and aerobic respiration under flooding with different adaptations to overcome oxygen and carbon dioxide deficiencies (Björn et al. 2022). Submerged plants may enhance plant ventilation via passive molecular diffusion processes (Colmer 2003), promote aeration of rhizosphere via buried leaves (Winkel et al. 2011), and perform direct exchange of gases between plant tissues and water (Mitsch and Gosselink 2007).

Free-floating and plants with floating leaves can improve O<sub>2</sub> supply to respiring tissues via thermodynamic gas transport systems (e.g., thermal transpiration; Schröder 1989; Björn et al. 2022). Solar warming and cooling by transpiration of the upper leaf surface in these plants generate a temperature gradient within the leaf, inducing a flow of pressurized gas (Grosse et al. 1991; Armstrong and Armstrong 2005; Richards et al. 2012); the 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 (Björn et al. 2022). Additionally, stomata in floating leaves and free-floating plants are found on the upper surface exposed to the air (Crang et al. 2018) favoring CO<sub>2</sub> uptake. Also, floating leaves contain air spaces that give the plant buoyancy allowing the leaves to float on the water surface. As in most aquatic species, ventilation is enabled by an extended system of air canals and intercellular spaces called aerenchyma (Justin and Armstrong 1987; Jackson and Armstrong 1999) that provide a diffusional pathway for oxygen transport to the roots (Crang et al. 2018). In addition to the atmosphere, gases in aerenchyma can originate from the rhizosphere or plant metabolism (Lambers and Oliveira 2019). All the aforementioned attributes help plants with floating leaves to resist flooding events derived from hydropeaks. Oxygen generated in the leaves of emergent plants during photosynthesis is transported to the submerged stem and roots, maintaining respiration when exposed to low environmental oxygen concentrations (Crang et al. 2018). In addition to aerenchyma, suction via old broken stems (Venturi-effect; e.g., Armstrong et al. 1992), air films on leaves when submerged (e.g., Armstrong and Armstrong 2014), water-repellent leaf surfaces; large air spaces inside leaves and roots, tissues remarkably porous, and barriers in roots to prevent radial O<sub>2</sub> loss from roots (Groot et al.

2005; Colmer et al. 2006; Herzog et al. 2018) are also special features allowing emergent plants to thrive in oxygen-deficient environments (Björn et al. 2022), similar to those imposed by HP submergence.

In contrast to aquatics, aerenchyma in terrestrial plants (i.e., rigid, non-floating, erect forms) has in general a reduced ventilation capacity, and therefore flooding will usually compromise their survival (see Björn et al. 2022). In aquatic species, intercellular spaces associated with aerenchyma contribute up to 60% of the leaf volume (Laan et al. 1989), while in non-aquatic species leaf volumes range from 2–7% (Larcher 2003). On the other hand, trees with large erect forms ensure that some parts of the plant will remain unscathed during submergence (Bejarano et al. 2018), which might help counterbalance their rather limited capacity to supply O<sub>2</sub> via ventilation.

While being good at resisting stress imposed by flooding conditions, aquatic plants (especially floating and submerged plants) usually present low tolerance to above-water conditions (Havens et al. 2004). This is in contrast to non-floating plants (e.g., erect stems or stems ascending to prostrate forms), which usually present stems of high density, and therefore more capable of reducing evapotranspiration and tolerate water stress.

Additionally, non-rigid, non-erect structures are less flexible and less resistant to mechanical disturbance during submergence and stages of rapid water fluctuations compared to large, erect shoot growth forms (Bejarano et al. 2018). Prostrate forms minimize the risk of breakage by mechanical forces by reducing plant frontal area (e.g., small growth forms; Puijalon et al. 2011), but will be more prone to be buried and experience mud coating. Conversely, erect stems will experience less mud coating, but their larger plant frontal area increases the risk of breakage.

### Woodiness (WD)

Woodiness is a soft trait which is a surrogate of the stem tissue density and flexibility. Three categories have been defined: (1) non-woody; (2) semi-woody; and (3) woody species. Non-woody plants have flexible organs and the ability to reconfigure shape with increasing flow velocity (e.g., through flattening and the alignment of shoots in the flow direction; Kouwen and Fathi-Moghadam 2000), therefore avoiding physical injury derived from HP forces (Bejarano et al. 2018). In contrast, denser branches can be a mechanical liability because they are less flexible and cannot adopt streamline shapes under flow, which increases the likelihood of breakage (Vogel 1988; Kouwen and Fathi-Moghadam 2000). The higher density of woody tissues, on the other hand, prevents xylem embolism derived from drought. Xylem embolism occurs when gaseous bubbles are aspirated into xylem conduits (e.g.,

Delzon et al. 2010), a phenomenon which becomes more likely during dry periods (Tyree and Sperry 1989; Nardini et al. 2011). Under drought conditions, bending stresses occur in the common wall between an embolized and a water-filled conduit generating a negative pressure that may cause conduit collapse (Hacke et al. 2001), ultimately reducing plant hydraulic conductance (Nardini and Pitt 1999; Nardini et al. 2011). In extreme cases, the reduction of hydraulic conductance may lead to complete failure of water transport and plant death (e.g., Brodribb and Cochard 2009). The thicker (or denser) the double wall between xylem conduits, the greater the reinforcement against collapse from bending (Young 1989; Hacke et al. 2001). For this reason, woody plants, with greater internal loads on the xylem conduit walls than non-woody plants, are likely to be more resistant to HP drought events.

### Leaf cuticle thickness (LCT)

The cuticle, a protective barrier of aerial surfaces of plants, acts as a diffusion barrier and, therefore, influences the diffusion of multiple molecules, including water, O<sub>2</sub> and CO<sub>2</sub> (e.g., Chen et al. 2011a, b). Leaf cuticle thickness (LCT) varies more than 100 times across species (Onoda et al. 2012), although most species present a LCT comprised between 1 and 10 µm (Riederer and Müller 2006). To our knowledge, there is no clear threshold defined in the scientific literature to accurately differentiate plant leaves based on their cuticle thickness. Scientific publications usually describe leaves with thicker cuticle layers as “thick”, “leathery” and/or “waxy”. On the contrary, leaves with rather thin cuticle layers are described as “thin”, “flat” and/or “broad” (e.g., Furlow 1979; Jermy et al. 1982; Hultén and Fries 1986; Tutin et al. 2001; López Gonzalez 2001; Clayton et al. 2006; Chytrý et al. 2021). Such adjectives may provide guidance to group species under two broad categories: (1) thin leaf cuticles (e.g., *Betula pubescens*, *Filipendula ulmaria*, *Viola palustris*, *Agrostis* sp., *Rosa* sp.; Baladrón et al. 2023) and (2) thick leaf cuticles (e.g., *Alnus incana*, *Pinus sylvestris*, *Ledum palustre*, *Salix* sp.; Baladrón et al. 2023). Thinner leaves facilitate underwater gas exchange (e.g., Maberly and Madsen 2002) and therefore photosynthesis (e.g., Pedersen et al. 2013) during hydropeaks. Maintenance of photosynthesis is key in sustaining both internal oxygen concentrations and carbohydrate contents in submerged plants (Mommer and Visser 2005), and it facilitates aerobic respiration (under submergence, anaerobic glycolysis can substitute aerobic respiration, but it is inefficient and toxic end products accumulate; Parolin 2012). On the other hand, plants with thicker cuticle layers enable plants to minimize water losses under drought conditions (Yul Yoo et al. 2009; Onoda et al. 2012; Arya et al. 2021),



including those derived from periods of low water release for hydropower production. Thick cuticles constitute a barrier to water movement because leaves' lipophilic barriers are very hydrophobic, which difficult water movement out of the leaf (e.g., Lambers and Oliveira 2019). Additionally, thicker cuticles can increase mechanical resistance (Onoda et al. 2012), potentially helping plants to cope with rapid water flow fluctuations linked to HP operations.

#### Leaf shape (LSH)

Plant leaf shape plays important roles in photosynthetic capacity, water use (Givnish 1979; Nicotra et al. 2011) and physiological tolerances to abiotic stresses (Demmings et al. 2019), including that imposed by extreme hydrological events derived from HP. Leaf shape can be divided into five general categories: (1) dissected leaves; (2) leaves finely divided into cylindrical pinnae; (3) finger-like leaves; (4) needle-like leaves; (5) others (e.g., egg-shaped, oblong, elliptical, obovate). Dissected leaves present a relatively thinner boundary layer that reduces diffusional resistance resulting in a greater gain of carbon, which is potentially beneficial for enhancing photosynthesis during HP submergence (Gurevitch and Schuepp 1990; Nicotra et al. 2007). Likewise, leaves finely divided into cylindrical pinnae allow for a greater and more uniform surface for the diffusion of carbon dioxide (Crang et al. 2018). Finger-like leaves also help to circulate dissolved gases (Crang et al. 2018), hence facilitating the plant's photosynthetic activity during prolonged submergence of aerial parts (Bejarano et al. 2018). Needle-like leaves are suited to dry environments (Du et al. 2020) and therefore can cope with HP drawdown periods. Simple leaves may not confer any clear advantage against HP disturbance.

#### Leaf size (LSI)

Leaf size is a key plant structural trait associated with plant growth, light interception, and photosynthetic efficiency (e.g., Rouphael et al. 2010). Raunkjær (1934) proposed the following classes of plant leaves based on their size: leptophyll (<25 mm<sup>2</sup>); nanophyll (25–225 mm<sup>2</sup>); microphyll (225–2025 mm<sup>2</sup>); mesophyll (2025–18,225 mm<sup>2</sup>); macrophyll (18,225–164,025 mm<sup>2</sup>); megaphyll (>164,025 mm<sup>2</sup>). Later authors have modified the classes (e.g., microphyll (<2025 mm<sup>2</sup>); notophyll (2025–4500 mm<sup>2</sup>); mesophyll (>4500 mm<sup>2</sup>); Webb 1959) and have sometimes used leaf length instead of leaf area (nanophyll (<2.5 cm); microphyll (2.5–7.6 cm); notophyll (7.6–12.7 cm); mesophyll (>12.7 cm); Boland et al. 2006). Whitten et al. (1996), Ingrouille (2012) and van der Maarel and Franklin (2012) have also provided definitions for leaf size categories. According to these classifications, three broad categories have been defined for

leaf size: (1) large (>4500 mm<sup>2</sup>); (2) medium (4500–2000 mm<sup>2</sup>); and (3) small (<2000 mm<sup>2</sup>). Generally, smaller leaves are advantageous in dry environments, while large leaves are so in cooler and lower irradiance environments (e.g., Tozer et al. 2015). Large leaves maximize light interception (e.g., Atwell et al. 1999), and therefore may help plants to maintain photosynthetic rates under presumably low irradiance levels and cooler temperatures resulting from HP submergence. Conversely, during prolonged HP drawdowns, plants may potentially benefit from having small leaves since these will reduce evapotranspiration under soil moisture deficits and water scarcity characterizing the no electricity production phases (e.g., Bejarano et al. 2018).

#### Leaf consistency (LCON)

Leaves can be categorized by referring to the hardness of the leaves (Shugart and Woodward 2011). Four general leaf consistency categories can be established: (1) succulent, ligneous (with woody photosynthetic parts); (2) papery (malacophyllous, herbaceous leaves); (3) between papery and coriaceous (hard and stiff, partially sclerophyllous leaves); and (4) coriaceous (thick, leathery, sclerophyllous leaves). Succulent leaves have specialized water-storing tissues to survive under water shortages (e.g., Eggli and Nyffeler 2009; Ogburn and Edwards 2010). Coriaceous leaves are more resistant to drought than malacophylls (soft, thin, papery leaves) because cells in sclerophyllous leaves have thick and rigid walls. This characteristic prevents cell collapse caused by negative turgor pressures (contraction of the cell wall) developing in them under water stress (e.g., Oertli et al. 1990), and therefore helping the plant to cope with HP drawdown periods. Additionally, coriaceous leaves usually exhibit a high tensile strength (Wang et al. 2010) compared to more papery leaves. An advantage of papery and flexible leaves is that they float above the water where gas exchange is optimum, which is advantageous during phases of up-ramping and continuous high peak discharge.

#### Leaf anatomy (LAN)

This trait classifies leaves according to their water relations, as follows: (1) helomorphic (i.e., leaves with well-developed aeration tissue (e.g., aerenchyma) as an adaptation to oxygen deficiency in swampy soils); (2) hygromorphic (i.e., leaves that depend on a large supply of moisture or grow partly or completely submerged in water); (3) mesomorphic (i.e., leaves that require abundant available soil water and a humid atmosphere); (4) xeromorphic (i.e., leaves adapted to dry habitats); and (5) Kranz leaf anatomy (leaves with specialized structures to

perform  $C_4$  photosynthesis, an adaptive feature for plants to cope with water stress (see Grigore et al. 2012; Crang et al. 2018).

Hygromorphic and helomorphic leaves are adapted to maximize the diffusion of  $CO_2$  from the water into the leaves for photosynthesis by means of ventilation systems (e.g., aerenchyma structures). Proper ventilation provides buoyancy to leaves and maintains them out of the water where gas exchange is faster. It also enables a diffusional pathway from emergent leaves to roots for oxygen transportation (Sculthorpe 1967; Crang et al. 2018). Hygromorphic and helomorphic leaves present characteristics that are key to cope with the slow gas exchange rates (Crang et al. 2018) presumably occurring under HP submergence. Some of these leaf characteristics are the presence epidermal cells with a single-layered mesophyll (or even lack of the entire mesophyll), finger-like shapes (or leaves presenting fine divisions into cylindrical pinnae), and stomata located on the leaves' upper surface (i.e., adaxial position, very common in floating leaves).

Xeromorphic and helomorphic leaves can minimize water losses under HP drawdown and water stress periods by adopting a number of anatomical adaptations, including: thick cuticles, dense covering of trichomes, reduced number of stomata, deeply sunken stomata (which allows reducing the diffusion gradient nearby the stomate area), leaf epidermis with thick lignified secondary walls, and the presence of epistomatal cavities (i.e., depression over guard cells of stomata) filled with deposits of wax particles. Some xeromorphic and helomorphic leaves also have the ability to roll exposing the thick, waterproof cuticle, and creates a humid space in the middle of the rolled leaf (Taiz et al. 2015; Crang et al. 2018). Xeromorphic leaves may also present needle (pines), scale-like (cedars, cypress), or flattened (spruces and firs) shapes to reduce the surface-to-volume ratio and likewise transpiration (Crang et al. 2018). Mesomorphic leaves are adapted to habitats intermediate between hydrophytic and xerophytic.

#### Leaf mass per leaf area (LMA)

This trait refers to the ratio between leaf dry mass and leaf area (e.g., Poorter et al. 2009). This morphological trait is highly correlated with leaf and whole-plant processes (de la Riva et al. 2016), including plant's maximum photosynthetic rates (e.g., Wright et al. 2004) and species' potential growth rate (e.g., Ruíz-Robledo and Villar 2005). In general, (1) aquatic plants may have the lowest LMA, followed by (2) ferns; (3) herbs/grasses; (4) deciduous shrubs and trees; (5) evergreen shrubs and trees; and (6) succulents, which usually present the highest LMA (Poorter et al. 2009; de la Riva et al. 2016).

Metabolic cost production of each single leaf in low LMA plants is low compared to high LMA leaves. A "low-cost" strategy is associated with leaves with short life spans and fast turnover rates (i.e., leaves that may not age in excess and display a high photosynthetic capacity during their entire lifespan; see Westoby et al. 2002). The production of short-lasting, low LMA leaves could be an advantageous strategy for plants under submergence, drag forces, and water stress derived from HP because the ratio of resource investment to photosynthetic function will be likely maximized; in relation to its photosynthetic activity, a leaf with a short lifespan will most likely have been amortized by the time it is damaged or dragged by high flow velocities derived from HP. In addition, low LMA leaves have more light-capture area deployed per mass (Reich et al. 1997), higher leaf nitrogen concentrations (Field and Mooney 1986; Lambers et al. 1998), and shorter diffusion paths from stomata to chloroplasts (Parkhurst 1994). All these characteristics may facilitate photosynthesis under light attenuation and slow gas exchange conditions likely occurring during HP submergence. On the other hand, high LMA, usually related to cuticle thickening, allows leaves to cope better with soil moisture deficits usually triggered by HP drawdown.

#### Rooting depth (RDE)

Rooting depth refers to the distribution of roots over sequential soil layers ranging from the soil surface to deeper horizons (Mueller et al. 2013; Ravenek et al. 2014; Freschet et al. 2021), and it is considered a trait of drought avoidance (Kashiwagi et al. 2005; Padilla and Pugnaire 2007).

Shallow and spreading rooting systems may help plants avoid deeper anoxic soil layers, and hence root hypoxia (Hosie 1969; Pedersen et al. 2021). This rooting pattern might be beneficial for plants to deal with waterlogged riverbanks derived from increasing and maximal water-level phases of HP. Conversely, deep-rooting systems contribute to an upward transport of water and nutrient from deeper soil layers (Bielak et al. 2014). Even a small number of roots deep in the soil profile may enable plants to capture water from deeper soil layers (Caldwell et al. 1998; Jackson and Armstrong 1999), which can be extremely relevant for plants to successfully cope with dry conditions associated to HP drawdown periods.

