



Woody plant adaptations to multiple abiotic stressors: Where are we?☆

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ARTICLE INFO

Edited by: Hermann Heilmeyer

Keywords:

Abiotic stress
Ecophysiology
Functional traits
Polytolerance
Stress tolerance
Trade-off

ABSTRACT

Interacting abiotic stresses exert a fundamental selective pressure on the adaptive syndromes of long-living organisms such as woody plants. However, general patterns and mechanisms describing woody plant adaptations to tolerate multiple abiotic stressors are yet to emerge. This hampers our ability to build predictive frameworks foreseeing species responses to stochastic changes in abiotic stress regimes due to climate change. With this Virtual Special Issue (VSI), we aimed to summarize what we know, and what we do not know, about woody plant adaptations to achieve tolerance to multiple abiotic limitations. To this end, we brought together studies exploring ecological or ecophysiological perspectives on woody plant adaptations to tolerate multiple abiotic stresses. Ecological studies suggest patterns associating trait trade-offs, climate, and biotic interactions with woody plants' multi-stress tolerance. Ecophysiological studies point to traits and conceptual frameworks that might explain some processes underpinning woody plant multi-stress tolerance. Here, we first revised the definitions of stress and stress tolerance used in ecological and ecophysiological research, providing a nomenclature of tolerance that could be used to unify definitions across research fields. Then, we summarized the main theories and evidence on woody plant adaptations to tolerate multiple abiotic stresses. Finally, we introduced the ecological and ecophysiological perspectives on this matter and placed the contributions to this VSI within the current state of the art. Altogether, this VSI allowed us to identify the lack of large-scale integration of patterns and processes describing woody plant adaptations to multiple abiotic stresses as a major gap in this field.

1. Introduction

Abiotic stressors are ubiquitous factors and exert fundamental constraints on species' distribution, form, and function. Such constraints are particularly relevant for sessile organisms, such as plants, especially woody ones. These are long-lived, perennial organisms continuously adjusting their resource acquisition, use, and conservation strategies to environmental and resource alterations (Smith and Huston, 1989; Niinemets and Valladares, 2006; Puglielli et al., 2021a). As a result, their adaptations to abiotic stress regimes in their natural habitat are reflective of different long-term environmental limitations, making woody plants important models for studying plant adaptation to multiple abiotic stressors (Niinemets, 2010a).

Habitats can be usually defined as having one overarching abiotic

limitation that mainly constraints plant performance (i.e., the law of the minimum). However, despite absolute polytolerance to two stressors is generally low for woody plants (Niinemets and Valladares, 2006), more recent evidence (Laanisto and Niinemets, 2015; Puglielli et al., 2021b) has shown that the degree of polytolerance to two stressors is influenced by the interaction with other stressors, meaning that polytolerance strategies cannot be defined in terms of absolute, but relative polytolerance (Puglielli et al., 2021b). Multiple abiotic (and biotic) limitations always act in concert in a single habitat, and, as a result, plant performance is co-limited by the interaction of multiple environmental limitations (Niinemets and Valladares, 2008). For instance, in several ecosystems (e.g., Mediterranean / savanna shrublands, bogs, and seasonally dry tropical forests), multiple abiotic stressors characterized by different severity and timing during a growing season differently

☆ This article is part of a special issue entitled: "Woody plants multi-stress" published at the journal *Flora*.