But in addition to giving access to permanent water, deep and wide root systems may provide mechanical stand stabilization (Bielak et al. 2014) to cope with drag forces derived from HP, therefore maximizing resistance to uprooting (see Bejarano et al. 2018).

Riverine species variation in mean rooting depth is extremely ample, ranging from 0.5 m (e.g., *Carex*) to



more than 10 m (*Acacia*) (Fan et al. 2017). Three rooting depth categories have been established according to the mean rooting depths (MRD) reported by Fan et al. (2017) for different plant genera: (1) shallow-rooted systems (i.e.,  $\text{MRD} < 1.5$  m; e.g., *Carex*, *Fagus*, *Picea*, *Salix*, *Festuca*, *Abies*, *Stipa*); (2) moderately deep-rooted systems ( $1.5 \text{ m} < \text{MRD} < 3$  m; e.g., *Populus*, *Juniperus*, *Andropogon*, *Acer*, *Pinus*) and (3) deep-rooted systems ( $\text{MRD} > 3$  m; e.g., *Ulmus*, *Quercus*, *Tamarix*, *Eucalyptus*, *Acacia*).

### Root morphology (RMO)

Root morphology is a trait tightly related to the root system architecture and provides spatial and structural information on the root system (e.g., Kallikowski 2011), including its capacity to support plant growth via water and nutrient absorption, and to provide anchorage to the plant (e.g., Tripathi et al. 2001). Types of root morphology can be classified into three groups: (1) lateral/fibrous systems; (2) lateral and taproot; and (3) taproot.

Taproots are characterized by the presence of a primary or dominant root that grows deep into the soil while developing lateral roots from the main root. On the contrary, fibrous root systems move more horizontally than vertically, and may not penetrate deeper into the soil (e.g., Mauseth 2009). Therefore, taproots may anchor the plant more tightly and firmly to the soil than fibrous roots (see Nair 2010), hence preventing plant uprooting during HP rapid water fluctuations. Taproots may also facilitate water uptake from deep soil layers under baseflow periods (see Brunner et al. 2015) as opposed to fibrous roots, which are considered surface feeders as they do not penetrate deep into the soil (e.g., Mauseth 2009). Conversely, fibrous roots may expose plants less to deeper anoxic soil layers than taproots, and hence to root hypoxia. In this regard, fibrous roots might help plants to cope with waterlogged soils resulting from HP operations.

### Shape reconfiguration (SHRE)

Some riverine plants are flexible and bend under high flow velocities. This reconfiguration can reduce drag forces acting on the plant (Vogel 1994; O'Hare et al. 2007), both by reducing the frontal area and by creating a more streamlined shape (Nikora 2010; Zhang and Nepf 2020).

In general terms, riverine plants can be categorized into the following groups: (1) plants presenting flexible, streamlined leaves and/or flapping leaves, as well as the elastic deformation of stems in response to current; (2) plants in which elastic deformation of stems likely occurring in response to current, but streamlined/flapping leaves are absent; and (3) plants with strong and rigid stems and leaves that may experience plastic deformation under strong water currents, and therefore

at risk of experiencing damage or breakage (see Nikora 2010). Plants belonging to category (1) will passively follow the flow (Nikora 2010) adopting a 'flexible and extensible' biomechanical strategy (Koehl 1979), which may significantly reduce injuries by drag forces derived from HP. Flapping leaves under high flow motion may also improve photosynthetic activity due to a decrease in self-shading and an increase in gas exchange (Koehl and Alberte 1988; Nikora 2010), which may benefit growth on plants during maximal HP water-level phases involving turbulent and fast water currents.

### Suberin barriers (SB)

Suberin is a structural lipophilic polyester of fatty acids, glycerol and some aromatics found in cell walls of plant tissues (Serra and Geldner 2022). The presence of suberin gives rise to radial  $\text{O}_2$ -loss barriers (i.e., apoplastic barriers in root outer cortex/exodermis; Manzur et al. 2015), which help plants tolerate anoxic conditions by preventing oxygen diffusion outward to the soil. Heavily suberized root tissues limit radial oxygen loss (ROL) from the root to the rhizosphere, supporting root growth in oxygen-depleted soils under flooded conditions (Armstrong et al. 2000; De Simone 2003). The content of suberin explains, in part, ROL rates from roots of riverine plants, and it is strongly species-dependent (Chen et al. 2022). For instance, the roots of wetland monocotyledonous species such as *Juncus effusus* and *Carex acuta* show very low ROL values ( $< 5 \text{ ng cm}^{-2} \text{ min}^{-1}$ ; measured 5 cm away from the root tip), whereas the dicotyledonous species *Caltha palustris*, *Ranunculus sceleratus* and *Rumex palustris* have roots relatively permeable to oxygen loss (ROL ranging between  $20\text{--}60 \text{ ng cm}^{-2} \text{ min}^{-1}$ ; measured 5 cm away from the root tip) (Laan et al. 1989; Visser et al. 2000). In general, low ROL rates are linked to the presence of non-permeable, 'strong' apoplastic barriers, whereas higher rates indicate a lower concentration of suberin and lignin in the roots, and therefore the presence of a 'partial' apoplastic barrier (Visser et al. 2000). ROL values higher than  $60 \text{ ng cm}^{-2} \text{ min}^{-1}$  indicate significant oxygen losses from the roots to the soil, and such values would correspond to species intolerant to flooding.

Taking the above into consideration, we define three categories: (1) presence of strong barriers (i.e., species presenting low ROL values, similar to those described for *Juncus effusus* and *Carex acuta*); (2) presence of partial barriers (i.e., plants showing ROL values similar to those described for *Caltha palustris*, *Ranunculus sceleratus* and *Rumex palustris*); and (3) absence of barriers aimed at preventing ROL from roots (i.e., species presenting ROL values superior to  $60 \text{ ng cm}^{-2} \text{ min}^{-1}$ ).

The stronger the barrier is, the more limited the oxygen loss through the root will be and, therefore, the more likely it is for the plant to withstand submergence and riverbank inundation derived from hydropeaks.

#### **Below-ground organs (BGOs) and root mass allocation**

Below-ground organs (i.e., rhizomes, tubers, stolons, buds and bulbs) constitute carbohydrates stockings and provide some plants with the ability to grow clonally and regenerate after disturbance (Klimešová et al. 2018), which may potentially have positive effects on plant survival under peak flow events derived from HP. Accumulation of carbohydrates on below-ground organs of perennial herbs and shrubs may likely help them to restore the above-ground biomass (Klimešová and Klimeš 2007; Clarke et al. 2013) damaged by HP mechanical forces. Species relying on below-ground organs to propagate will also have an advantage under HP regimes because a large portion of their structures will remain hidden on the ground, hence minimizing exposure to drag and lift forces and to scouring derived from HP rapid water-level fluctuations (Bejarano et al. 2018). Below-ground organs are also involved on a number of strategies and mechanisms that should help avoid or minimize damages on plants exposed to HP, including the geotropic growth, the adoption of multi-stemmed growth forms, or the presence of contractile roots under the soil surface (Pütz 2002, 2006). Finally, thigmomorphogenetic responses (Goodman and Ennos 1997; Mickovski and Ennos 2003) might be a key adaptive mechanism to cope with HP stress. Specifically, the application of horizontal forces on the stem of a plant during up-ramping and peak flow HP stages may induce changes in the allocation of below-ground root biomass, or even change the mechanical properties of roots, contributing to increasing the plant's stability and hence to avoid uprooting during the hydropeaks.

Plant species without any of the characteristics and mechanisms described above will potentially be much more vulnerable to HP disturbance than those that do have them.

#### **Plant height (PHE)**

Tall plants can avoid flood and HP drag forces from reaching green parts and meristems in the canopy, where most photosynthesis happens (e.g., Lambers et al. 2008). In general, trees will have their green parts and meristems more protected from HP disturbances than shrubs, and shrubs slightly more protected than herbaceous plants (i.e., grasses and forbs).

#### **Leaf venation network (LVN)**

Leaf venation is the distribution and arrangement pattern of a leaf vein system (Li et al. 2013a, b). Plant resistance to flooding, drought, and rapid water-level fluctuations might vary depending on LVN's architectural features, including the distribution, density, diameter, length, and loopiness of veins (i.e., vein topology), vein tapering, distance between veins, and structures supporting LVN's functioning (i.e., accessory transport elements).

LVNs might be classified under three broad groups: (1) LVNs making plants vulnerable to HP (i.e., non-hierarchical, non-reticulate LVNs; craspedodromous leaves, low vein length per unit area (VLA), large vein diameters (VD), absence of vein tapering, presence of bundle sheath extensions (BSEs) and accessory transport elements); (2) LVNs conferring plants partial-resistance to HP (i.e., evidence of at least one characteristic described in (1)); and (3) LVNs conferring plant resistance to HP disturbance: hierarchical, reticulate LVNs; brochidodromous leaves, high VLA, small VD, low venation density, and presence of vein tapering.

Reticulate LVNs tend to increase the length of all vein paths (Price and Weitz 2014), including that of major veins. It is believed that major veins act as water transport superhighways (Sack and Scoffoni 2013) enabling the plant to tolerate hydraulic system disruptions caused by drought. Therefore, reticulate systems will likely help plants to maintain water supply under water stress conditions, and hence to successfully cope with drought events resulting from HP (Brodribb et al. 2016).

Vein topology may also play a role under HP disturbance. Brochidodromous leaves present leaf vein topologies that display loops in second order veins. This topology may prevent the propagation of embolisms that reduce conductance under low water potential (Brodribb et al. 2016). Therefore, the presence of loops in the network (Katifori et al. 2010) may help to tolerate better hydraulic system disruptions resulting from vein mechanical damage or drought, as opposed to craspedodromous leaves, in which second order veins run to the leaf's margin (Sack and Scoffoni 2013). Eucamptodromous leaves (i.e., mix of brochidodromous and craspedodromous patterns) would provide partial resistance to HP disturbance.

Length, diameters and density of LVNs can help plants to deal with submergence and drought derived from HP events. High VLA allows higher rates of gas exchange per unit leaf area (Sack and Scoffoni 2013) and may provide benefits for biomechanical support. Smaller conduits are also less vulnerable to drought (Sack and Scoffoni 2013), while veins with larger diameters provide

additional mechanical support to leaves (Niklas 1992; Méndez-Alonzo et al. 2013) exposed to HP drag forces. Additionally, large mid-veins allow flexural bending along the midrib reducing mechanical load (e.g., Cooley et al. 2004), and potentially making leaves more resistant to drag forces. Finally, low LVNs densities decelerate water flow within the leaf and, consequently, reduce evaporation under conditions of moisture deficiency (Migalina et al. 2010) such as those occurring during HP baseflow stages.

Vein tapering (i.e., veins' cross-sections narrow along their length, from first to second order veins) can make plants more resistant to drought since they reduce the spread of embolism bubbles (under drought stress, capillary forces that prevent air from bursting into the xylem are exceeded, causing a bubble to invade the water-filled lumen that blocks the xylem conduit in the leaf network). Susceptibility to embolism increases proportionally with the size of veins, with minor veins being the last to lose function (Brodrribb et al. 2016).

Accessory transport and support tissues (e.g., elements such as sclereids, transfusion tracheids, and idioblasts) can act as water storage to buffer cell water potentials from transiently high transpiration rates likely occurring during HP drawdown events. Support tissues may also increase the mechanical strength of leaves by providing resistance to shrinkage under dehydration conditions (see Sack and Scoffoni 2013).

BSEs may allow stomata to respond more quickly to changes in xylem water potential, which should be beneficial when soil moisture (and therefore leaf hydraulic conductance) changes rapidly (Sack and Scoffoni 2013), as it may occur in riverbanks affected by HP. BSEs may also play a role in guiding light inside the leaf favoring higher photosynthetic rates under the low light intensities likely occurring under HP submergence. Additionally, BSEs may increase the mechanical strength of the leaf, especially when fibers or scleroids are present.

#### Presence of chloroplasts in epidermis (PCHE)

Submerged aquatic plant species cope with submergence owing to a suite of traits that favor gas exchange, such as leaves with epidermal chloroplasts (Maberly and Madsen 2002; Bailey-Serres and Voesenek 2008). The transfer of chloroplasts to the outer epidermal layer of submerged and floating plants reduces the distance for CO<sub>2</sub> transport from the medium toward the carboxylation centers and improves the illumination conditions in submerged leaves (e.g., Pedersen et al. 2013). Conversely, in terrestrial plants (e.g., riparian trees), the epidermis exerts a protective function, and the epidermal chloroplasts are poorly developed in most species (Ronzhina and

P'yankov 2001). These characteristics do not favor gas exchange under HP submergence. We have considered PCHE a trait of binary nature, and therefore plants are classified as those with chloroplasts in epidermis (1) "present" or (2) "absent".

#### Location of stomata (LSTO)

Leaf stomata (i.e., small pores responsible for gas exchange in vascular plants) can be present (1) on the upper surface of the leaf (stomata on adaxial position, or epistomatic); (2) on the lower surface of the leaf (stomata on abaxial position, or hypostomatic); or (3) on both sides of the leaf (amphistomatic).

Aquatic plants have stomata present in adaxial position, which helps to reduce the contact of stomata with the water and maintain them in contact with air, where gas exchange is faster (Maberly and Madsen 2002; Lambers et al. 2008). Riverine plants can experience episodes of complete submergence in HP rivers, and therefore facilitation of gas exchange via adaxial stomata might be critical for them to sustain photosynthetic activity and below-ground organs respiration (Pedersen et al. 2013). On the other hand, abaxial stomata are more sensitive than adaxial stomata to water-stress signals. Externally applied ABA or Ca<sup>2+</sup> has much less of an effect on the regulation of adaxial stomatal movement compared with their effects on abaxial stomata (Wang 1998). A higher sensitivity to water-stress signals might help to close stomata guard cells faster during HP drought episodes, hence favoring a better control of plant water losses. Amphistomaty may optimize both photosynthetic rates and plant respiration under HP submergence, and control water losses under HP drought. Additionally, there is evidence that amphistomaty may have evolved in response to increasing aridity during the Tertiary, as it is considered to be a highly xeromorphic trait (e.g., Parkhurst 1978); therefore, amphistomatic stomata will likely help plants to cope with water scarcity during HP baseflows.

#### Presence of trichomes (PTRI)

Trichomes (i.e., appendages present on the surface of many plants that originate from the outer epidermal cell tissue of the plant; e.g., Johnson 1975) protect plants from being damaged by drought stress, and the density and types of trichomes are related to plant stress resistance (Sandquist and Ehleringer 2003; Kenzo et al. 2008). Based on trichomes characteristics, we propose a classification of plants structured in three broad categories: (1) plants lacking hairs or trichomes; with a smooth surface (i.e., glabrous or glabrate); (2) plants with a "moderate" trichome density (i.e., leaves with sparse, soft hairs, puberulent, pulverulent, setose, stellate, hoary leaves,

velvety plant tissues); and (3) plants with a high trichome density (i.e., leaves with quite hairy leaves; covered in coarse, stiff hairs, bristly hairs, woolly hairs (hirsute, hispid, lanate, tomentose, velutinous, pilose, downy leaves)). It is expected that plants belonging to category (3) will be more protected from HP drought episodes than plants classified under category (2), and those in category (2) may in turn resist drought conditions better than plants grouped under category (1).

#### Leaf persistence (LPER)

LPER describes whether species lose their foliage over the year and when it happens. Leaf persistence can be divided into three general categories: (1) hibernial (i.e., leaves which arise in fall, persist through the winter, and die back in the heat and dryness of summer); (2) vernal and/or aestival (i.e., green from early spring to the end of the summer, or just during the warm period, then usually decaying); and (3) evergreen leaves (i.e., leaves that persist throughout the year and last at least two years) (see Grime et al. 1988).

Evergreen leaves, usually tougher and endowed with thicker mechanical tissues than deciduous leaves (Givnish 2002), make a more conservative use of water and may tolerate better drought conditions linked to HP drawdown. Evergreens might also make a more efficient use of nutrients compared to deciduous leaves. During leaf senescence, plants recover nutrients (e.g., N, P, K) and leaf proteins from chloroplasts before the leaf is shed by the end of the abscission process, and the fraction of nutrients not recovered must be replaced when new leaves are produced (Chabot and Hicks 1982). Unexpected weather events such as late summer droughts or heavy fall rainstorms may disrupt the abscission process by accelerating or modifying the timing of abscission, ultimately affecting nutrient recapture from leaves (see Crang et al. 2018). In a similar fashion, hydrological alterations derived from HP (i.e., drought, rapid and short-term water-level fluctuations, and inundation) may potentially disrupt the leaf abscission process. During drought, leaves are shed to conserve water and avoid damages to plant central organs, which are more costly than peripheral organs for plants to replace (Tyree et al. 1993; Wolfe et al. 2016). During inundation events, as a result of slow gas diffusion underwater, submerged plant tissues rapidly accumulate ethylene (e.g., Hartman et al. 2019), a gaseous hormone that triggers a number of flood-adaptive responses (Jackson 2008), including leaf abscission (Denny 1924). Mechanical forces associated to rapid water-level fluctuations triggered by HP operations can cause breakage and removal of plant biomass (Bejarano et al. 2020), including leaves. In short, unexpected drought, submergence and rapid water-level

fluctuations linked to HP may limit the recovery of nutrients from leaves since these might be shed or mechanically removed before the nutrient recovery takes place. Given that the cost of leaf construction in deciduous plants is higher than in evergreens, disruptions in nutrient recapturing implies higher metabolic losses for deciduous species and therefore, under HP disturbance, evergreens might have an advantage over deciduous plants.