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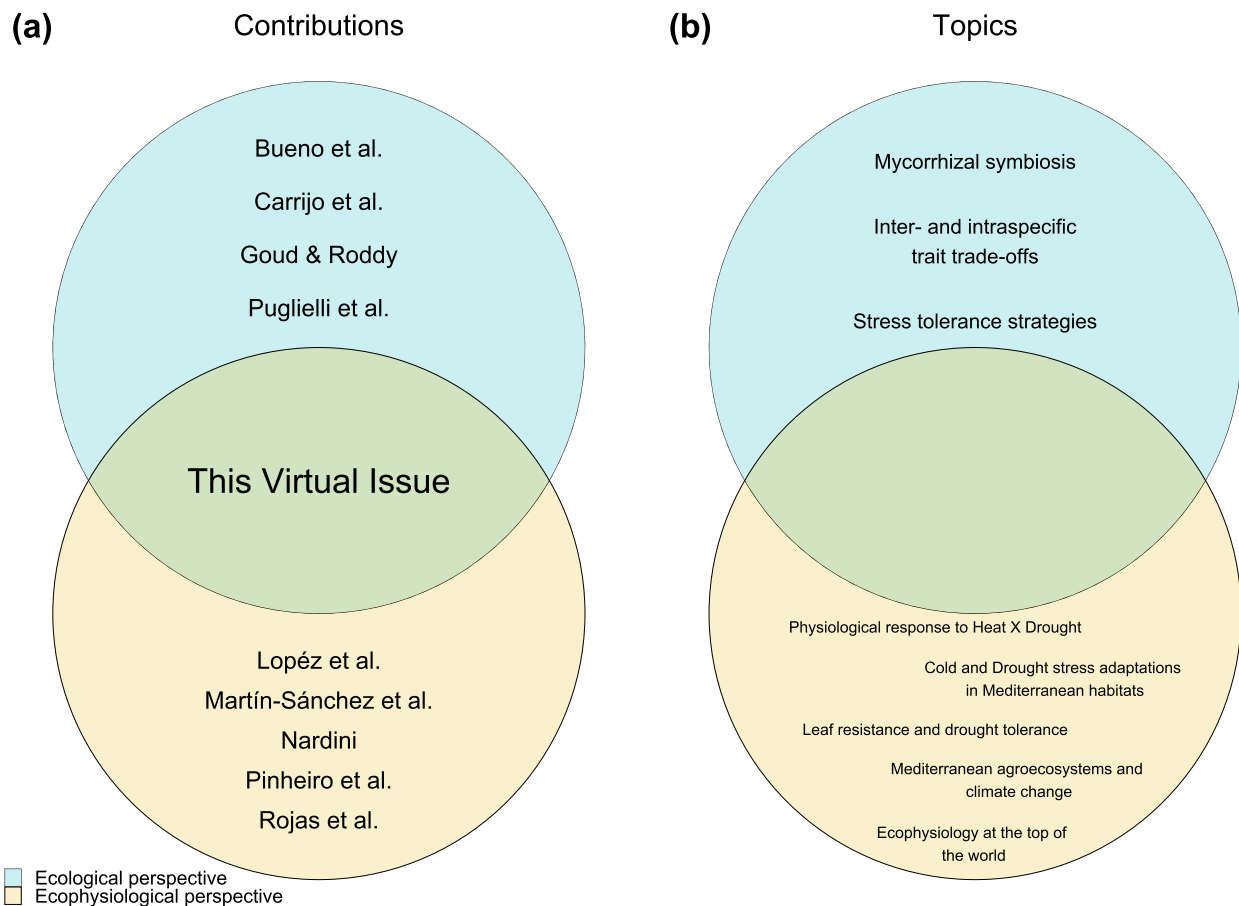


Fig. 1. Venn diagram mapping the contributions and the topics included in this Virtual Special Issue according to their ecological or ecophysiological perspective on woody plant adaptations to tolerate multiple stressors.

alter species ability to grow and reproduce (Niinemets, 2010a). Even drought spans a combination of multiple abiotic limitations besides water deficit stress (Volaire, 2018). These interacting and/or alternating abiotic limitations, which often have non-additive effects on plant performance, have shaped the adaptive evolution of woody plants (Larcher, 1987; Niinemets, 2010a), eventually defining their adaptive and acclimation potentials. Identifying the general patterns of woody plant adaptations to multiple abiotic stressors and disentangling the underlying processes (*sensu* Volaire et al., 2020) is necessary to pave the path towards generalization and predictions. This herculean task is particularly needed in the context of global climate change where long-term plant adaptations to the major abiotic stress, as well as their acclimation limits, have been, and will likely continue to be, challenged by novel and often unpredictable abiotic stress combinations.

In this Virtual Special Issue (VSI), we aimed at bringing together multi-taxon evidence on woody plants' adaptations to complex environmental matrices, where multiple abiotic stressors occur. We also brought together opinions and review articles to suggest how future research alleys on this topic should be built from the current knowledge. Importantly, the contributions that constitute this VSI span ecological and ecophysiological perspectives on woody plants' adaptations to achieve multi-stress tolerance (Fig. 1), increasing the possibility of directly comparing how different and yet interconnected fields of research try to address similar questions.