Whether deciduous hibernial plants are more vulnerable to HP than vernal or aestival species (or vice versa) may depend on annual patterns of electricity demand. In principle, peaks of hydropower demand may dictate to which extent leaf nutrient recapture is disrupted. For instance, in Northern Europe, nutrient recovery in hibernial plants might be more disrupted by HP than in aestival species, because higher electricity demands will likely occur in winter, when hibernial species' peak foliage occurs. Conversely, in Southern Europe, especially during summer periods of record-breaking temperatures, it may occur the opposite; aestival species might be more vulnerable since peak foliage may coincide with periods of increased hydropower production for building cooling.

#### Resprouting ability (RA)

Resprouting is the capacity of some plants to survive and regenerate vegetatively (e.g., Clarke et al. 2013) and permits recovery from disturbance by means of dormant buds that consume below-ground reserves even when all above-ground biomass has been removed (e.g., Bond and Midgley 2001; Paula and Pausas 2006). We established three categories to classify plants according to their resprouting ability: (1) resprouters (i.e., the plant is efficient at resprouting, or it has the following characteristics: deep-root system, presence of underground storage organs (e.g., rhizomes) and non-sclerophylly characters; see Paula and Pausas 2006; see Clarke et al. 2013); (2) relative potential to resprout (i.e., the species presents some of the characteristics described in (1)); and (3) non-resprouters (i.e., none of the characteristics described in (1) are present in the species).

In theory, resprouters will be capable to regenerate biomass damages derived from anoxia periods, breakage, burial, mud coating and desiccation resulting from HP (see Bejarano et al. 2018). However, although resprouting favors plant regrowth (Pate et al. 1990; Schwilk and Ackery 2005), and this should help plants to thrive under HP, this strategy may also present downsides. For instance, resprouters tend to be deep-rooted species, whereas non-resprouters are usually shallow-rooted (e.g., Bell 2001; Paula and Pausas 2006). In this regard, resprouters might be more exposed than non-resprouters to the negative effects of frequent waterlogging resulting from HP.



Likewise, resprouters usually have lower drought resistance than non-resprouters at leaf level because they have lower water use efficiency and lower leaf mass per area (i.e., lower sclerophylly). These characteristics may constitute a disadvantage to cope with desiccation derived from HP baseflow periods.

Considering all the above, it is likely that resprouters may present full resistance to certain elements of HP (e.g., mechanical damages derived from drag and lift forces), but only partial resistance to others (e.g., submergence, waterlogging, and desiccation).

### CO<sub>2</sub> concentrating mechanisms (CO<sub>2</sub>-CM)

Some plants have evolved ATP-dependent mechanisms to concentrate CO<sub>2</sub> around Rubisco (i.e., active CO<sub>2</sub> concentrating mechanisms) as well as other concentration strategies (i.e., CO<sub>2</sub>-recycling, generation of suberin barriers; Lambers and Oliveira 2019) that may be key for plant survival in riparian areas affected by HP operations.

Plants preferentially take up the lighter isotope of carbon <sup>12</sup>C during photosynthesis and <sup>13</sup>C accumulates (Fogel and Cifuentes 1993; Evans 2001). Submergence and drought resulting from HP may constrain CO<sub>2</sub> supply within plants' leaves, ultimately forcing plants to fix <sup>13</sup>C during photosynthesis instead of <sup>12</sup>C, which implies a higher metabolic cost for plants (Farquhar and Richards 1984). Switching from <sup>12</sup>C to <sup>13</sup>C fixation might potentially translate into lower plant morphological performance (e.g., reduced leaf, stem, and root biomass) and limited energy readily available to maintain plant internal processes (Baladrón et al. 2022).

Physical and physiological concentrating mechanisms (CO<sub>2</sub>-CMs) help to increase and optimize the available pool of CO<sub>2</sub> within the plants' leaves. These mechanisms may potentially have an impact in reducing energy expenses linked to photosynthesis (Farquhar and Richards 1984; Lambers and Oliveira 2019) under limited gas diffusion conditions likely occurring during HP submergence. CO<sub>2</sub>-CMs can be divided as "soft" or "hard". Common soft mechanisms are suberin barriers (i.e., apoplastic barriers in root outer cortex/exodermis to prevent oxygen diffusion outward to the soil; Manzur et al. 2015) and stem recycling photosynthesis (i.e., a syndrome in which chlorophyllous cells in the cortex of shrub and tree species re-fix a portion of the CO<sub>2</sub> respired by the underlying tissues or carried into the stem segment by the transpiration stream; Avila et al. 2014; Cernusak and Cheesman 2015; Wittmann and Pfanz 2018). Common hard mechanisms are C<sub>4</sub>, C<sub>3</sub>-C<sub>4</sub> and C<sub>2</sub> (glycine (Gly) shuttling) photosynthetic pathways (see Sage et al. 2014). As opposed to C<sub>3</sub> photosynthesis (which undergoes the standard mechanism of the Calvin cycle), C<sub>4</sub> plants increase photosynthetic efficiency via compartmentation of CO<sub>2</sub>

assimilation and fixation by increasing PEP carboxylase activity (e.g., Schuler et al. 2016) in the mesophyll cells and limiting Rubisco only to bundle sheath chloroplasts (Sage et al. 2014); during the dark period, CO<sub>2</sub> is fixed in the form of HCO<sub>3</sub><sup>-</sup> by PEPC and stored in large vacuoles in the form of malate (Poschenrieder et al. 2018). The CO<sub>2</sub> for fixation with Rubisco is obtained by decarboxylation of malate during the following day-light period (Lüttge 2004; Poschenrieder et al. 2018). The C<sub>3</sub>-C<sub>4</sub> photosynthesis are common to species that are intermediates between C<sub>3</sub> and C<sub>4</sub> photosynthesis (Mercado and Studer 2022). These plants have intermediate leaf anatomies that contain bundle sheath cells that are less distinct and developed than the C<sub>4</sub> plants (e.g., Moore et al. 1995). Although probably less efficient than C<sub>4</sub> physiology, C<sub>3</sub>-C<sub>4</sub> might help plants to partially cope with limited CO<sub>2</sub> supply associated to HP submergence. In C<sub>2</sub> photosynthesis, glycine (Gly) produced in photorespiration diffuses from the mesophyll to sheath cells for metabolism, and photorespiratory CO<sub>2</sub> is re-assimilated; this mechanism elevates CO<sub>2</sub> levels in the bundle sheath two to three times that of the mesophyll cells, thereby improving Rubisco efficiency (Sage and Khoshravesh 2016) and the chances of plant survival under HP submergence.

Considering all the above, we have established the following trait categories: (1) absence of traits to concentrate CO<sub>2</sub> (i.e., plants that perform photosynthesis using the C<sub>3</sub> photosynthetic pathway, lacking CO<sub>2</sub>-CMs); (2) presence of a "soft" CO<sub>2</sub>-CM; (3) species equipped with more than one "soft" CO<sub>2</sub>-CM (i.e., presence of suberin barriers and stem recycling photosynthesis); and (4) presence of "hard" CO<sub>2</sub>-CMs.

### Antioxidant mechanisms (AM)

Antioxidant mechanisms allow the removal of reactive oxygen species (ROS) that may occur during phases of anaerobic energy production (Blokina et al. 2003; Turkan 2018). ROS act as secondary messengers when plants are exposed to environmental stress (e.g., drought or flooding), but they also induce plant cell damages (i.e., degradation of biomolecules like pigments, proteins, lipids, carbohydrates, DNA) and, ultimately, may cause plant cellular death (Das and Roychoudhury 2014; Bhatla and Lal 2018). Under flooding, ATP is produced via glycolysis; this metabolic pathway also triggers the production of acetaldehyde, a potent toxin that enhances the formation of ROS (Lambers and Oliveira 2019). There is also evidence that ROS in plants can increase as a response to drought (e.g., Noctor et al. 2014) and trigger different types of cellular damage, including the oxidation of protein sulfhydryl groups, photosystem damage, enzyme inhibition, lipid peroxidation, free fatty acid accumulation in membranes and activation of programmed cell

death (McKersie 1991; Sharma and Dubey 2005; Sharma et al. 2012). Therefore, it is key for plants to eliminate ROS excess derived from exposure to anoxia and drought episodes associated to HP operations.

Plants have defense systems (i.e., non-enzymatic and enzymatic antioxidant mechanisms) implicated in lowering the amount of ROS and overcome their oxidative damage, as well as in maintaining redox homeostasis (Bhatla and Lal 2018; Das and Roychoudhury 2014). Other mechanisms of some plants (e.g., *Salix martiana*) involve building up a several millimeter thick oxygenated layer around the roots that help eliminate phytotoxins via radial oxygen loss (ROL) (see Haase et al. 2003). In other species, toxic products are transported upward and excreted (e.g., through branch lenticels and leaf stomata; Kenefick 1962; Chirkova and Gutman 1972; Hook 1984; or through well-oxygenated aerenchyma structures; e.g., Haase et al. 2003).

According to what is described above, five general antioxidant mechanisms categories can be established: (1) enzymatic systems; (2) non-enzymatic systems; (3) transportation of toxic products by excretion; (4) presence of enzymatic, non-enzymatic or excretion systems, but of limited efficacy to remove ROS; and (5) absence of antioxidant mechanisms.

#### Presence of coleoptile (PCOL)

Coleoptiles (i.e., the cylindrical, soda straw-like first structure that emerges from graminoids; e.g., Parodi 1987) allow grasses to bend toward the light via phototropism, a mechanism that may potentially help riverine plants to adapt their growth and development under changing environments (Estelle 1996; Holland et al. 2009). Plants in fluvial habitats affected by changing flow regimes associated to HP operations can potentially benefit from this mechanism because it can help the plant to grow towards the surface and “escape” from light-attenuated environments resulting from submergence, where photosynthesis might be difficult. Phototropism is triggered by light perception, followed by the synthesis and translocation of signal molecules (i.e., auxins) in the tip of photo-stimulated grass coleoptiles. Differential accumulation of auxin in response to tropic stimulation, and the activity of auxin transport and auxin receptor proteins in plants (see Liscum et al. 2014) might in turn potentially translate into differences in phototropism performance between plant species, therefore affecting its capacity to escape from submergence under HP.

In addition, the coleoptile constitutes a tube within which the cotyledon grows upward to the surface, potentially offering graminoids some degree of protection against physical injury and biomass loss provoked by drag

and lift forces occurring during phases of rapid rise in discharge. The coleoptile may also protect the cotyledon from desiccation resulting from HP baseflow periods.

We have considered PCOL a trait of binary nature, and therefore plants will be classified under the categories (1) “present” or (2) “absent”.

#### Seed germination (SG)

Seed germination under HP is reduced by constant soil waterlogging and riverbank erosion resulting from highly fluctuating waters, as well as by soil desiccation resulting from fast drawdowns (Stella et al. 2010; Sarneel et al. 2014; Bejarano et al. 2020). The risk of desiccation during HP phases of low water levels is especially high in arid regions characterized by long drought periods (Bejarano et al. 2018).

Plants that germinate on a yearly basis may present a high vulnerability to HP disturbances, as germination is required every year and seed exposure will be maximum. On the contrary, perennial plants complete a single life cycle in three or more growing seasons, and hence particularly sensitive life stages are not faced every year (Bejarano et al. 2018).

In addition, the availability of light for riverine plants under HP submergence may be limited to short time windows comprised between the end of a hydropeak (i.e., down-ramping stage) and the beginning of a new hydropeak (i.e., up-ramping stage). Plants capable of germinating under “fleeting time windows” of sunlight (see Kettenring et al. 2006) between two hydropeaks may have an advantage over species that need “long-lived gaps” of multiple days or weeks (‘low-risk’ germination strategy; Kettenring et al. 2006). We foresee that (1) perennial plants might display the highest tolerance to HP, followed by (2) biennials, (3) annuals capable to germinate under short “fleeting time windows” of sunlight, and (4) annual plants adopting a ‘low-risk’ germination-based strategy. Plants under category 4 may likely experience the greatest difficulties to germinate under HP submergence.

#### Stomatal control (STOC)

Stomatal control determines the water use efficiency (WUE) of a plant by optimizing water lost against carbon gained (Cowan and Farquhar 1977; Yang et al. 2021). The effectiveness of stomatal control depends on the regulation of the stomatal aperture (i.e., speed and ‘tightness’ of closure). Fast opening and closing allow optimizing CO<sub>2</sub> influx into the leave and H<sub>2</sub>O losses. But in addition, the faster the stomatal closure is, the most effective photosynthetic induction will be (e.g., Urban et al. 2007), which in turn will determine an effective utilization of fluctuating irradiance (Kaiser et al. 2015; Morales and Kaiser



2020), a phenomenon likely occurring under flooding and water fluctuations derived from HP (i.e., "fleeting time windows" of sunlight; see Kettenring et al. 2006).

Plants can be classified under three stomatal control categories (see Shtein et al. 2017; Haworth et al. 2011): (1) Type I (i.e., kidney-shaped stomata with passive stomatal control), which corresponds to the least efficient stomatal control, usually present in ferns and gymnosperms; (2) Type II (i.e., kidney-shaped stomata with an active stomatal control), which corresponds to plants with moderately efficient control, commonly found in angiosperms; and (3) Type III (i.e., dumbbell-shaped stomata with an active stomata control) are "morphologically innovative" stomata highly efficient at opening and closing, and are common in grasses (Poaceae). This 'graminoid' morphology is associated with faster stomatal movements leading to more efficient gas exchange in changing environments (e.g., Shtein et al. 2017), for instance, riverine areas affected by episodic submergence and drought, constant waterlogging and frequent water-level variations derived from HP.

#### Non-structural carbohydrates and flooding acclimation responses (NSC)

The amount of non-structural carbohydrates (NSC, i.e., starch) in plant tissues is the result of carbon gain (photosynthesis) minus consumption (growth and maintenance respiration) (Chapin et al. 1990; Li et al. 2013a, b). Plant energy metabolism under HP submergence stress can likely be maintained with the degradation of NSC reserves, which is used by some plants (e.g., rice) to produce energy for the maintenance of basic metabolic processes (Jackson and Ram 2003; Parolin 2009), including plant respiration in anaerobic tissues (Perata et al. 1992; Colmer and Greenway 2005). This is known as a quiescence strategy (e.g., Bailey-Serres and Voesenek 2008; Voesenek and Bailey-Serres 2015), where plants do not elongate shoots under flooding to minimize carbohydrate consumption. Instead, quiescent plants use their reserves to maintain underwater metabolism and to regrow after stress (see Manzur et al. 2009; Zhao et al. 2021). Mobilization of NSC reserves differ greatly among plant species (e.g., Crawford 1992), allowing them to survive underwater from several days (e.g., *Juncus effusus*) to nearly 3 months (e.g., *Scirpus maritimus*) (Manzur et al. 2009; see Crawford 1992). Therefore, the larger the NSC reserves are, the more chances of survival during complete HP submergence. A second flooding-induced acclimation response is known as the escape strategy (Bailey-Serres and Voesenek 2008; Zhao et al. 2021) useful under relatively shallow submergence. To facilitate the escape strategy, starch reserves can be mobilized so the plant can rapidly extend their petioles or stems to allow

leaves to reach the water surface to aerate the remainder of the plant (Colmer and Voesenek 2009; Nagai et al. 2010; Zhao et al. 2021). In theory, the higher is the capacity of the plant to mobilize starch granules, the more soluble sugar available will be as an energy source for the plant to elongate and "escape" from HP submergence (see Striker et al. 2008). Operational HP regimes generating deep and long-lasting flooding in riverbanks may select against species relying on escape strategies because elongation growth competes with maintenance processes involved in plant survival during complete submergence (Ram et al. 2002). Under deep and long-lasting HP flooding, elongation growth may not be sufficient for shoots to regain contact with the air, and if that were the case, high carbohydrate consumption will likely lead to an energy deficit, severe tissue damage, and mortality (see Pierik et al. 2009; Chen et al. 2011a, b; 2019).

Based on the aforementioned, four categories can be established to classify plants based on their NSC reserves and flooding acclimation responses: (1) plants using carbohydrates to enable a quiescence strategy and with large carbohydrate reserves (species that will likely tolerate deep and long-lasting flooding); (2) plants adopting a quiescence strategy with limited carbohydrate reserves (species likely capable to thrive under deep (but short-lasting) HP submergence); (3) plants adopting an escape strategy and with large carbohydrate reserves (these plants will likely tolerate prolonged (but relatively shallow) HP submergence); and (4) plants without the capacity to adopt flooding-induced acclimation responses (i.e., quiescence or escape) and without large starch reserves.