In this mini-review, we first revise the classical definitions of plant stress and stress tolerance to summarize how 'stress' and 'stress tolerance' are differently perceived by ecologists and ecophysiologicalists. In doing that, we highlight 'time' as an important addition to the definition of stress to better define the differences in which ecologists and ecophysiologicalists define stress (see Volaire et al., 2020 for an extensive

review on this topic). When revising the concept of stress tolerance, we focus on the distinction between 'physiological tolerance' and 'ecological tolerance' (*sensu* Niinemets and Valladares, 2008), as we argue this to be one of the major obstacles in generalizing the concept of tolerance across different research fields. Second, we briefly review evidence supporting the existence of a single stress tolerance syndrome in woody plants. Finally, in the last two sections, we present the contributions of our VSI in the context of the more general research trends and approaches that have so far characterized the ecological and ecophysiological research on woody plant adaptations to tolerate multiple abiotic stressors. This mini-review introduces our VSI and does not provide a detailed review of the literature on woody plant adaptations to multiple abiotic stressors. For this we refer to the extensive review by Niinemets (2010a), and to the context introduced by the contributions in our VSI.

1.1. Some definitions of 'plant stress' and 'stress tolerance'

Levitt (1972) defined stress as a reduction in individual plant performance as environmental conditions become unfavorable on a (relatively) short timescale (see also Larcher, 1987 and Lichtenthaler, 1996 for similar definitions). This definition is easily interpreted from an acclimation perspective, as it suggests a dynamic response of plant performance in relation to varying abiotic factors. For this reason, this definition was promptly adopted by plant (eco)physiologists, who often build dose-response curves or temporal trends of how physiological / morphological traits dynamically adjust when the level of the abiotic limitation changes during a short time scale (Volaire, 2018; Volaire et al., 2020). In this context, tolerance can be interpreted as the breadth of a dose-response curve, or of a temporal trend, set by the upper and lower levels of a given abiotic factor either corresponding to a minimum

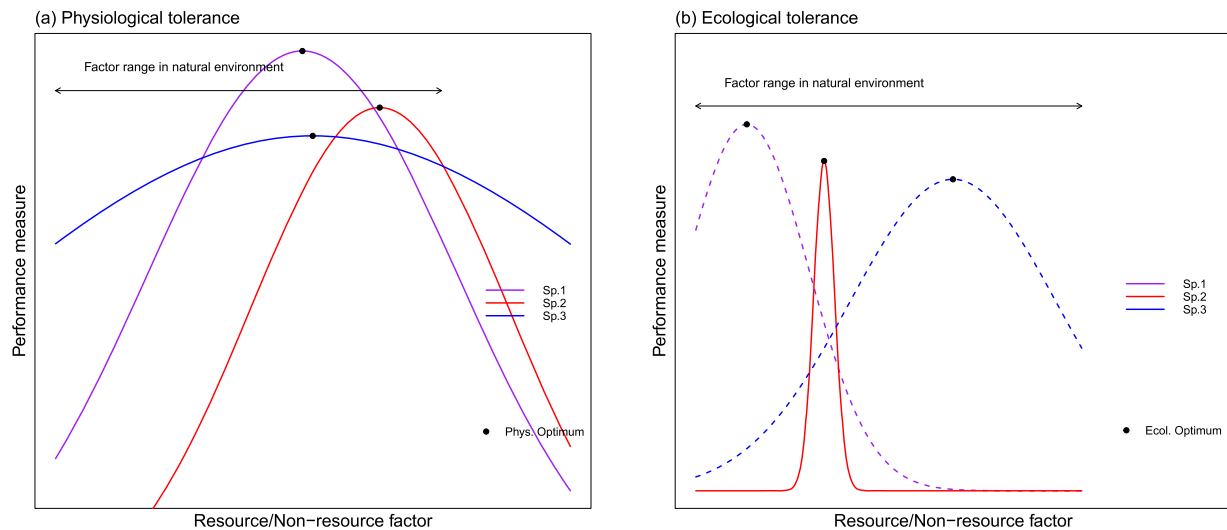


Fig. 2. Conceptual difference between (a) physiological tolerance, and (b) ecological tolerance. Performance curves for three virtual species (Sp.1–Sp.3) along a resource/non-resource gradient of an abiotic factor are shown. The black dots in each panel correspond to the physiological or ecological tolerance optimum for each species (i.e., where the performance function is maximized). The theoretical range of resource/non-resource factor in the natural environment is also shown to highlight the conceptual difference between physiological and ecological tolerance. Dashed lines represent truncated tolerance functions for species in the field (see main text). Curves were drawn following Niinemets and Valladares (2008) with permission.

or disrupted plant performance. This is what is usually referred to as ‘physiological tolerance’, and the maximum of this function is then called the ‘physiological optimum’ (Niinemets and Valladares, 2008; Fig. 2a). Comparing ‘physiological tolerance’ curves between species allows interpreting the adaptive value of plant acclimation limits to given abiotic factors (Lichtenthaler, 1996; Poorter et al., 2010; Garnier et al., 2015).

Grime (1977) defined stress as the constraint imposed by the chronic (i.e., long-term) lack of resources over biomass production in a habitat. The term ‘chronic’ brings a clearer adaptive perspective to this definition compared to Levitt’s one. That is plants adapted to chronically resource-limited habitats have an inherent slow biomass accumulation compared to plants adapted to resource-rich habitats, even if it were to grow them under the same environmental conditions. Grime’s definition of stress, usually referred to as ‘resource stress’, is the most common definition of stress used in plant ecological research. Later, Chapin (1991) nuanced Grime’s definition of stress to accommodate the ‘non-resource stress’, referring to the stress imposed by environmental factors that are not resources for a plant (e.g., temperature). Despite the distinction between resource and non-resource stress is still in use in the field of functional ecology (see Craine et al., 2012 for a review), the two stress types constantly interact in natural environments because non-resource stress directly alters a plant’s demand for resources (Craine et al., 2012). Therefore, multiple stressors interact to shape a species’ realized tolerance strategy to both resource and non-resource stress (Puglielli et al., 2021b).

Given these considerations, the concept of tolerance in ecological research (hereafter ecological tolerance, *sensu* Niinemets and Valladares, 2008) refers to a curve that has both a breadth and an ‘ecological optimum’ that might differ from the physiological one (Niinemets and Valladares, 2008; Fig. 2b). This is because in their natural environment, species do not only chronically face a narrower range of a resource compared to the ones supplied when building physiological response curves (Niinemets and Valladares, 2008), but they also compete interspecifically for that resource (Fig. 2b). Additionally, interacting non-resource stresses further alter a species ability to use a given resource, contributing to shape a species’ ecological tolerance. In other words, multiple long-term selective pressures at a given habitat have shaped a species’ ecological tolerance.

To clarify the difference between ‘physiological’ and ‘ecological’

tolerance definitions, we can try to re-express them by using the dichotomy ‘fundamental’ vs. ‘realized’ niche (*sensu* Hutchinson, 1957). The fundamental niche is loosely defined as the potential set of environmental conditions where a species can grow, survive, and reproduce, while the realized niche is where a species thrives in the presence of other species and dispersal barriers. In other words, the realized niche is the shrunk/skewed/truncated version of the fundamental niche. Similarly, we can define ‘physiological tolerance’ as the potential plants’ performance to a given abiotic factor, and it can be interpreted as a measure of ‘fundamental tolerance’. On the other hand, the ‘ecological tolerance’ for a given abiotic factor reflects how the fundamental tolerance is shrunk / skewed / truncated in the real world – i.e., where other species, abiotic and biotic factors have shaped, during evolution, the tolerance breadth and the ecological optimum of a given species (Niinemets and Valladares, 2008). Therefore, we define ecological tolerance as a measure of ‘realized tolerance’. As such, the physiological and the ecological optima will represent a measure of potential and realized niche position for a given abiotic stress factor, when optima are compared across species.

Overall, it is evident that physiological and ecological tolerance of a given species are subject to different biological interpretations. As a result, there is no general agreement on the definition of tolerance, and ecologists and ecophysiologicals inherently rely on different definitions. To this purpose we have provocatively used the differentiation ‘fundamental’ vs. ‘realized’ stress tolerance, highlighting the similarities with the ‘fundamental’ vs. ‘realized’ niche concepts, as these concepts are, on the contrary, rarely confused. Similar conceptual differences can also be found in other research fields, such as biogeography, where differences between ‘potential’ vs. ‘realized’ range size are often defined following Hutchinson’s concept of ‘fundamental’ vs. ‘realized’ niche (e.g., Nogués-Bravo et al., 2014). Here we call for a switch towards the ‘fundamental’ vs. ‘realized’ tolerance definition to set immediately the conceptual similarities between definitions while stressing their different biological interpretation. By building on the universal niche nomenclature, our proposal to redefine tolerance has the potential to unify the concept of tolerance across research fields.

Finally, we want to point the attention to an important limitation of the above-described approaches: they rarely account for the effect of ontogeny, which is necessary to compare tolerances across species (Niinemets, 2010a). However, Niinemets and Valladares (2006) argued

Table 1

The main adaptations of stress-tolerant plants defining the stress tolerance syndromes proposed by Grime (1977) and by Chapin et al. (1993).