#### Plant ventilation systems (PVS)

Ventilation mechanisms such as aerenchyma (i.e., extended system of air canals and intercellular spaces aimed at enabling ventilation in roots and plant rhizomes anchored in water-saturated soils; e.g., Björn et al. 2022), heat pumps (i.e., convections, or 'internal winds', generated across stomata that drive gasses from the atmosphere via young natant leaves, petioles to roots and back, via older leaves to the atmosphere; Dacey and Klug 1982; Armstrong and Armstrong 2011), pneumatophores, knee roots, stilt roots (i.e., roots of plants that grow vertically above the water level to get oxygen for respiration; e.g., McKee 1993; Pallardy 2008), formation of lenticels (i.e., large cracks on the surface of stems and roots which facilitates O<sub>2</sub> entry into the aerenchyma; Jackson et al. 2009), and snorkeling (e.g., Rogers 2021), are crucial for plants to thrive in water-saturated soils (Björn et al. 2022) such as those located in riverbanks of HP rivers. Based on their capacity to maintain optimal conditions for photosynthesis and respiration under oxygen-deficient environments, plants may be classified under three

categories: (1) those presenting aerenchyma; (2) those with alternative ventilation systems (usually less efficient than aerenchyma structures); and (3) those without aerenchyma or any other alternative ventilation mechanism.

Aerenchyma enables a diffusional pathway from emergent leaves to roots to transport oxygen, nitrogen, and various metabolically generated gases such as CO<sub>2</sub> and ethylene (Parolin 2012) under flooded and oxygen-deficient conditions (e.g., Steffens and Rasmussen 2016). In addition, it provides buoyancy to floating-leaves maintaining them out of the water where gas exchange is faster. Different aerenchyma types arise from the combination of four general root structural types. The shape of these root types resembles a bicycle wheel (graminaceous), a spider web (cyperaceous), a honeycomb (*Rumex*) and a non-organized structure with irregular aerenchyma lacunae (*Apium*) (e.g., Justin and Armstrong 1987; Striker et al. 2007).

Alternative ventilation systems may also facilitate O<sub>2</sub> entry from the atmosphere into the plant (see Jackson et al. 2009), but they might be slightly less efficient than aerenchyma. Plants with reduced aerenchyma production and without alternative ventilation mechanisms to facilitate oxygen diffusion between shoots and roots will likely be vulnerable to soil waterlogging and submergence derived from HP.

#### Presence of adventitious roots (ADV)

Adventitious roots grow from any non-root tissue (Esau 1953; Lovell and White 1986) and can be produced in response to stress conditions (Bannoud and Bellini 2021), such as flooding. Emergent adventitious roots grow in the oxygenated layer at the surface of the flood-water table facilitating the entry of oxygen into the root and the stem by the shortest possible pathway (e.g., Parolin 2012), therefore helping plants to avoid anoxia under submergence (e.g., Steffens and Rasmussen 2016). While under experimental conditions with stable water levels most species are able to develop adventitious roots, it is rare to find such ability in field plants, probably because their adaptive value with rapidly changing water levels is in question (Parolin et al. 2004). Regarding HP, this means that anoxia avoidance via adventitious roots might be achieved by plants located upstream the HP dam, where surface water levels may not rise rapidly. Downstream HP dams surface water levels will rapidly rise during every hydropeak and, in such case, adventitious roots may not constitute a strong advantage, especially when HP water-level fluctuations are high and frequent. Nonetheless, while adventitious roots may not offer strong protection to anoxia under rapidly changing water levels, they may help plants tolerate burial effects resulting from frequent and fast water fluctuations (Bejarano et al. 2018);

if high sedimentation rates occur during down-ramping HP stages, adventitious roots can replace the function of the ordinary root system, which often dies under several decimetres of sediment (Parolin 2012).

Adventitious roots are produced vigorously and rapidly in some species, but much less readily in others, and plants can be grouped according to their ease of rooting (Jackson 1985). Herbaceous plants with prostrate stems such as *Veronica filiformis* and *V. persica* (Harris and Lovell 1980), species presenting rhizomes or stolons (e.g., *Agropyron repens* (Palmer and Sagar 1963) and *Ranunculus repens* (Ginzo and Lovell 1973)), and climbers are often vigorous adventitious root formers (Jackson 1985). On the contrary, woody plants, especially older individuals, may present limited adventitious root production (e.g., Haissig 1974).

Based on the aforementioned, we have considered ADV a trait of binary nature, and plants are classified under the categories (1) “well-developed” adventitious roots (i.e., herbaceous plants, species with rhizomes or stolons, climbers) or (2) “poorly developed” adventitious roots (i.e., woody plants).

#### Chloroplasts movement under changing light intensities (CHMOV)

Plants can deal with changing light intensities through light-induced chloroplast movements (Wada et al. 2003). Under low light intensities, such as those likely received by plants under HP submergence, chloroplasts move toward light-irradiated area (i.e., the “accumulation response”) and situate along the cellular edges perpendicular to the incident light to optimize absorption, ensuring the capture of the maximum amount of light (Zurzycki 1955), and enhancing leaf photosynthesis and biomass production (Gotoh et al. 2018). Two phototropins (phot1 and phot2; e.g., Liscum et al. 2014) drive chloroplast movement during the “accumulation response”. By contrast, under high-intensity light, which may potentially affect aquatic plants during baseflow periods, phot2 activation causes chloroplasts to move away from the irradiated edge of the cell in a so-called “avoidance response” to prevent photodamage (e.g., Kasahara et al. 2002). Leaves of most shade-grown plants tend to exhibit stronger chloroplast movement than sun-grown plants (Davis et al. 2011; Higa and Wada 2016; Gotoh et al. 2018) and therefore should be more efficient at enhancing photosynthesis under HP submergence, and preventing photodamage under baseflow periods.

According to the aforementioned, two categories can be established to classify plants based on CHMOV: (1) shade-grown plants (strong chloroplast movement); and (2) sun-grown plants (weak chloroplast movement).

### Corticular photosynthesis (COPH)

Chlorophyll-containing bark tissue can be found in stems and branches of trees, shrubs and bushes. Several authors have demonstrated that the bark chlorenchyme in woody trees is able to photosynthetically reduce the flux of respiratory CO<sub>2</sub> to the atmosphere, a process that has been termed "CO<sub>2</sub>-refixation" or alternatively "corticular photosynthesis" (Foote and Schaedle 1976; Berveiller et al. 2007; Ávila et al. 2014; Wittmann and Pfanz 2018). The prerequisites necessary for a working reductive CO<sub>2</sub> assimilation metabolism (e.g., an effective chloroplast structure, enzymatic equipment, nutrients, water, light and carbon dioxide) are present in sufficient amounts and quantities within the chlorenchymal bark tissues of trees (Pfanz et al. 2002). Corticular photosynthesis improves plant-scale water-use efficiency due to the low water loss from the stems compared with the losses associated with foliar photosynthesis (Cernusak and Hutley 2011; Avila et al. 2014; Tarvainen et al. 2017). This is beneficial for trees to cope with water shortages linked to dry HP periods. Additionally, corticular photosynthesis may provide means for maintaining hydraulic function during drought (Vandegehuchte et al. 2015; Bloemen et al. 2016). Likewise, corticular photosynthesis may help avoiding oxygen deficiency in plants (Pfanz et al. 2002; Wittmann and Pfanz 2018) exposed to repeated HP inundations. In addition, leaf photosynthesis might be lost or severely impaired when mechanical forces resulting from fast HP currents break or damage plants' leaves. In such cases, corticular photosynthesis might help the plant to maintain a favorable carbon balance (see Ivanov et al. 2006) until it recovers the aerial elements lost.

We have considered COPH a trait of binary nature, and therefore plants will be classified under the categories (1) "present" or (2) "absent".

### Mycorrhizal symbioses (MS)

Mycorrhizal symbioses refer to the association between fungi and plants (e.g., Kirk et al. 2001). The roots of over 90% of all plant species establish these relationships with fungal taxa (Bonfante and Genre 2010). Mycorrhizas can be broadly classified as ectomycorrhizas (ECMs), when the fungus surrounds the root tip and colonizes the root intercellular spaces, and endomycorrhizas (e.g., ericoid (ERs) and arbuscular mycorrhizas (AMs)), when the fungus develops inside the root cells (Smith and Read 2008; Bonfante and Genre 2010). Four categories have been established for this trait: (1) presence of AM; (2) presence of ER; (3) presence of ECM; and (4) absence of mycorrhizal symbioses.

AMs (the commonest mycorrhizas) are associated with roots of about 80% of plant species, and facilitate host plants to grow vigorously under stressful

conditions by mediating a series of complex communication events between the plant and the fungus leading to enhanced photosynthetic rate (Birhane et al. 2012), as well as increased water uptake (Begum et al. 2019); this means that AM can help the plant to cope with photosynthetic and gas exchange limitations that may occur during HP flooding events, as well as to withstand desiccation derived from drawdown periods, and waterlogging resulting from frequent surface water-level fluctuations.

ERs are mycorrhizas of *Erica* (heather), *Calluna* (ling) and *Vaccinium* (bilberry), that is, plants that endure moorlands and similar environments where consecutive waterlogging and desiccation stages may occur. Therefore, ER may likely help plants to cope with the repeated wetting and drying cycles affecting soil riverbanks in HP systems.

ECMs are the most advanced symbiotic association between higher plants and fungi, involving the majority of forest trees (Moore 2011), and including common riparian species such as *Alnus* spp., *Betula* spp. and *Salix* spp. (Iversen et al. 2014; Weemstra et al. 2016; Chen et al. 2020). ECM symbioses may improve the water status of trees under drought conditions, through an increased absorbing surface, enhanced hydraulic conductivity at the soil–root interface, and hormonal and nutritional effects modifying stomatal regulation (Breda et al. 2006; Brunner et al. 2015). Some ECM fungi have a high resilience to drying and, therefore, plants that establish associations may increase their tolerance to drought conditions (Jarvis et al. 2013) derived from baseflow HP periods.

### Main findings, challenges and further research

Plant functional traits can help predict species resistance to fluvial alterations derived from HP, and hence to better understand the fate of local community structure, biodiversity, and ecosystem function in rivers affected by the use of this hydropower generation mode. This study provides new ideas and hypotheses on how plants may respond to HP, and brings together literature items (e.g., empirical or theoretical) that were previously disconnected. Our effort was to compile data available from multiple literature sources on plant functional traits, but here synthesized and interpreted to facilitate its use in assessing the resistance of riverine plants to common HP disturbances (i.e., flooding, water stress, and water fluctuations).

The establishment of categories for each functional trait has proven to be a challenging task. The type and number of categories defined for the traits here presented are constrained by the information and data available in the original sources. For some traits there is little data available, while for others the published studies may be contradictory, making it necessary to establish

categories based on expert judgement. Before using the information here presented, it is wise to consider if the categories as provided here are suitable for the questions asked (see Tyler et al. 2021), or if they should better be adjusted or modified. For instance, in our work, three categories were defined to classify plants based on their resprouting ability: (1) resprouter species; (2) species with relative potential to resprout; and (3) non-resprouters. If for research purposes clear cut differences between plant species want to be avoided, and rather need to classify species under a “continuous resprouting spectrum”, we may have to switch from qualitative to quantitative-based categories (e.g., measure species resprouting ability based on the number, volume, length and/or diameter of resprouts). Further improvements in the definition of trait categories will benefit any future attempt to rank riverine species based on their resistance to HP disturbance.

Our work addresses a combination of physiological (hard) and morpho-anatomical (soft) traits (Hodgson et al. 1999; Zakharova et al. 2019), and the theoretical importance of each of them in helping species to grow and survive under HP. In general, the availability of data on physiological traits in the literature is substantially lower than for morphological traits. As evidenced by Bejarano et al. (2016), traditionally, information on plant traits has focused on morphological characteristics, which were merged into local floras and field guides (e.g., Linnaeus 1745; British Ecological Society 1941), and much less attention has been paid to physiological traits. This fact represents a problem because physiological traits are better predictors of species habitat affinities than morpho-anatomical traits (see Belluau and Shipley 2018).

Processes such as the biosynthesis, metabolism, transport, and signal transduction of plant hormones (i.e., key regulators of plant growth and development such as auxin, cytokinin, brassinolide, gibberellin, ethylene, abscisic acid, jasmonate, and salicylic acid; e.g., Li et al. 2017; Bhatla and Lal 2018) involved in plant adaption to drought, waterlogging and flooding stress have been progressively studied (Jia et al. 2021) in plants. Studies on signaling pathways linked to plant hydrological stress have been conducted in the past using species of commercial or scientific interest (e.g., *Arabidopsis thaliana*; Yeung et al. 2018), but few or none in wild plants, including those growing in riparian corridors. The lack of these type of experimental studies on riverine plants complicates their grouping based on their greater or lesser capacity to trigger physiological processes potentially critical to withstand HP. Hence, it still is necessary to further clarify how physiological mechanisms operate in most riverine plants and, furthermore, how they may provide them an advantage in HP environments.

New experiments aimed at understanding stress signaling pathways and hormone synthesis involved in riverine plant resistance to fluvial disturbances would be helpful in order to incorporate new physiological traits into our analysis framework, and to determine connections between functional categories and their theoretical capacity to confer plant resistance to HP. Similarly, numerical datasets from such experiments would allow shifting from qualitative trait categories to quantitative-based classification systems.

Due to the reasons stated above, physiological traits of interest had to be discarded from our trait set due to a lack of information in the scientific literature either to define functional trait categories, or to accurately classify riverine species under any specific trait category. Shoot growth rate is an example of an understudied trait that had to be discarded from this study. Plants that grow fast may avoid submergence or at least stay closer to water surface to avoid light attenuation, potentially facilitating photosynthesis under HP submergence. Plants adopting the so-called low-O<sub>2</sub> escape strategy (Bailey-Serres and Voesenek 2008; Voesenek and Bailey-Serres 2015) can rapidly produce elongated shoots that emerge out of the water functioning as ‘snorkels’. This strategy can help plants to restore gas exchange (Voesenek and Sasidharan 2013; Sasidharan et al. 2018) when exposed to shallow HP inundation, and to avoid erosion, burial, and mud coating derived from fast water currents resulting from hydropeaks. However, with the exception of some species for which submergence-induced shoot growth responses have been studied (e.g., elongation in *Rumex palustris* (Voesenek et al. 2003), there is a lack of information on riverine plants’ shoot elongation responses, and therefore this trait cannot be currently used for HP assessment purposes.

Groups of traits intercorrelated (e.g., He et al. 2020), functionally redundant, and probably common, across sets of species within riverine communities should be kept in mind when assessing the resistance of species to HP. Traits strongly correlated are usually part of major plant adaptive strategies (Li et al. 2022), and can be considered as part of a single spectrum (He et al. 2020). Therefore, having information of part of the traits within a spectrum may allow inferring the attributes of the remaining traits for which information is not available.

Some of the traits presented in this work are strongly correlated. For instance, thick leaf cuticles, dense covering of trichomes, high leaf mass per area, and reduced number of stomata in leaves of xerophytic plants belong to the leaf economic spectrum (LES; Reich et al. 1997; Wright et al. 2004), and all of them allow plants to reduce water losses under drought conditions (Crang et al. 2018). Likewise, the formation of aerenchyma, increased



gas exchange through reduced leaf thickness, and chloroplasts that lie directed toward the epidermis are part of the low-oxygen escape syndrome (LOES), a strategy adopted by some plant species to avoid submergence (Bailey-Serres and Voisenek 2008).

Principal components analysis (PCA) and Pearson's correlation coefficients can be used to identify associations among plant traits (e.g., Bontemps et al. 2017; Fyllas et al. 2020). The application of these methods can provide a better understanding of trait intercorrelation, and improve trait-based index calculations aimed at determining riverine plant resistance to HP.

The database here presented can be expanded to cover all possible traits related to hydrological and hydraulic processes triggered by HP. Future additions to it may include a better understanding of trait–disturbance interactions, as well as additional advantages not reported in this work that may likewise confer plants resistance to HP disturbance (Baladrón et al. 2023). Future initiatives can also build on our work integrating information on traits and species (i.e., filling “(multi-) species by (multi) traits” matrices to rank species based on their differential tolerance to HP).

## Conclusions

Despite its limitations, this study is unique in that it comprehensively provides the rationale supporting the theoretical resistance of riverine species according to the presence/absence of specific functional traits, or the expression of a given trait attribute (i.e., value or modality taken by each trait). Using trait-based groups of species instead of individual species may simplify the evaluation of HP impacts on riverine plant communities worldwide and guarantee transferability of results across regions. Additionally, restoration of river margins suffering from HP impacts involving revegetation may benefit from our study. Revegetation prevents the establishment of invasive plant species, reduces the leakage of nutrients and sediments from riparian areas, and may increase in-stream habitats and stabilize water temperature and provide cover for fish and macroinvertebrate communities (Jowett et al. 2009; Peng et al. 2014). Consequently, correctly selected species for revegetation purposes may improve the chances of restoration success (Jowett et al. 2009; Peng et al. 2014).