Adaptation	Grime (1977)	Chapin et al. (1993)
Enhanced nutrient retention	Yes	
Evergreen habit	Yes	–
Growth rate	Slow	Slow
Photosynthesis	Low	Low
Organ longevity	Long	Long
Secondary metabolites concentration	High	High
Stomatal conductance	–	Low
Tissue N	–	Low
Tissue turnover	Slow	Slow
Transpiration	–	Low
Water conservation	High	High

(and partly tested) that despite ecological and physiological tolerance values changing with ontogeny (e.g., Niinemets, 2006; Sendall and Reich, 2013; Sendall et al., 2015), relative differences among species are going to remain largely constant in a comparative context. As of today, we still miss large cross-species data on ontogenetic changes in species tolerances, hindering our ability to test for the ontogenetic effect explicitly and conclusively (Puglielli et al., 2021a). Thus, the ‘ontogenetic assumption’ remains reasonable because it is the only one possible at this stage.

1.2. A single syndrome to tolerate them all?

The definition of a single, general stress tolerance syndrome that is valid for all plants is a long-standing goal of ecological and ecophysiological research on plants’ abiotic stress tolerance (e.g. Grime, 1977; Chapin et al., 1993; Table 1). The predictions reported in Table 1 are quite clear and point to the idea that a single stress tolerance syndrome must be inherently linked to traits favoring slow growth, slow acquisition of resources, and slow organ turnover. Despite some criticism of this idea (Grubb, 1998), as of today, we know that traits linked to a conservative acquisition and use of resources are found in unproductive, harsh habitats (Wright et al., 2004, 2005; Moles, 2018; Yang et al., 2019), and this is usually referred to as the ‘slow’ strategy of stress tolerators. The identification of trait trade-offs reflecting plant strategies in relation to habitat characteristics is a major advancement provided by the advent of trait-based ecology (sensu Westoby and Wright, 2006).

1.2.1. The importance of plant phenology

Despite the idea of a general stress tolerance syndrome represents a successful framework in a broad comparative context, some considerations need to be made. At the leaf level, for instance, the ‘slow’ strategy of stress tolerators might be more reflective of evergreen broad- and needle-leaved species’ strategies. This is because of the long leaf-life span of evergreen leaves, which allows sorting of clear large-scale interspecific differences in leaf trait–environment relationships. In other words, a longer leaf-life span means probably more year-to-year exposure to adverse environmental conditions, marking more evident leaf morpho-functional local adaptations along broad gradients in evergreens (Wright et al., 2005).

On the other hand, deciduousness represents an equally successful alternative strategy for temporally avoiding, and therefore surviving, highly stressful periods (Zanne et al., 2014, 2018). For instance, deciduous species become particularly successful in highly seasonal environments – e.g., seasonally dry tropical forests (e.g., Poorter and Markesteijn, 2008), or where the growing season becomes particularly short. Deciduousness can decouple the leaf trait–environment relationships for the species belonging to this functional type, as the leaves are formed under favorable environmental conditions, potentially missing leaf-level adaptations to the stress imprint in their natural habitat. Therefore, it is of uttermost relevance considering how the leaf types (or

more generally functional types), as well as their related phenological events (Volaire et al., 2020), integrate in the trait syndromes that woody plants have evolved under regimes of multiple abiotic stressors. For instance, plant functional type is considered the main determinant of biomass allocation in relation to shade or drought tolerance in woody plants globally (Puglielli et al., 2021a). Contrasting strategies between functional types, or time-dependent processes, can blur the emergence of patterns trying to link traits and tolerances across species. Numerous previous studies have in fact already pointed out the constraints imposed by differences among plant functional types in generalizing trait–tolerance and trait–environment relationships (e.g., Lusk et al., 2008; Hallik et al., 2009; Markesteijn and Poorter, 2009; Stahl et al., 2013; Tomlinson et al., 2013a, 2013b; Rueda et al., 2018; Puglielli et al., 2021a).

Other studies have stressed the need to account for time-dependent processes to disentangle patterns of plant adaptations to abiotic stress (Volaire, 2018; Volaire et al., 2020). This aspect is highly relevant for choosing the right trait framework depending on the timescale of the analysis, and this is indeed the most striking difference between the ecological and the ecophysiological approach. According to Volaire (2018), the ecological approach uses functional traits or ecological tolerances to describe species ecological strategies, but these might fail to reveal plant adaptations to short-term fluctuations in resource and non-resource stressors. In line with this, a recent meta-analysis by Wang and Wang (2023) showed that the acclimation responses of woody plants to the interacting effect of shade and drought are more evident in terms of process traits compared to functional traits (sensu Volaire et al., 2020). On the other hand, functional traits better characterized the adaptive value of the differences in the acclimation responses of shade or drought tolerant vs. intolerant species in response to the same shade × drought treatment. Thus, ecophysiological adaptive strategies of woody plants, that is the group of mechanisms that operate at the temporal scale of multiple abiotic stress fluctuations (e.g., during a growing season; Volaire, 2018), represent an additional adaptive dimension requiring urgent integration in the research agenda on woody plant adaptations to tolerate multiple stressors.

1.2.2. The search for a shade tolerance adaptive syndrome

The identification of a general shade tolerance syndrome for woody plants is another important obstacle in identifying a single stress tolerance syndrome, as being shade-tolerant does not necessarily imply embracing the previously described ‘slow’ strategy. On the contrary, the evidence is quite heterogeneous when coming to plants’ adaptations to low light environments (see Valladares and Niinemets, 2008; Niinemets, 2010b; Valladares et al., 2016; Poorter et al., 2019 for extensive reviews on this topic). One interesting aspect is that plants’ responses to low light seem to display opposite patterns when comparing acclimation and adaptive responses (e.g., Lusk et al. 2008 for leaf mass per area; Puglielli et al. 2021a for biomass allocation to leaves, stems, and roots), and this aspect deserves further research.

While for plant morpho-physiological acclimation responses to low-light (and their adaptive value) we recommend reading Poorter et al. (2019), here we report the two main competing hypotheses on the achievement of shade tolerance from a purely adaptive perspective: (i) the ‘carbon-gain hypothesis’, and (ii) the ‘stress tolerance hypothesis’. The carbon gain hypothesis (Givnish, 1988) predicts that shade-tolerant species enhance net energy capture in low light, mainly by allocating carbon to leaf production to maximize leaf area compared to intolerant species. The second hypothesis assumes high stress tolerance in shade and lower carbon losses (Kitajima, 1994), and predicts that shade-tolerant species construct more robust leaves with greater dry mass per unit leaf area compared to intolerant species. Currently, there is no consensus on the general (trait) syndrome (Poorter et al., 2019), or on biomass allocation patterns (Puglielli et al., 2021a), associated with high shade tolerance in woody plants. However, the available evidence (e.g., Lusk et al., 2008; Hallik et al., 2009; Puglielli et al., 2021a)