## Abbreviations

HP	Hydropeaking
ROS	Reactive oxygen species
ATP	Adenosine triphosphate
PGF	Plant growth-form
SGF	Shoot growth-form
PGF	Plant growth-form
SGF	Shoot growth-form

WD	Woodiness
LCT	Leaf cuticle thickness
LSH	Leaf shape
LSI	Leaf size
LCON	Leaf consistency
LAN	Leaf anatomy
LMA	Leaf mass per leaf area
RDE	Rooting depth
MRD	Mean rooting depth
RMO	Root morphology
SHRE	Shape reconfiguration
SB	Suberin barriers
BGOs	Below-ground organs and root mass allocation
PHE	Plant height
LVN	Leaf venation network
PCHE	Presence of chloroplasts in epidermis
LSTO	Location of stomata
PTRI	Presence of trichomes
LPER	Leaf persistence
RA	Resprouting ability
CO <sub>2</sub> -CM	CO <sub>2</sub> concentrating mechanisms
AM	Antioxidant mechanisms
PCOL	Presence of coleoptile
SG	Seed germination
STOC	Stomatal control
NSC	Non-structural carbohydrates and flooding acclimation responses
PVS	Plant ventilation systems
ADV	Presence of adventitious roots
CHMOV	Chloroplasts movement under changing light intensities
COPH	Cortical photosynthesis
MS	Mycorrhizal symbioses
AMs	Arbuscular mycorrhizas
ERs	Ericoid mycorrhizas
ECMs	Ectomycorrhizas
F	Flooding
WS	Water stress
WF	Water fluctuations
ROL	Radial oxygen loss
VLA	Vein length per unit area
BSEs	Bundle sheath extensions
VD	Vein diameters
Gly	Glycine
PEPC	Phosphoenolpyruvate carboxylase
Rubisco	Ribulose-1,5-bisphosphate carboxylase/oxygenase
WUE	Water use efficiency

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## Author contributions

AB and MDB conceived the study. AB collected and analyzed the data, and wrote the paper with contributions from MDB and IB. All authors contributed critically and gave final approval for publication.

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## Availability of data and materials

All data generated or analyzed during this study are included in this manuscript.

## Declarations

## Ethics approval and consent to participate

Not applicable.

**Consent for publication**

Not applicable.

**Competing interests**

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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**References**

- Aguiar FC, Fábão A, Bejarano MD, Merritt D, Nilsson C, Martins MJ (2013) FLOWBASE—a riparian plant traitbase. Instituto Superior de Agronomia, Universidade de Lisboa, Lisboa. <http://www.isa.ulisboa.pt/proj/flowbase>. Accessed 12 Feb 2023
- Armstrong W, Armstrong J (2005) Stem photosynthesis not pressurized ventilation is responsible for light-enhanced oxygen supply to submerged roots of alder (*Alnus glutinosa*). *Ann Bot* 96:591–612
- Armstrong J, Armstrong W (2011) Reasons for the presence or absence of convective (pressurized) ventilation in the genus *Equisetum*. *New Phytol* 190:387–397. <https://doi.org/10.1111/j.1469-8137.2010.03539.x>
- Armstrong W, Armstrong J (2014) Plant internal oxygen transport (diffusion and convection) and measuring and modelling oxygen gradients. *Plant Cell Monogr* 21:267–297. [https://doi.org/10.1007/978-3-7091-1254-0\\_14](https://doi.org/10.1007/978-3-7091-1254-0_14)
- Armstrong J, Armstrong W, Beckett PM (1992) *Phragmites Australis*: Venturi- and humidity-induced pressure flows enhance rhizome aeration and rhizosphere oxidation. *New Phytol* 120:197–207
- 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*. *Ann Bot* 86:687–697
- Arya GC, Sarkar S, Manashero E, Aharoni A, Cohen H (2021) The plant cuticle: an ancient guardian barrier set against long-standing rivals. *Front Plant Sci* 12:663165. <https://doi.org/10.3389/fpls.2021.663165>
- Atwell BJ, Kriedemann PE, Turnbull CGN (1999) Plants in action: adaptation in nature, performance in cultivation. Macmillan Publishers, Australia
- Ávila E, Herrera A, Tezara W (2014) Contribution of stem CO<sub>2</sub> fixation to whole-plant carbon balance in nonsucculent species. *Photosynthetica* 52:3–15
- Bailey-Serres J, Voisenek LACJ (2008) Flooding stress: acclimations and genetic diversity. *Annu Rev Plant Biol* 59:313–339. <https://doi.org/10.1146/annurev.arplant.59.03>
- Baladrón A, Bejarano MD, Sarneel JM, Boavida I (2022) Trapped between drowning and desiccation: riverine plants under hydropeaking. *Sci Total Environ* 829:154451. <https://doi.org/10.1016/j.scitotenv.2022.154451>
- Baladrón A, Bejarano MD, Boavida I (2023) Why do plants respond differently to hydropeaking disturbance? A functional approach. *Ecol Indic* 150:110237. <https://doi.org/10.1016/j.ecolind.2023.110237>
- Bannoud F, Bellini C (2021) Adventitious rooting in *Populus* species: update and perspectives. *Front Plant Sci*. <https://doi.org/10.3389/fpls.2021.668837>
- Baralotto C, Caraglio Y, Goret J-Y, Scherberich D (2011) MARIWENN—Guiana species database. EcoFoG (Joint Research Unit Ecology of Guiana Forests), Center for the Study of Biodiversity in Amazonia. Mariwenn—UMR EcoFoG. Accessed 3 Feb 2023
- Begum N, Qin C, Ahanger MA, Raza S, Khan MI, Ashraf M et al (2019) Role of arbuscular mycorrhizal fungi in plant growth regulation: implications in abiotic stress tolerance. *Front Plant Sci* 10:1068. <https://doi.org/10.3389/fpls.2019.01068>
- Bejarano MD, Maroto J, Nilsson C, Aguiar FC (2016) Traits of riparian woody plants responding to hydrological and hydraulic conditions: a northern Swedish database. *Ecology* 97:2892–2892. <https://doi.org/10.1002/ecy.1533>
- Bejarano MD, Jansson R, Nilsson C (2018) The effects of hydropeaking on riverine plants: a review. *Biol Rev* 93:658–673
- Bejarano MD, Sordo-Ward A, Alonso C, Jansson R, Nilsson C (2020) Hydropeaking affects germination and establishment of riverbank vegetation. *Ecol Appl* 30:e02076. <https://doi.org/10.1002/eap.2076>
- Bell DT (2001) Ecological response syndromes in the flora of southwestern Western Australia: fire resprouters versus reseeder. *Bot Rev* 67:417–440
- Belluau M, Shipley B (2018) Linking hard and soft traits: physiology, morphology and anatomy interact to determine habitat affinities to soil water availability in herbaceous dicots. *PLoS ONE* 13:e0193130. <https://doi.org/10.1371/journal.pone.0193130>
- Bernhardt-Römermann M, Römermann C, Nuske R, Parth A, Klotz S, Schmidt W, Stadler J (2008) On the identification of the most suitable traits for plant functional trait analyses. *Oikos* 117:1533–1541. <https://doi.org/10.1111/j.0030-1299.2008.16776.x>
- Berveiller D, Kierzkowski D, Damesin C (2007) Interspecific variability of stem photosynthesis among tree species. *Tree Physiol* 27:53–61
- Bhatla SC, Lal MA (2018) Plant physiology, development and metabolism. Springer, Cham
- Bielak K, Dudzinska M, Pretzsch H (2014) Mixed stands of Scots pine (*Pinus sylvestris* L.) and Norway spruce [*Picea abies* (L.) Karst.] can be more productive than monocultures. Evidence from over 100 years of observation of long-term experiments. *For Syst* 23:573–589
- Birhane E, Sterck F, Fetene M, Bongers F, Kuyper T (2012) Arbuscular mycorrhizal fungi enhance photosynthesis, water use efficiency, and growth of frankincense seedlings under pulsed water availability conditions. *Oecologia* 169:895–904. <https://doi.org/10.1007/s00442-012-2258-3>
- Björn LO, Middleton BA, Germ M, Gaberščik A (2022) Ventilation systems in wetland plant species. *Diversity* 14:517. <https://doi.org/10.3390/d14070517>
- Bloemen J, Vergenst LL, Overlaet-Michiels L, Steppe K (2016) How important is woody tissue photosynthesis in poplar during drought stress? *Trees* 30:63–72
- Blokhina O, Virolainen E, Fagerstedt KV (2003) Antioxidants, oxidative damage and oxygen deprivation stress: a review. *Ann Bot* 91:179–194. <https://doi.org/10.1093/aob/mcf118>
- Boenisch G, Kattge J (2014) TRY—plant trait database: quantifying and scaling global plant trait diversity. Max Planck Institute for Biogeochemistry and Diversitas/IGBP. TRY References (try-db.org). Accessed 6 Sep 2022
- Boland DJ, Brooker MIH, Chippendale GM, Hall N, Hyland BPM, Johnston RD, Kleinig DA, McDonald MW, Turner JD (2006) Forest Trees of Australia. Csiro Publishing
- Bond WJ, Midgley JJ (2001) Ecology of sprouting in woody plants: the persistence niche. *Trends Ecol Evol* 16:45–51
- Bonfante P, Genre A (2010) Mechanisms underlying beneficial plant–fungus interactions in mycorrhizal symbiosis. *Nat Commun* 1:48. <https://doi.org/10.1038/ncomms1046>
- Bontemps A, Davi H, Lefèvre F, Rozenberg P, Muratorio S (2017) How do functional traits syndromes covary with growth and reproductive performance in a water-stressed population of *Fagus sylvatica*? *Oikos* 126:1472–1483. <https://doi.org/10.1111/oik.04156>
- Breda N, Huc R, Granier A, Dreyer E (2006) Temperate forest trees and stands under severe drought: a review of ecophysiological responses, adaptation processes and long-term consequences. *Ann For Sci* 63:625–644. <https://doi.org/10.1051/forest:2006042>
- British Ecological Society (1941) Biological flora of the British Isles. *J Ecol* 29:356–357
- Brodrribb TJ, Cochard H (2009) Hydraulic failure defines the recovery and point of death in water-stressed conifers. *Plant Physiol* 149:575–584
- Brodrribb TJ, Bienaimé D, Marmottant P (2016) Revealing catastrophic failure of leaf networks under stress. *Proc Natl Acad Sci USA* 113:4865–4869. <https://doi.org/10.1073/pnas.1522569113>
- Bruder A, Tonolla D, Schweizer SP, Vollenweider S, Langhans SD, Wüest A (2016) A conceptual framework for hydropeaking mitigation. *Sci Total Environ* 568:1204–1212. <https://doi.org/10.1016/j.scitotenv.2016.05.032>
- Bruehlheide H, Dengler J, Purschke O, Lenoir J, Jiménez-Alfaro B, Hennekens SM et al (2018) Global trait–environment relationships of plant communities. *Nat Ecol Evol* 2:1906–1917. <https://doi.org/10.1038/s41559-018-0699-8>
- Brunner I, Herzog C, Dawes MA, Arend M, Sperisen C (2015) How tree roots respond to drought. *Front Plant Sci* 6:547. <https://doi.org/10.3389/fpls.2015.00547>
- Bunn SE, Arthington AH (2002) Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. *Environ Manag* 30:492–507



- Caldwell MM, Dawson TE, Richards JH (1998) Hydraulic lift: consequences of water efflux from the roots of plants. *Oecologia* 113:151–161
- Cernusak LA, Cheesman AW (2015) The benefits of recycling: how photosynthetic bark can increase drought tolerance. *New Phytol* 208:995–997
- Cernusak LA, Hutley LB (2011) Stable isotopes reveal the contribution of cortical photosynthesis to growth in branches of *Eucalyptus miniata*. *Plant Physiol* 155:515–523. <https://doi.org/10.1104/pp.110.163337>
- Chabot BF, Hicks DJ (1982) The ecology of leaf life spans. *Annu Rev Ecol Syst* 13:229–259
- Chapin FS, Schulze E-D, Mooney HA (1990) The ecology and economics of storage in plants. *Annu Rev Ecol Syst* 21:423–447
- Chen G, Komatsuda T, Ma JF, Li C, Yamaji N, Nevo E (2011a) A functional cutin matrix is required for plant protection against water loss. *Plant Signal Behav* 6:1297–1299. <https://doi.org/10.4161/psb.6.9.17507>
- Chen X, Visser EJJW, de Kroon H, Pierik R, Voeselek LA, Huber H (2011b) Fitness consequences of natural variation in flooding-induced shoot elongation in *Rumex palustris*. *New Phytol* 190:409–420. <https://doi.org/10.1111/j.1469-8137.2010.03639.x>
- Chen X-S, Li Y-F, Cai Y-H, Xie Y-H, Deng Z-M, Li F, Hou Z-Y (2019) Differential strategies to tolerate flooding in *Polygonum hydropiper* plants originating from low- and high-elevation habitats. *Front Plant Sci* 9:1970. <https://doi.org/10.3389/fpls.2018.01970>
- Chen W, Tape KD, Euskirchen ES, Liang S, Matos A, Greenberg J, Fraterigo JM (2020) Impacts of arctic shrubs on root traits and belowground nutrient cycles across a northern Alaskan climate gradient. *Front Plant Sci* 11:588098. <https://doi.org/10.3389/fpls.2020.588098>
- Chen A, Liu T, Wang Z, Chen X (2022) Plant root suberin: A layer of defence against biotic and abiotic stresses. *Front Plant Sci*. 13:1056008. <https://doi.org/10.3389/fpls.2022.1056008>
- Chirkova TV, Gutman TS (1972) Physiological role of branch lenticels in willow and poplar under conditions of root anaerobiosis. *Sov Plant Physiol* 19:289–295
- Chytrý M, Danihelka J, Kaplan Z, Wild J, Holubová D, Novotný P, Řezníčková M, Rohn M, Dřevojan P, Grulich V et al (2021) Pladias database of the Czech Flora and vegetation. *Preslia* 93:1–87
- Clarke PJ, Lawes MJ, Midgley JJ, Lamont BB, Ojeda F, Burrows GE, Enright NJ, Knox KJE (2013) Resprouting as a key functional trait: how buds, protection and resources drive persistence after fire. *New Phytol* 197:19–35. <https://doi.org/10.1111/nph.12001>
- Clayton WD, Harman KT, Williamson H. 2006. World Grass Species—Synonymy database. The Board of Trustees of the Royal Botanic Gardens, Kew
- Colmer TD (2003) Long-distance transport of gases in plants: a perspective on internal aeration and radial oxygen loss from roots. *Plant Cell Environ* 26:17–36
- Colmer TD, Greenway H (2005) Oxygen transport, respiration, and anaerobic carbohydrate catabolism in roots in flooded soils. In: Lambers H, Rivas-Carbo M (eds) *Plant respiration: from cell to ecosystem*. Springer, Netherlands
- Colmer TD, Voeselek LAJ (2009) Flooding tolerance: suites of plant traits in variable environments. *Funct Plant Biol* 36:665–681
- Colmer TD, Cox MCH, Voeselek LAJ (2006) Root aeration in rice (*Oryza sativa*): evaluation of oxygen, carbon dioxide, and ethylene as possible regulators of root acclimatizations. *New Phytol* 170:767–778
- Cooley AM, Reich A, Rundel P (2004) Leaf support biomechanics of neotropical understory herbs. *Am J Bot* 91:573–581
- Cornelissen JHC, Lavorel S, Garnier E, Díaz S, Buchmann N, Gurvich DE, Reich PB, ter Steege H, Morgan HD, van der Heijden MGA, Pausas JG, Poorter H (2003) A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Aust J Bot* 51:335–380
- Costa MJ, Pinheiro A, Boavida I (2019) Habitat enhancement solutions for Iberian cyprinids affected by hydropeaking: insights from flume research. *Sustainability* 11:6998. <https://doi.org/10.3390/su11246998>
- Cowan IR, Farquhar GD (1977) Stomatal function in relation to leaf metabolism and environment. *Symp Soc Exp Biol* 121:471–505
- Crang R, Lyons-Sobaski S, Wise R (2018) Leaves. In: *Plant anatomy: a concept-based approach to the structure of seed plants*. Springer, Cham
- Crawford RMM (1992) Oxygen availability as an ecological limit to plant distribution. *Adv Ecol Res* 23:95–185
- Cushman RM (1985) Review of ecological effects of rapidly varying flows downstream from hydroelectric facilities. *N Am J Fish Manage* 5:330–339. [https://doi.org/10.1577/15488659\(1985\)5%3C330:ROEEOR%3E2.0.CO;2](https://doi.org/10.1577/15488659(1985)5%3C330:ROEEOR%3E2.0.CO;2)
- Dacey JWH, Klug MJ (1982) Ventilation by floating leaves in Nuphar. *Am J Bot* 69:999–1003
- Das K, Roychoudhury A (2014) Reactive oxygen species (ROS) and response of antioxidants as ROS-scavengers during environmental stress in plants. *Front Environ Sci* 2:53. <https://doi.org/10.3389/fenvs.2014.00053>
- Davis PA, Caylor S, Whippe CW, Hangerter RP (2011) Changes in leaf optical properties associated with light-dependent chloroplast movements. *Plant Cell Environ* 34:2047–2059
- De la Riva EG, Olmo M, Poorter H, Uberta JL, Villar R (2016) Leaf mass per area (LMA) and its relationship with leaf structure and anatomy in 34 Mediterranean woody species along a water availability gradient. *PLoS ONE* 11:e0148788. <https://doi.org/10.1371/journal.pone.0148788>
- De Simone O (2003) Apoplastic barriers and oxygen transport properties of hypodermal cell walls in roots from four Amazonian tree species. *Plant Physiol* 132:206–217
- Delzon S, Douthé C, Sala A, Cochard H (2010) Mechanism of water-stress-induced cavitation in conifers: bordered pit structure and function support the hypothesis of seal-capillary seeding. *Plant Cell Environ* 33:2101–2111
- Demmings EM, Williams BR, Lee C-R, Barba P, Yang S, Hwang C-F et al (2019) Quantitative trait locus analysis of leaf morphology indicates conserved shape loci in grapevine. *Front Plant Sci* 10:1373. <https://doi.org/10.3389/fpls.2019.01373>
- Denny FE (1924) Effect of ethylene upon respiration of lemons. *Bot Gaz* 77:322–329
- Díaz S, Cabido M, Casanoves F (1998) Plant functional traits and environmental filters at a regional scale. *J Veg Sci* 9:113–122. <https://doi.org/10.2307/3237229>
- Diehl RM, Merritt DM, Wilcox AC, Scott ML (2017) Applying functional traits to ecogeomorphic processes in riparian ecosystems. *Bioscience* 67:729–743. <https://doi.org/10.1093/biosci/bix080>
- Du H, Ran JH, Feng YY, Wang X-Q (2020) The flattened and needlelike leaves of the pine family (Pinaceae) share a conserved genetic network for adaxial-abaxial polarity but have diverged for photosynthetic adaptation. *BMC Evol Biol* 20:131. <https://doi.org/10.1186/s12862-020-01694-5>
- Eggle U, Nyffeler R (2009) Living under temporarily arid conditions: succulence as an adaptive strategy. *Bradleya* 27:13–36
- Esau K (1953) *Plant Anatomy*. John Wiley and Sons, New York
- Estelle M (1996) Plant tropisms: the ins and outs of auxin. *Curr Biol* 6:1589–1591
- Evans RD (2001) Physiological mechanisms influencing plant nitrogen isotope composition. *Trends Plant Sci* 6:121–126
- Fan Y, Miguez-Macho G, Jobbágy EG, Jackson RB, Otero-Casal C (2017) Hydrologic regulation of plant rooting depth. *Proc Nat Acad Sci* 114:10572–10577. <https://doi.org/10.1073/pnas.1712381114>
- Farquhar GD, Richards RA (1984) Isotopic composition of plant carbon correlates with water use efficiency of wheat genotypes. *Aust J Plant Physiol* 11:539–552
- Field C, Mooney HA (1986) The photosynthesis–nitrogen relationship in wild plants. In: Givnish T (ed) *On the economy of plant form and function*. Cambridge University Press, Cambridge
- Fitter AH, Hay RKM (2002) *Environmental physiology of plants*. Academic Press, London
- Fitter AH, Peat HJ (1994) The ecological flora database. *J Ecol* 82:415–425
- Flowers T, Santos J, Jahns M, Warburton B, Reed P (2015) Halophytes—eHALOPH database. University of Sussex, Brighton, United Kingdom. eHALOPH (uc.pt). <http://www.sussex.ac.uk/affiliates/halophytes/>. Accessed 10 Jan 2023
- Fogel ML, Cifuentes LA (1993) *Isotope fractionation during primary production*. In: Engel MH, Macko SA (eds) *Organic geochemistry*. Plenum Press, New York
- Foot KC, Schaedle M (1976) Diurnal and seasonal patterns of photosynthesis and respiration by stems of *Populus tremuloides* Michx. *Plant Physiol* 58:651–655
- Freschet GT, Pagès L, Iversen CM, Comas LH, Rewald B, Roumet C, Klimešová J, Zadworny M, Poorter H, Postma JA et al (2021) A starting guide to root ecology: strengthening ecological concepts and standardising root classification, sampling, processing and trait measurements. *New Phytol* 232:973–1122
- Furlow JJ (1979) The systematics of the American species of *Alnus* (Betulaceae). *Rhodora* 81:151–248

- Fyllas NM, Michelaki C, Galanidis A, Evangelou E, Zaragoza-Castells J, Dimitrakopoulos PG, Lloyd J et al (2020) Functional trait variation among and within species and plant functional types in mountainous mediterranean forests. *Front Plant Sci*. <https://doi.org/10.3389/fpls.2020.00212>
- Garnier E, Cortez J, Billès G, Navas M-L, Roumet C, Debussche M et al (2004) Plant functional markers capture ecosystem properties during secondary succession. *Ecology* 85:2630–2637. <https://doi.org/10.1890/03-0799>
- Gayraud S, Statzner B, Bady P, Haybach A (2003) Invertebrate traits for the bio-monitoring of large European rivers: an initial assessment of alternative metrics. *Freshwater Biol* 48:2045–2064
- Geigenberger P (2003) Response of plant metabolism to too little oxygen. *Curr Opin Plant Biol* 6:247–256. [https://doi.org/10.1016/s1369-5266\(03\)00038-4](https://doi.org/10.1016/s1369-5266(03)00038-4)
- Gibbs J, Greenway H (2003) Mechanisms of anoxia tolerance in plants. I. Growth, survival and anaerobic catabolism. *Func Plant Biol* 30:1–47. [https://doi.org/10.1071/PP98095\\_ER](https://doi.org/10.1071/PP98095_ER)
- Givnish T (1979) On the adaptive significance of leaf form. In: Solbrig OT, Jain S, Johnson GB, Raven PH (eds) Topics in plant population biology. Macmillan Education, London. [https://doi.org/10.1007/978-1-349-04627-0\\_17](https://doi.org/10.1007/978-1-349-04627-0_17)
- Givnish TJ (2002) Adaptive significance of evergreen vs. deciduous leaves: solving the triple paradox. *Silva Fennica* 36:703–743
- Goodman AM, Ennos AR (1997) The response of roots to mechanical stimulation. In: Jeronimidis G, Vincent JFV (eds) Plant biomechanics (Conference Proceedings I: papers). Centre for Biomimetics, University of Reading, Reading
- Gotoh E, Suetsugu N, Yamori W, Ishishita K, Kiyabu R, Fukuda M, Higa T, Shirouchi B, Wada M (2018) Chloroplast accumulation response enhances leaf photosynthesis and plant biomass production. *Plant Physiol* 178:1358–1369. <https://doi.org/10.1104/pp.18.00484>
- Grigore MN, Toma C, Zamfirache M, Boscaiu M, Olteanu Z, Cojocaru D (2012) Ecological anatomy in halophytes with  $C_4$  photosynthesis: discussing adaptive features in endangered ecosystems. *Carpath J Earth Env* 7:13–21
- Grime JP, Hodgson JG, Hunt R (1988) Comparative plant ecology. A functional approach to common British species. Unwin Hyman, London
- Groot TT, van Bodegom PM, Meijer HAJ, Harren JFM (2005) Gas transport through the root–shoot transition zone of rice tillers. *Plant Soil* 277:107–116
- Grosse W, Bernhard BH, Tiebel H (1991) Pressurized ventilation in wetland plants. *Aquat Bot* 39:89–98
- Gurevitch J, Schuepp PH (1990) Boundary layer properties of highly dissected leaves: an investigation using an electrochemical fluid tunnel. *Plant Cell Environ* 13:783–792
- Haase K, De Simone O, Junk WJ, Schmidt W (2003) Internal oxygen transport in cuttings from flood-adapted varzea tree species. *Tree Physiol* 23:1069–1076. <https://doi.org/10.1093/treephys/23.15.1069>
- Hacke UG, Sperry JS, Pockman WT, Davis SD, McCulloh KA (2001) Trends in wood density and structure are linked to prevention of xylem implosion by negative pressure. *Oecologia* 126:457–461. <https://doi.org/10.1007/s004420100628>
- Haissig BE (1974) Origins of adventitious roots. *N Z J For Sci* 4:299–310
- Harby A, Noack M (2013) Rapid flow fluctuations and impacts on fish and the aquatic ecosystem. In: Maddock J, Harby A, Kemp P, Wood P (eds) Ecohydraulics: an integrated approach. Wiley, Chichester
- Harris GR, Lovell PH (1980) Adventitious root formation in *Veronica* spp. *Ann Bot* 45:459–468
- Hartman S, Sasidharan R, Voesenek LACJ (2019) The role of ethylene in metabolic acclimations to low oxygen. *New Phytol* 229:64–70. <https://doi.org/10.1111/nph.16378>
- Havens KE, Sharfstein B, Brady MA, East TL, Harwell MC, Maki RP, Rodusky AJ (2004) Recovery of submerged plants from high water stress in a large subtropical lake in Florida, USA. *Aquat Bot* 78:67–82
- Haworth M, Elliott-Kingston C, McElwain JC (2011) Stomatal control as a driver of plant evolution. *J Exp Bot* 62:2419–2423
- He N, Li Y, Liu C, Xu L, Li M, Zhang J et al (2020) Plant trait networks: improved resolution of the dimensionality of adaptation. *Trends Ecol Evol* 35:908–918. <https://doi.org/10.1016/j.tree.2020.06.003>
- Herzog M, Konnerup D, Pedersen O, Winkel A, Colmer TD (2018) Leaf gas films contribute to rice (*Oryza sativa*) submergence tolerance during saline floods. *Plant Cell Environ* 41:885–897
- Higa T, Wada M (2016) Chloroplast avoidance movement is not functional in plants grown under strong sunlight. *Plant Cell Environ* 39:871–882
- Hodgson JG, Wilson PJ, Hunt R, Grime JP, Thompson K (1999) Allocating C–S–R plant functional types: a soft approach to a hard problem. *Oikos* 85:282–294
- Holland JJ, Roberts D, Liscum E (2009) Understanding phototropism: from Darwin to today. *J Exp Bot* 60:1969–1978
- Hook DD (1984) Adaptations to flooding with fresh water. In: Kozlowski TT (ed) Flooding and plant growth. Academic Press, New York
- Hosie RC (1969) Native trees of Canada, 7th edn. Canadian Forestry Service, Department of Fisheries and Forestry, Ottawa
- Hultén E, Fries M (1986) Atlas of North European vascular plants, north of the Tropic of Cancer. 3 vols. Koeltz scientific books
- Ingrouille M (2012) Diversity and Evolution of Land Plants. Springer Science and Business Media
- Ivanov AG, Krol M, Sveshnikov D, Malmberg G, Gardeström P, Hurry V, Öquist G, Huner NPA (2006) Characterization of the photosynthetic apparatus in cortical bark chlorenchyma of Scots pine. *Planta* 223:1165–1177. <https://doi.org/10.1007/s00425-005-0164-1>
- Iversen CM, Sloan VL, Sullivan PF, Euskirchen ES, McGuire AD, Norby RJ et al (2014) The unseen iceberg: plant roots in arctic tundra. *New Phytol* 205:34–58. <https://doi.org/10.1111/nph.13003>
- Jackson MB (1985) Ethylene and responses of plants to soil waterlogging and submergence. *Annu Rev Plant Physiol* 36:145–174
- Jackson MB (2008) Ethylene-promoted elongation: an adaptation to submergence stress. *Ann Bot* 101:229–248
- Jackson MB, Armstrong W (1999) Formation of aerenchyma and the processes of plant ventilation in relation to soil flooding and submergence. *Plant Biol* 1:274–287
- Jackson MB, Ram PC (2003) Physiological and molecular basis of susceptibility and tolerance of rice plants to complete submergence. *Ann Bot* 91:227–241
- Jackson MB, Ishizawa K, Osamu I (2009) Evolution and mechanisms of plant tolerance to flooding stress. *Ann Bot* 103:137–142
- Jager HJ, De Silva T, Uria-Martinez R, Pracheil BM, Macknick J (2022) Shifts in hydropower operation to balance wind and solar will modify effects on aquatic biota. *Water Biol Secur* 1:100060. <https://doi.org/10.1016/j.watbs.2022.100060>
- Jarvis S, Woodward S, Alexander IJ, Taylor AFS (2013) Regional scale gradients of climate and nitrogen deposition drive variation in ectomycorrhizal fungal communities associated with native Scots pine. *Glob Change Biol* 19:1688–1696. <https://doi.org/10.1111/gcb.12178>
- Jerry AC, Chater AO, David RW (1982) Sedges of the British Isles. Botanical Society of the British Isles Handbook no. 1, 2nd ed. Botanical Society of Britain and Ireland
- Jia W, Ma M, Chen J, Wu S (2021) Plant morphological, physiological and anatomical adaptation to flooding stress and the underlying molecular mechanisms. *Int J Mol Sci* 22:1088. <https://doi.org/10.3390/ijms22031088>
- Johnson HB (1975) Plant pubescence: An ecological perspective. *Bot Rev* 41:233–258. <https://doi.org/10.1007/BF02860838>
- Jowett IG, Richardson J, Boubée JAT (2009) Effects of riparian manipulation on stream communities in small streams: two case studies. *N Z J Mar Fresh* 43:763–774
- Justin SHFW, Armstrong W (1987) The anatomical characteristics of roots and plant response to soil flooding. *New Phytol* 106:465–495
- Kaelke CM, Dawson JO (2003) Seasonal flooding regimes influence survival, nitrogen fixation, and the partitioning of nitrogen and biomass in *Alnus incana* ssp. *rugosa*. *Plant Soil* 254:167–177. <https://doi.org/10.1023/a:1024903912325>
- Kaiser E, Morales A, Harbinson J, Kromdijk J, Heuvelink E, Marcelis LFM (2015) Dynamic photosynthesis in different environmental conditions. *J Exp Bot* 66:2415–2426. <https://doi.org/10.1093/jxb/eru406>
- Kalliokoski T (2011) Root system traits of Norway spruce, Scots pine, and silver birch in mixed boreal forests: an analysis of root architecture, morphology and anatomy. *Dissertationes Forestales*. <https://doi.org/10.14214/df.121>
- Kasahara M, Kagawa T, Oikawa K, Suetsugu N, Miyao M, Wada M (2002) Chloroplast avoidance movement reduces photodamage in plants. *Nature* 420:829–832