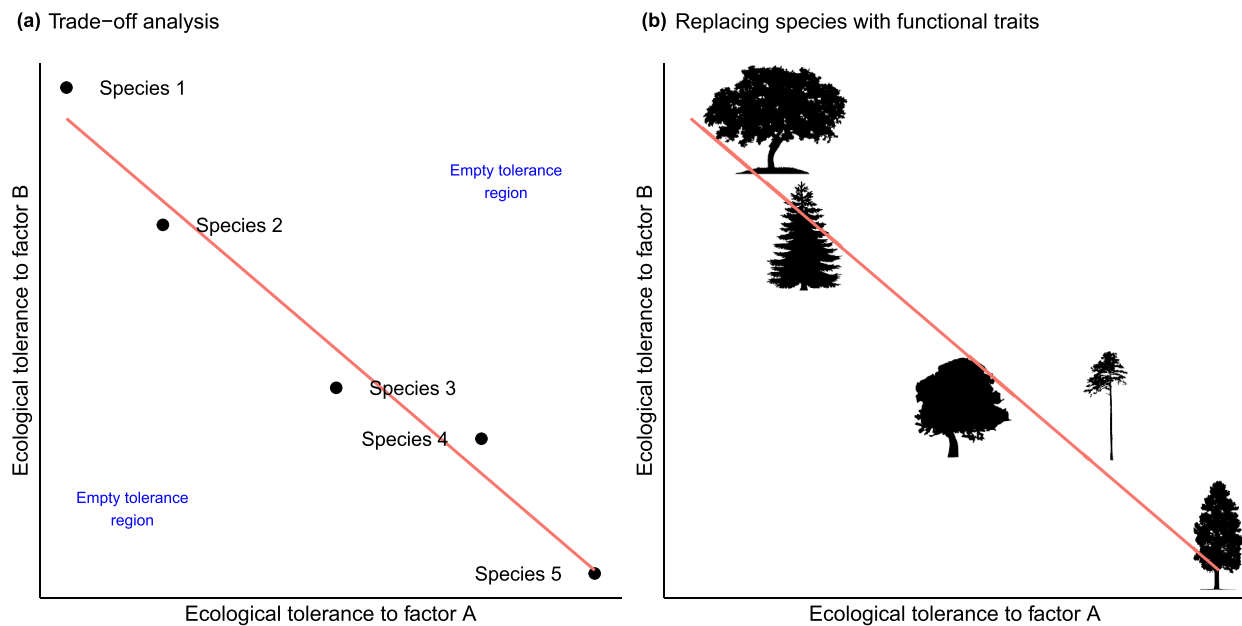


Fig. 3. Main approaches used in the ecological research on plant abiotic stress tolerance. **(a)** Identifying the tolerance patterns through trade-off analyses involving ecological tolerances. This approach identifies not viable tolerance combinations – i.e., empty tolerance regions. **(b)** Replacing species with their traits (usually done through a trait-based approach) to identify the trait combinations underlying the pattern.

suggests that to finally disentangle the trait syndrome(s) of shade-tolerant vs. -intolerant woody plants in the field, we need to consider the interaction between the biome/ecosystem (e.g., tropical vs. temperate) where a species occurs and the plant functional type it belongs. This further stresses the previous considerations on the importance of accounting for plant functional type's effect when studying plant adaptations to abiotic stresses. Another important body of evidence suggests that the traits linked to shade tolerance can display pronounced changes with ontogeny (Delagrange et al., 2004; Niinemets, 2006; Lusk et al., 2011; Sendall and Reich, 2013; Sendall et al., 2015; Puglielli et al., 2021a), which is likely to interact with the above-mentioned determinants (Puglielli et al., 2021a). In this context, however, the same previous considerations on the lack of large-scale ontogenetic data on stress tolerance apply as well.

1.2.3. The need for multiple trait dimensions

The search for general adaptive syndromes evolved by woody plants to tolerate multiple co-occurring or subsequent abiotic stressors is of uttermost importance to foresee species responses to current and future climatic changes (Niinemets, 2010a). Some patterns such as the Leaf Economics Spectrum (Wright et al., 2004) are largely accepted, and, for instance, the Leaf Economics Spectrum was already shown to be linked, weakly though, to species ecological tolerance to shade and drought (Hallik et al., 2009). However, new patterns have emerged – i.e., the Global Spectrum of Plant Form and Function (Díaz et al., 2016). Others, instead, have been only envisioned, such as the Whole-Plant Economic Spectrum (Reich, 2014), predicting that a 'fast-slow' traits trade-off can explain all the trait combinations for above- and belowground plant organs, including the hydraulic trait dimension. These new patterns have never been analyzed alongside species tolerance towards multiple abiotic stresses.

Nevertheless, there is evidence that the hydraulic dimension (e.g., Li et al., 2015) and the fine-root two-dimensional space (Carmona et al., 2021) are independent of the Leaf Economics Spectrum and of the Global Spectrum of Plant Form and Function, respectively, requiring an integration of the idea of a 'Whole-Plant Economic Spectrum' (Reich, 2014). Independent trait dimensions can, in fact, result in much more trait combinations than those expected based on trait trade-offs

(Laughlin, 2014), possibly resulting in unpredictable trait syndrome–tolerance relationships. Overall, we call for more analyses linking measures of abiotic stress tolerance to multiple pattern and process trait dimensions (*sensu* Voltaire et al., 2020) carefully selected from independent trait planes / axes in order to more efficiently identify general tolerance syndromes (see Laughlin, 2014 for a discussion on the importance of trait independence for identifying plant strategies). This endeavor is strongly needed to finally tackle the inherent multidimensional nature of multi-stress tolerance in woody plants.

2. Ecological perspective on woody plant multi-stress tolerance

The ecological perspective on stress in woody plants has typically been focusing on two broad directions: trade-offs, especially between different abiotic stress factors; and functional trait correlations with and within different stress levels (Fig. 3). The first direction is best described as a top-down theoretical approach, presuming strict trade-offs between woody plant's capability of tolerating different stress factors (e.g. Smith and Huston, 1989) due to physicochemical constraints restricting adaptations and acclimatizations (Laanisto and Niinemets, 2015; Puglielli et al., 2021b). The second direction has emerged more from local scale case studies trying to assess how much different stress factors affect various functional traits. This approach rapidly developed over time into global assessments of economic spectra describing the functional spaces of above- and below-ground plant organs to assess the full functionality of plants (Wright et al., 2004; Diaz et al., 2016; Carmona et al., 2021; Weigelt et al., 2021).