- Kashiwagi J, Krishnamurthy L, Upadhyaya H, Krishna H, Chandra S, Vadez V, Serraj R (2005) Genetic variability of drought-avoidance root traits in the mini-core germplasm collection of chickpea (*Cicer arietinum* L.). *Euphytica* 146:213–222. <https://doi.org/10.1007/s10681-005-9007-1>
- Katifori E, Szöllösi GJ, Magnasco MO (2010) Damage and fluctuations induce loops in optimal transport networks. *Phys Rev Lett* 104:048704. <https://doi.org/10.1103/PhysRevLett.104.048704>
- Kattge K, Diaz S, Lavorel S, Prentice IC, Leadley P et al (2011) TRY—a global database of plant traits. *Glob Change Biol* 17:2905–2935. <https://doi.org/10.1111/j.1365-2486.2011.02451.x>
- Kawecki TJ, Ebert D (2004) Conceptual issues in local adaptation. *Ecol Lett* 7:1225–1241. <https://doi.org/10.1111/j.1461-0248.2004.00684.x>
- Kearney MR, Simpson SJ, Raubenheimer D, Helmuth B (2010) Modelling the ecological niche from functional traits. *Philos Trans R Soc B Biol Sci* 365:3469–3483. <https://doi.org/10.1098/rstb.2010.0034>
- Keddy PA (1992) Assembly and response rules: two goals for predictive community ecology. *J Veg Sci* 3:157–164
- Kenefick DG (1962) Formation and elimination of ethanol in sugar beet roots. *Plant Physiol* 37:434–439. <https://doi.org/10.1104/pp.37.3.434>
- Kenzo T, Yoneda R, Azani MA, Majid NM (2008) Changes in leaf water use after removal of leaf lower surface hairs on *Mallotus macrostachyus* (Euphorbiaceae) in a tropical secondary forest in Malaysia. *J For Res* 13:137–142
- Kettenring KM, Gardner G, Galatowitsch SM (2006) Effect of light on seed germination of eight wetland *Carex* species. *Ann Bot* 98:869–874. <https://doi.org/10.1093/aob/mcl170>
- Kirk PM, Cannon PF, David JC, Stalpers J (2001) Ainsworth and Bisby's dictionary of the Fungi, 9th edn. CAB International, Wallingford
- Kleyer M (1995) Biological traits of vascular plants—a database. University of Stuttgart, Arbeitsberichte, Stuttgart. Biological traits of vascular plants // University of Oldenburg (uol.de). Accessed 4 Feb 2023
- Kleyer M, Bekker RM, Knevel IC, Bakker JP, Thompson K, Sonnenschein M et al (2008) The LEDA Traitbase—a database on the life history traits of the Northwest European flora. *J Ecol* 96:1266–1274. <https://doi.org/10.1111/j.1365-2745.2008.01430.x>
- Klimešová J, Klimeš L (2007) Bud banks and their role in vegetative regeneration—a literature review and proposal for simple classification and assessment. *Perspect Plant Ecol* 8:115–129
- Klimešová J, Martinková J, Ottaviani G (2018) Belowground plant functional ecology: towards an integrated perspective. *Funct Ecol* 32:2115–2126. <https://doi.org/10.1111/1365-2435.13145>
- Klotz S, Kühn I, Durka W (2002) BIOFLOR: Eine Datenbank zu biologischökologischen Merkmalen der Gefäßpflanzen in Deutschland. Schriftenreihe für Vegetationskunde 38. Bundesamt für Naturschutz, Bonn. BiolFlor search system (ufz.de). Accessed 8 Feb 2023
- Koehl MAR, Alberte RS (1988) Flow, flapping, and photosynthesis of *Nereocystis luetkeana*: a functional comparison of undulate and flat blade morphologies. *Mar Biol* 99:435–444
- Koehl MAR (1979) Stiffness or extensibility of intertidal algae: a comparative study of modes of withstanding wave action. *J Biomech* 12:634
- Kouwen N, Fathi-Moghadam M (2000) Friction factors for coniferous trees along rivers. *J Hydraul Eng* 126:732–740. [https://doi.org/10.1061/\(ASCE\)0733-9429\(2000\)126:10\(732\)](https://doi.org/10.1061/(ASCE)0733-9429(2000)126:10(732))
- Laan P, Berrevoets MJ, Lythe S, Armstrong W, Blom CWPM (1989) Root morphology and aerenchyma formation as indicators of the flood-tolerance of *Rumex* species. *J Ecol* 77:693–703
- Lambers H, Oliveira RS (2019) Photosynthesis, respiration, and long-distance transport: long distance transport of assimilates. *Plant physiological ecology*, 3rd edn. Springer, Cham. <https://doi.org/10.1007/978-3-030-29639-1>
- Lambers H, Chapin FS III, Pons TL (1998) Plant physiological ecology. Springer Verlag, Berlin
- Lambers H, Raven JA, Shaver GR, Smith SE (2008) Plant nutrient-acquisition strategies change with soil age. *Trends Ecol Evol* 23:95–103. <https://doi.org/10.1016/j.tree.2007.10.008>
- Larcher W (2003) Physiological plant ecology: ecophysiology and stress physiology of functional groups, 4th edn. Springer, Berlin
- Lavorel S, Garnier E (2002) Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Funct Ecol* 16:545–556. <https://doi.org/10.1046/j.1365-2435.2002.00664.x>
- Lavorel S, McIntyre S, Landsberg J, Forbes TDA (1997) Plant functional classifications: from general groups to specific groups based on response to disturbance. *Trends Ecol Evol* 12:474–478. [https://doi.org/10.1016/s0169-5347\(97\)01219-6](https://doi.org/10.1016/s0169-5347(97)01219-6)
- Li MH, Cherubini P, Dobberty PM, Arend M, Xiao WF, Rigling A (2013a) Responses of leaf nitrogen and mobile carbohydrates in different *Quercus* species/provenances to moderate climate changes. *Plant Biol* 15:177–184. <https://doi.org/10.1111/j.1438-8677.2012.00579.x>
- Li L, Zeng H, Guo D-L (2013b) Leaf venation functional traits and their ecological significance. *Chin J Plant Ecol* 37:691–698
- Li J, Li C, Smith SM (2017) Hormone metabolism and signaling in plants. Woodhead Publishing, Elsevier
- Li J, Chen X, Niklas KJ, Sun J, Wang Z, Zhong Q et al (2022) A whole-plant economics spectrum including bark functional traits for 59 subtropical woody plant species. *J Ecol* 110:248–261
- Linnaeus C (1745) *Flora Svecica*. Lars Salvius, Stockholm
- Liscum E, Askinosie SK, Leuchtman DL, Morrow J, Willenburg KT, Coats DR (2014) Phototropism: growing towards an understanding of plant movement. *Plant Cell* 26:38–55. <https://doi.org/10.1105/tpc.113.119727>
- Lovell PH, White J (1986) Anatomical changes during adventitious root formation. In: Jackson MB (eds) *New Root Formation in Plants and Cuttings*. Developments in Plant and Soil Sciences, vol 20. Springer, Dordrecht. [https://doi.org/10.1007/978-94-009-4358-2\\_4](https://doi.org/10.1007/978-94-009-4358-2_4)
- López Gonzalez G (2001) *Los Árboles y Arbustos De La Península Ibérica e Islas Baleares*. 2ª Ed. (2 Vols.). Mundi Prensas Libros, Madrid
- Lubbe FC, Henry HAL (2020) The role of perennation traits in plant community soil frost stress responses. *Ann Bot* 126:873–881. <https://doi.org/10.1093/aob/mcaa104>
- Lüttge U (2004) Ecophysiology of Crassulacean acid metabolism (CAM). *Ann Bot* 93:629–652. <https://doi.org/10.1093/aob/mch087>
- Maberly SC, Madsen TV (2002) Freshwater angiosperm carbon concentrating mechanisms: processes and patterns. *Funct Plant Biol* 29:393–405
- Manzur ME, Grimaldi AA, Insausti P, Striker GG (2009) Escape from water or remain quiescent? *Lotus tenuis* changes its strategy depending on depth of submergence. *Ann Bot* 104:1163–1169. <https://doi.org/10.1093/aob/mcp203>
- Manzur ME, Grimaldi AA, Insausti P, Striker GG (2015) Radial oxygen loss and physical barriers in relation to root tissue age in species with different types of aerenchyma. *Funct Plant Biol* 42:9–17
- Mauseth JD (2009) *Botany: an introduction to plant biology*, 2/e, Multimedia Enhanced. Jones and Bartlett Publishers, Sudbury
- McGill BJ, Enquist BJ, Weiher E, Westoby M (2006) Rebuilding community ecology from functional traits. *Trends Ecol Evol* 21:178–185
- McKee KL (1993) Soil physicochemical patterns and mangrove species distribution—reciprocal effects? *J Ecol* 81:477–487
- McKersie BD (1991) The role of oxygen free radicals in mediating freezing and desiccation stress in plants. In: Pell EJ, Steffen KL (eds) *Active oxygen/oxidative stress and plant metabolism*. American Society of Plant Physiology, Rockville
- Méndez-Alonzo R, Ewers FW, Sack L (2013) Ecological variation in leaf biomechanics and its scaling with tissue structure across three Mediterranean-climate plant communities. *Funct Ecol* 27:544–554. <https://doi.org/10.1111/1365-2435.12059>
- Mercado MA, Studer AJ (2022) Meeting in the middle: lessons and opportunities from studying C3–C4 intermediates. *Annu Rev Plant Biol* 73:43–65
- Merritt DM, Scott ML, Leroy Poff N, Auble GT, Lytle DA (2010) Theory, methods and tools for determining environmental flows for riparian vegetation: riparian vegetation-flow response guilds. *Freshwater Biol* 55:206–225. <https://doi.org/10.1111/j.1365-2427.2009.02206.x>
- Mickovski SB, Ennos AR (2003) The effect of unidirectional stem flexing on shoot and root morphology and architecture in young *Pinus sylvestris* trees. *Can J For Res* 33:2202–2209. <https://doi.org/10.1139/x03-139>
- Miedema Brown L, Anand M (2022) Plant functional traits as measures of ecosystem service provision. *Ecosphere* 13:e3930. <https://doi.org/10.1002/ecs2.3930>
- Migalina SV, Ivanova LA, Makhnev AK (2010) Changes of leaf morphology in *Betula pendula* Roth and *B. pubescens* Ehrh. along a zonal-climatic transect in the Urals and Western Siberia. *Russ J Ecol* 41:263–271. <https://doi.org/10.1134/S106741361004003X>
- Mitsch WJ, Gosselink JG (2007) *Wetlands: human history, use, and science*, 4th edn. Wiley, Hoboken

- Mommer L, Visser EJW (2005) Underwater photosynthesis in flooded terrestrial plants: a matter of leaf plasticity. *Ann Bot* 96:581–589. <https://doi.org/10.1093/aob/mci212>
- Moor H, Rydin H, Hylander K, Nilsson MB, Lindborg R, Norberg J, Vesik P (2017) Towards a trait-based ecology of wetland vegetation. *J Ecol* 105:1623–1635
- Moore D (2011) Ectomycorrhizae. <http://www.world-of-fungi.org/>. Accessed 25 Jan 2023.
- Moore R, Clark WD, Kingsley RS, Vodopich D (1995) Botany. Wm. C Brown Publishers, Dubuque
- Morales A, Kaiser E (2020) Photosynthetic acclimation to fluctuating irradiance in plants. *Front Plant Sci* 11:268. <https://doi.org/10.3389/fpls.2020.00268>
- Morrison HA, Smokorowski KE (2000) The applicability of various frameworks and models for assessing the effects of hydropeaking on the productivity of aquatic ecosystems. Canadian Technical Report of Fisheries and Aquatic Sciences No. 2322. Department of Fisheries and Oceans, Canada
- Mouillot D, Graham NAJ, Villéger S, Mason NWH, Bellwood DR (2013) A functional approach reveals community responses to disturbances. *Trends Ecol Evol* 28:167–177. <https://doi.org/10.1016/j.tree.2012.10.004>
- Mueller K, Tilman D, Fornara D, Hobbie S (2013) Root depth distribution and the diversity-productivity relationship in a long-term grassland experiment. *Ecology* 94:787–793. <https://doi.org/10.1890/12-1399.1>
- Nagai K, Hattori Y, Ashikari M (2010) Stunt or elongate? Two opposite strategies by which rice adapts to floods. *J Plant Res* 123:303–309
- Nair KPP (2010) Agronomy and economy of important tree crops of the developing world. Elsevier Science, Burlington
- Nardini A, Pitt F (1999) Drought resistance of *Quercus pubescens* as a function of root hydraulic conductance, xylem embolism and hydraulic architecture. *New Phytol* 143:485–493
- Nardini A, Salleo S, Jansen S (2011) More than just a vulnerable pipeline: xylem physiology in the light of ion-mediated regulation of plant water transport. *J Exp Bot* 62:4701–4718. <https://doi.org/10.1093/jxb/err208>
- Nicotra AB, Cosgrove MJ, Cowling A, Schlichting CD, Jones CS (2007) Leaf shape linked to photosynthetic rates and temperature optima in South African *Peltargonium* species. *Oecologia* 154:625–635
- Nicotra AB, Leigh A, Boyce KC, Jones CS, Niklas KJ, Royer DL, Tsukaya H (2011) The evolution and functional significance of leaf shape in the angiosperms. *Funct Plant Biol* 38:535–552. <https://doi.org/10.1071/FP11057>
- Niklas KJ (1992) Plant biomechanics: an engineering approach to plant form and function. University of Chicago Press, Chicago
- Nikora V (2010) Hydrodynamics of aquatic ecosystems: an interface between ecology, biomechanics and environmental fluid mechanics. *River Res Appl* 26:367–384
- Nock CA, Vogt RJ, Beisner BE (2016) Functional traits. In: eLS. Wiley, Chichester
- Noctor G, Mhamdi A, Foyer CH (2014) The roles of reactive oxygen metabolism in drought: not so cut and dried. *Plant Physiol* 164:1636–1648. <https://doi.org/10.1104/pp.113.233478>
- O'Hare MT, Hutchinson KA, Clarke RT (2007) The drag and reconfiguration experienced by five macrophytes from a lowland river. *Aquat Bot* 86:253–259
- Oertli JJ, Lips SH, Agami M (1990) The strength of sclerophyllous cells to resist collapse due to negative turgor pressure. *Acta Oecol* 11:281–290
- Ogburn RM, Edwards EJ (2010) The ecological water-use strategies of succulent plants. *Adv Bot Res* 55:179–225. [https://doi.org/10.1016/S0065-2296\(10\)55004-3](https://doi.org/10.1016/S0065-2296(10)55004-3)
- Onoda Y, Richards L, Westoby M (2012) The importance of leaf cuticle for carbon economy and mechanical strength. *New Phytol* 196:441–447. <https://doi.org/10.1111/j.1469-8137.2012.04263.x>
- Padilla FM, Pugnaire FI (2007) Rooting depth and soil moisture control Mediterranean woody seedling survival during drought. *Funct Ecol* 21:489–495
- Pallardy SG (2008) Physiology of woody plants, 3rd edn. Academic Press, Burlington
- Palmquist EC, Ralston BE, Sarr D, Merritt DM, Shafroth PB, Scott JA (2017) Functional traits and ecological affinities of riparian plants along the Colorado River in Grand Canyon. *West N Am Nat* 77:22–30. <https://doi.org/10.3398/064.077.0104>
- Parkhurst DF (1978) The adaptive significance of stomatal occurrence on one or both surfaces of leaves. *J Ecol* 66:367–383. <https://doi.org/10.2307/2259142>
- Parkhurst DF (1994) Diffusion of CO<sub>2</sub> and other gases inside leaves. *New Phytol* 126:449–479
- Parodi LR (1987) Gramíneas. In: Enciclopedia Argentina de Agricultura y Jardinería. Editorial ACME S.A.C.I., Buenos Aires
- Parolin P (2009) Submerged in darkness: adaptations to prolonged submergence by woody species of the Amazonian floodplains. *Ann Bot* 103:359–376. <https://doi.org/10.1093/aob/mcn216>
- Parolin P (2012) Diversity of adaptations to flooding in trees of Amazonian floodplains. *Revista Pesquisas-Botânica* 63:7–28
- Parolin P, de Simone O, Haase K, Waldhoff D, Rottenberger S, Kuhn U, Kesselmeier J, Schmidt W, Piedade MTF, Junk WJ (2004) Central Amazon floodplain forests: tree survival in a pulsing system. *Bot Rev* 70:357–380
- Pate JS, Froend RH, Bowen BJ, Hansen A, Kuo J (1990) Seedling growth and storage characteristics of seeder and resprouter species of Mediterranean-type ecosystems of SW Australia. *Ann Bot* 65:585–601
- Paula S, Pausas JG (2006) Leaf traits and resprouting ability in the Mediterranean basin. *Funct Ecol* 20:941–947
- Paula S, Pausas JG (2013) BROTE: a plant trait database for Mediterranean Basin species. Centro de Investigaciones sobre Desertificación del Consejo Superior de Investigaciones Científicas. <http://www.uv.es/jgpausas/brote.htm>. Accessed 7 Nov 2022
- Pedersen O, Colmer TD, Sand-Jensen K (2013) Underwater photosynthesis of submerged plants—recent advances and methods. *Front Plant Sci* 4:140. <https://doi.org/10.3389/fpls.2013.00140>
- Pedersen O, Sauter M, Colmer TD, Nakazono M (2021) Regulation of root adaptive anatomical and morphological traits during low soil oxygen. *New Phytol* 229:42–49. <https://doi.org/10.1111/nph.16375>
- Peng C, Zhang L, Qin H, Li D (2014) Revegetation in the water level fluctuation zone of a reservoir: an ideal measure to reduce the input of nutrients and sediment. *Ecol Eng* 71:574–577
- Perata P, Pozueta-Romero J, Akazawa T, Yamaguchi J (1992) Effect of anoxia on starch breakdown in rice and wheat seeds. *Planta* 188:611–618. <https://doi.org/10.1007/BF00197056>
- Pfanz H, Aschan G, Langenfeld-Heyser R, Wittmann C, Loose M (2002) Ecology and ecophysiology of tree stems: cortical and wood photosynthesis. *Naturwissenschaften* 89:147–162
- Pierik R, van Aken JM, Voesenek LACJ (2009) Is elongation-induced leaf emergence beneficial for submerged *Rumex* species? *Ann Bot* 103:353–357. <https://doi.org/10.1093/aob/mcn143>
- Pollock LJ, Morris WK, Vesik PA (2012) The role of functional traits in species distributions revealed through a hierarchical model. *Ecography* 35:716–725. <https://doi.org/10.1111/j.1600-0587.2011.07085.x>
- Poorter H, Niinemets Ü, Poorter L, Wright IJ, Villar R (2009) Causes and consequences of variation in leaf mass per area (LMA): a meta-analysis. *New Phytol* 182:565–588. <https://doi.org/10.1111/j.1469-8137.2009.02830.x>
- Poschenrieder C, Fernández J, Rubio L, Pérez L, Terés J, Barceló J (2018) Transport and use of bicarbonate in plants: current knowledge and challenges ahead. *Int J Mol Sci* 5:1352. <https://doi.org/10.3390/ijms19051352>
- Poschlod P, Kleyer M, Jackell AK, Dannemann A, Tackenberg O (2003) BIOPOP: a database of plant traits and internet application for nature conservation. *Folia Geobot* 38:263–271
- Price CA, Weitz JS (2014) Costs and benefits of reticulate leaf venation. *BMC Plant Biol* 14:234. <https://doi.org/10.1186/s12870-014-0234-2>
- Pujalón S, Bouma TJ, Douady C, van Groenendael J, Anten NPR, Martel E, Bornette G (2011) Plant resistance to mechanical stress: evidence of an avoidance-tolerance trade-off. *New Phytol* 191:1141–1149. <https://doi.org/10.1111/j.1469-8137.2011.03763.x>
- Pütz N (2002) Contractile roots. In: Waisel Y, Eshel A, Kafkafi U (eds) Plant roots: the hidden half, 3rd edn. CRC Press, Boca Raton. <https://doi.org/10.1201/9780203909423>
- Pütz N (2006) Seedling establishment, underground kinetics, and clonal reiteration: How do *Potentilla inclinata* and *Inula ensifolia* get their multifunctional subterranean systems? *Flora* 201:298–306. <https://doi.org/10.1016/j.flora.2005.08.006>
- Ram PC, Singh BB, Singh AK, Ram P, Singh PN, Singh HP, Boamfa EI, Harren FJM, Santosa E, Jackson MB (2002) Physiological basis of submergence tolerance in rainfed lowland rice: prospects for germplasm improvement through marker aided breeding. *Field Crops Res* 76:131–152
- Raunkiaer C (1934) The life forms of plants and statistical plant geography. Oxford University Press, Oxford



- Regos A, Gagne L, Alcaraz-Segura D, Honrado JP, Domínguez J (2019) Effects of species traits and environmental predictors on performance and transferability of ecological niche models. *Sci Rep* 9:4221. <https://doi.org/10.1038/s41598-019-40766-5>
- Reich PB, Walters MB, Ellsworth DS (1997) From tropics to tundra: global convergence in plant functioning. *Proc Natl Acad Sci USA* 94:13730–13734
- Riederer M, Müller C (2006) *Biology of the plant cuticle*. Ann Plant Rev. Blackwell, Oxford
- Reich PB, Ackerly DD, Wright I, Westoby M (2009) GLOPNET: Global Plant Trait Network. Macquarie University, Sydney. [glopnnet \(mq.edu.au\)](http://glopnnet.mq.edu.au). Accessed 10 Feb 2023
- Ravenek J, Bessler H, Engels C, Mommer L (2014) Long-term study of root biomass in a biodiversity experiment reveals shifts in diversity effects over time. *Oikos* 123:1528–1536. <https://doi.org/10.1111/oik.01502>
- Richards JH, Kuhn DN, Bishop K (2012) Interrelationships of petiolar air canal architecture, water depth, and convective air flow in *Nymphaea odorata* (Nymphaeaceae). *Am J Bot* 99:1903–1909
- Rogers GK (2021) Bald cypress knees, *Taxodium distichum* (Cupressaceae): an anatomical study, with functional implications. *Flora* 278:151788
- Ronzina DA, P'yankov VI (2001) Structure of the photosynthetic apparatus in leaves of freshwater hydrophytes: general characteristics of the leaf mesophyll and a comparison with terrestrial plants. *Russ J Plant Physiol.* <https://doi.org/10.1023/A:1016733015194>
- Rouphael Y, Mouneimne AH, Ismail A, Gyves MD, Rivera CM, Colla G (2010) Modeling individual leaf area of rose (*Rosa hybrida* L.) based on leaf length and width measurement. *Photosynthetica* 48:9–15. <https://doi.org/10.1007/s11099-010-0003-x>
- Ruiz-Obledo J, Villar R (2005) Relative growth rate and biomass allocation in ten woody species with different leaf longevity using phylogenetic independent contrasts. *Plant Biol* 7:484–494
- Sack L, Scoffoni C (2013) Leaf venation: structure, function, development, evolution, ecology and applications in the past, present and future. *New Phytol* 198:983–1000. <https://doi.org/10.1111/nph.12253>
- Sage RF, Khoshravesh R (2016) Passive CO<sub>2</sub> concentration in higher plants. *Curr Opin Plant Biol* 31:58–65. <https://doi.org/10.1016/j.pbi.2016.03.016>
- Sage RF, Khoshravesh R, Sage TL (2014) From proto-Kranz to C<sub>4</sub> Kranz: building the bridge to C<sub>4</sub> photosynthesis. *J Exp Bot* 65:3341–3356. <https://doi.org/10.1093/jxb/eru180>
- Sandquist DR, Ehleringer JR (2003) Population- and family-level variation of brittlebush (*Encelia farinosa*, Asteraceae) pubescence: Its relation to drought and implications for selection in variable environments. *Am J Bot* 90:1481–1486
- Sarnecki JM, Janssen RH, Rip WJ, Bender I, Bakker E (2014) Windows of opportunity for germination of riparian species after restoring water level fluctuations: a field experiment with controlled seed banks. *J Appl Ecol* 51:1006–1014
- Sasidharan R, Hartman S, Liu Z, Martopawiro S, Sajeev N, van Veen H, Yeung E, Voeselek LACJ (2018) Signal dynamics and interactions during flooding stress. *Plant Physiol* 176:1106–1117. <https://doi.org/10.1104/pp.17.01232>
- Schröder P (1989) Characterization of a thermo-osmotic gas transport mechanism in *Alnus glutinosa* (L.). *Trees* 3:38–44
- Schuler ML, Mantegazza O, Weber APM (2016) Engineering C<sub>4</sub> photosynthesis into C<sub>3</sub> chassis in the synthetic biology age. *Plant J* 87:51–65
- Schwilk DW, Ackerly DD (2005) Is there a cost to resprouting? Seedling growth rate and drought tolerance in sprouting and nonsprouting *Ceanothus* (Rhamnaceae). *Am J Bot* 92:404–410
- Sculthorpe CD (1967) *The biology of aquatic vascular plants*. Edward Arnold Publication Ltd, London
- SER, INSR, RBGK (2023) Seed Information Database (SID). Society for Ecological Restoration, International Network for Seed Based Restoration and Royal Botanic Gardens Kew. <https://ser-sid.org/>. Accessed 15 Feb 2023
- Serra O, Geldner N (2022) The making of suberin. *New Phytol* 235:848–866
- Shan R, Sasthav C, Wang XX, Lima LMM (2020) Complementary relationship between small-hydropower and increasing penetration of solar photovoltaics: evidence from CAISO. *Renew Energy* 155:1139–1146
- Sharma P, Dubey RS (2005) Drought induces oxidative stress and enhances the activities of antioxidant enzymes in growing rice seedlings. *Plant Growth Regul* 46:209–221
- Sharma P, Jha AB, Dubey RS, Pessarakli M (2012) Reactive oxygen species, oxidative damage, and antioxidative defense mechanism in plants under stressful conditions. *J Bot* 2012:1–26. <https://doi.org/10.1155/2012/217037>
- Shtein I, Shelef Y, Marom Z, Zelinger E, Schwartz A, Popper ZA et al (2017) Stomatal cell wall composition: distinctive structural patterns associated with different phylogenetic groups. *Ann Bot* 119:1021–1033
- Shugart HH, Woodward FI (2011) *Global change and the terrestrial biosphere: achievements and challenges*. Wiley-Blackwell, West Sussex
- Sloey TM, Ellis VS, Kettenring KM (2023) Using plant functional traits to inform wetland restoration. *Wetlands* 43:92. <https://doi.org/10.1007/s13157-023-01741-z>
- Smith SE, Read DJ (2008) *Mycorrhizal symbiosis*, 3rd edn. Academic Press, London
- Smokorowski KE (2022) The ups and downs of hydropowering: a Canadian perspective on the need for, and ecological costs of, peaking hydropower production. *Hydrobiologia* 849:421–441. <https://doi.org/10.1007/s10750-020-04480-y>
- Steffens B, Rasmussen A (2016) The physiology of adventitious roots. *Plant Physiol* 170:603–617. <https://doi.org/10.1104/pp.15.01360>
- Stella JC, Battles JJ, McBride JR, Orr BK (2010) Riparian seedling mortality from simulated water table recession, and the design of sustainable flow regimes on regulated rivers. *Res Ecol* 18:284–294
- Striker GG, Insausti P, Grimoldi AA, Vega AS (2007) Trade-off between root porosity and mechanical strength in species with different types of aerenchyma. *Plant Cell Environ* 30:580–589
- Striker GG, Insausti P, Grimoldi AA (2008) Flooding effects on plant recovery from defoliation in the grass *Paspalum dilatatum* and the legume *Lotus tenuis*. *Ann Bot* 102:247–254
- Stromberg JC, Merritt DM (2015) Riparian plant guilds of ephemeral, intermittent and perennial rivers. *Freshw Biol* 61:1259–1275. <https://doi.org/10.1111/fwb.12686>
- Suding K, Lavorel S, Chapin FS, Cornelissen JHC, Díaz S, Garnier E et al (2008) Scaling environmental change through the community-level: a trait-based response-and-effect framework for plants. *Glob Change Biol* 14:1125–1140
- Taiz L, Zeiger E, Møller IM, Murphy A (2015) *Plant physiology and development*, 6th edn. Sinauer Associates Publishers, Sunderland
- Tang L, Morris WK, Zhang M, Shi F, Vesik PA (2022) Exploring how functional traits modulate species distributions along topographic gradients in Baxian Mountain, North China. *Sci Rep* 12:994. <https://doi.org/10.1038/s41598-021-04210-x>
- Tarvainen L, Wallin G, Lim H, Linder S, Oren R, Ottosson L, Mikael RM, Torngern P, Marshall J (2017) Photosynthetic refixation varies along the stem and reduces CO<sub>2</sub> efflux in mature boreal *Pinus sylvestris* trees. *Tree Physiol* 38:558–569. <https://doi.org/10.1093/treephys/tpx130>
- Tonolla D, Bruder A, Schweizer S (2017) Evaluation of mitigation measures to reduce hydropowering impacts on river ecosystems—a case study from the Swiss Alps. *Sci Total Environ* 574:594–604. <https://doi.org/10.1016/j.scitotenv.2016.09.101>
- Tozer WC, Rice B, Westoby M (2015) Evolutionary divergence of leaf width and its correlates. *Am J Bot* 102:367–378. <https://doi.org/10.3732/ajb.1400379>
- Tripathi P, Abdullah JS, Kim J, Chung Y-S, Kim S-H, Hamayun M, Kim Y (2001) Investigation of root morphological traits using 2D-imaging among diverse soybeans (*Glycine max* L.). *Plants* 10:2535. <https://doi.org/10.3390/plants10112535>
- Turkan I (2018) ROS and RNS: key signalling molecules in plants. *J Exp Bot* 69:3313–3315. <https://doi.org/10.1093/jxb/ery198>
- Tutin TG, Heywood VH, Burges NA, Valentine DH, Walters SM, Webb DA (2001) *Flora Europaea*. Cambridge University Press, Cambridge
- Tyler T, Herbertsson L, Olofsson J, Olsson PA (2021) Ecological indicator and traits values for Swedish vascular plants. *Ecol Indic* 120:106923. <https://doi.org/10.1016/j.ecolind.2020.106923>
- Tyree MT, Sperry JS (1989) Vulnerability of xylem to cavitation and embolism. *Annu Rev Plant Phys* 40:19–38
- Tyree MT, Cochard H, Cruziat P, Sinclair B, Ameglio T (1993) Drought induced leaf shedding in walnut: evidence for vulnerability segmentation. *Plant Cell Environ* 16:879–882
- Urban O, Kosvancova M, Marek MV, Lichtenthaler HK (2007) Induction of photosynthesis and importance of limitations during the induction phase in sun and shade leaves of five ecologically contrasting tree species from the temperate zone. *Tree Physiol* 27:1207–1215. <https://doi.org/10.1093/treephys/27.8.1207>

- [USDA] United States Department of Agriculture (2010) The PLANTS Database. USDA National Resources Conservation Service. USDA Plants Database. Accessed 10 Dec 2022
- Valladares F, Gianoli E, Gómez JM (2007) Ecological limits to plant phenotypic plasticity. *New Phytol* 176:749–763. <https://doi.org/10.1111/j.14698137.2007.02275.x>
- Van der Maarel E, Franklin J (2012) *Vegetation Ecology*, 2nd edn. Wiley-Blackwell, West Sussex
- Vandegehuchte MW, Bloemen J, Vergenst LL, Steppe K (2015) Woody tissue photosynthesis in trees: salve on the wounds of drought? *New Phytol* 208:998–1002
- Vartapetian BB, Jackson M (1997) Plant adaptations to anaerobic stress. *Ann Bot* 79:3–20
- Venn SE, Green K, Pickering CM, Morgan JW (2011) Using plant functional traits to explain community composition across a strong environmental filter in Australian alpine snowpatches. *Plant Ecol* 212:1491–1499. <https://doi.org/10.1007/s11258-011-9923-1>
- Verberk WCEP, van Noordwijk CGE, Hildrew AG (2013) Delivering on a promise: integrating species traits to transform descriptive community ecology into a predictive science. *Freshw Sci* 32:531–547. <https://doi.org/10.1899/12-092.1op>
- Violle C, Navas M-L, Vile D, Kazakou E, Fortunel C, Hummel I, Garnier E (2007) Let the concept of trait be functional! *Oikos* 116:882–892
- Visser EJW, Colmer TD, Blom CWPM, Voeselek LACJ (2000) 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* 23:1237–1245. <https://doi.org/10.1046/j.1365-3040.2000.00628.x>
- Voeselek LACJ, Bailey-Serres J (2015) Flood adaptive traits and processes: an overview. *New Phytol* 206:57–73. <https://doi.org/10.1111/nph.13209>
- Voeselek LACJ, Sasidharan R (2013) Ethylene—and oxygen signalling—drive plant survival during flooding. *Plant Biol* 15:426–435
- Voeselek LA, Benschop JJ, Bou J, Cox MC, Groeneveld HW, Millenaar FF, Vreeburg RA, Peeters AJ (2003) Interactions between plant hormones regulate submergence-induced shoot elongation in the flooding-tolerant dicot *Rumex palustris*. *Ann Bot* 91:205–211. <https://doi.org/10.1093/aob/mcf116>
- Voeselek LACJ, Colmer TD, Pierik R, Millenaar FF, Peeters AJM (2006) How plants cope with complete submergence. *New Phytol* 170:213–226. <https://doi.org/10.1111/j.1469-8137.2006.01692.x>
- Vogel S (1988) *Life's devices*. Princeton University Press, Princeton
- Vogel S (1994) *Life in moving fluids*. Princeton University Press, Princeton
- Wada M, Kagawa T, Sato Y (2003) Chloroplast movement. *Annu Rev Plant Biol* 54:455–468
- Wang X-Q (1998) Differential responses of abaxial and adaxial guard cells of broad bean to abscisic acid and calcium. *Plant Physiol* 118:1421–1429. <https://doi.org/10.1104/pp.118.4.1421>
- Wang S, Ren L, Liu Y, Han Z, Yang Y (2010) Mechanical characteristics of typical plant leaves. *J Bionic Eng* 7:294–300. [https://doi.org/10.1016/s1672-6529\(10\)60253-3](https://doi.org/10.1016/s1672-6529(10)60253-3)
- Webb LJ (1959) A physiognomic classification of australian rain forests. *J Ecol* 47:551–570. <https://doi.org/10.2307/2257290>, [JSTOR2257290](https://www.jstor.org/stable/2257290)
- Weemstra M, Mommer L, Visser EJW, van Ruijven J, Kuyper TW, Mohren GMJ, Sterck FJ (2016) Towards a multidimensional root trait framework: a tree root review. *New Phytol* 211:1159–1169. <https://doi.org/10.1111/nph.14003>
- Westoby M, Falster DS, Moles AT, Vesk PA, Wright IJ (2002) Plant ecological strategies: some leading dimensions of variation between species. *Annu Rev Ecol Syst* 33:125–159. <https://doi.org/10.1146/annurev.ecolsys.33.010802.150452>
- Whitten T, Soeriaatmadja RE, Afiff SA (1996) *The ecology of Java and Bali: the ecology of Indonesia series, vol 2*. Periplus Editions, Singapore
- Winkel A, Colmer TD, Pedersen O (2011) Leaf gas films of *Spartina anglica* enhance rhizome and root oxygen during tidal submergence. *Plant Cell Environ* 34:2083–2092
- Wittmann C, Pfanz H (2018) More than just CO<sub>2</sub>-recycling: cortical photosynthesis as a mechanism to reduce the risk of an energy crisis induced by low oxygen. *New Phytol* 219:551–564. <https://doi.org/10.1111/nph.15198>
- Wolfe BT, Sperry JS, Kursar TA (2016) Does leaf shedding protect stems from cavitation during seasonal droughts? A test of the hydraulic fuse hypothesis. *New Phytol* 212:1007–1018. <https://doi.org/10.1111/nph.14087>
- Wright IJ, Reich PB, Westoby M, Ackerly DD, Baruch Z, Bongers F et al (2004) The worldwide leaf economics spectrum. *Nature* 428:821–827
- Yang Y-J, Bi M-H, Nie Z-F, Jiang H, Liu X-D, Fang X-W, Brodribb TJ (2021) Evolution of stomatal closure to optimize water-use efficiency in response to dehydration in ferns and seed plants. *New Phytol* 230:2001–2010
- Yeung E, van Veen H, Vashisht D, Sobral Paiva AL, Hummel M, Rankenberr T, Steffens B, Steffen-Heins A, Sauter M, de Vries M, Schuurink RC, Bazin J, Bailey-Serres J, Voeselek LACJ, Sasidharan R (2018) A stress recovery signaling network for enhanced flooding tolerance in *Arabidopsis thaliana*. *Proc Natl Acad Sci U S A* 115:E6085–E6094. <https://doi.org/10.1073/pnas.1803841115>
- Yin Q, Wang L, Lei M, Dang H, Quan J, Tian T et al (2018) The relationships between leaf economics and hydraulic traits of woody plants depend on water availability. *Sci Total Environ* 621:245–252. <https://doi.org/10.1016/j.scitotenv.2017.11.171>
- Young WC (1989) *Roark's formulas for stress and strain*. McGraw Hill, New York
- Yul Yoo C, Pence HE, Hasegawa PM, Mickelbart MV (2009) Regulation of transpiration to improve crop water use. *Crit Rev Plant Sci* 6:410–431
- Zakharova L, Meyer KM, Seifan M (2019) Trait-based modelling in ecology: a review of two decades of research. *Ecol Model* 407:108703. <https://doi.org/10.1016/j.ecolmodel.2019.05.008>
- Zhang X, Nepf H (2020) Flow-induced reconfiguration of aquatic plants, including the impact of leaf sheltering. *Limnol Ocean* 65:2697–2712. <https://doi.org/10.1002/lno.11542>
- Zhao Y, Zhang W, Abou-Elwafa SF, Shabala S, Xu L (2021) Understanding a mechanistic basis of ABA involvement in plant adaptation to soil flooding: the current standing. *Plants* 10:1982. <https://doi.org/10.3390/plant10101982>
- Zurzycki J (1955) Chloroplast arrangement as a factor in photosynthesis. *Acta Soc Bot Pol* 24:27–63

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