Trade-offs have traditionally been defined through negative relationships between two traits (or features or parameters, etc.) of living organisms. The constraint of having just two traits against each other limits the potential insightfulness of such analyses due to the multifaceted nature of stress and its tolerance and effect patterns (Puglielli et al., 2021b). In this context, another significant aspect is the nature of the trade-off relationship (Grubb, 2016). While the earlier conceptual trade-off models of abiotic stress tolerance expected a strict "boundary line" type (*sensu* Grubb, 2016) of trade-offs, the analysis with empirical data have shown high variability of polytolerance patterns of abiotic stress tolerance (e.g. Niinemets and Valladares, 2006; Laanisto and

Niinemets, 2015), with the trade-off type clearly being “trend line” (*sensu* Grubb, 2016).

The dispersion around both sides of the trade-off line clearly indicates a larger, if not dominant, role of adaptation and acclimatization in shaping the trade-offs (which are still present, just not as omnipresent as traditionally thought) in woody species abiotic stress tolerance patterns. Trend line trade-off suggests that adapting to further tolerance might still be possible, but that would depend on the attainability of favorable combinations of functional traits; while boundary line trade-off indicates the absolute tolerance limit. Thus, further studies on this topic discovering that tolerating multiple stress factors at the same time, or polytolerance, in woody species sometimes tends to cross some trend lines and have to pay more attention to the nature of the trade-off line. Such crossings can only happen in a trend line trade-off space, not in a boundary line one (Puglielli et al., 2021b).

This VSI includes two perspective studies that describe two broad directions to approach this new perspective. The first one is treating the advancement of knowledge from within the abiotic stress tolerance space (Puglielli et al., 2022 this issue). These authors point out the need for a more comprehensive and holistic approach in stress tolerance trade-off studies, and they say that studying species tolerance or adaptations to multiple stressors is highly complicated because of the inherent multidimensionality of plants' strategies in coping with multiple stresses. This is why they propose a potential roadmap towards the development of a “periodic table” for abiotic stress tolerance of woody plants. The roadmap is based on a theoretical framework of Winemiller et al. (2015), where five key ecological dimensions are selected (habitat, strategy, trophic, defense, and metabolic dimensions) that ought to provide sufficient wholesome insight for describing an organism's position in a virtual “periodic table” of stress tolerance. Using this approach dramatically reduces the number of biological dimensions to tackle the multidimensional nature of woody plant adaptations to tolerate abiotic stresses (*sensu* Puglielli et al., 2021b), where the limits of abiotic stress tolerance strategies of woody plants were defined on a global scale.

The second perspective brings into play the biotic interactions for explaining tolerance towards multiple stresses (Bueno et al., 2022 this issue). Their review provides a short evolutionary timescale on when and how mycorrhiza developed on woody species and then provides more detailed accounts of how this symbiotic relationship helps mitigate different abiotic stress factors (drought, cold, heat, nutrient deficiency, and shade). They present key mechanisms for how mycorrhiza can help tolerate a specific abiotic stress factor, but also the crucial trade-offs related to mitigation processes (e.g., from limitations related to fungal life strategies and growth forms to concurring nutrient dynamics and biogeographical constraints related to stress mitigation).

Bueno et al. (2022 this issue) also provide a useful theoretical framework on how the symbiosis between mycorrhiza and woody species could function in multiple abiotic stress situations. They point out that such experimental and observational research is scarce, which is why they lay out the first steps to take toward understanding the complexity of plant responses to multiple stress factors and their mediation strategies by mycorrhizal fungi. According to their conclusions, the first step would be to identify how severely different combinations of abiotic stress can limit the set of mitigation resources available to mycorrhiza. Thus, this complex and underexplored topic would require a geographically and environmentally diverse approach.

Tolerating abiotic stress is one of the countless research areas that have been dominated by functional ecology in recent decades. On a larger spatial scale, the effect of abiotic stress on plant functional traits is relatively well known on the main climatic gradients and is linked to plant strategies (Wright et al., 2004; Reich, 2014; Díaz et al., 2016; Carmona et al., 2021), while local scale variations both within and between species are largely unknown (Goud and Roddy, 2022 this issue). Local-scale variations in intra- and interspecific trait variability of the most frequently used functional traits on both leaf and plant level in

contrasting environmental conditions are presented in two papers in this VSI.

Carrijo et al. (2021 this issue) studied functional traits in Brazilian savanna within the framework of the global spectrum of plant form and function (Díaz et al., 2016) – one habitat was characterized by old lowland alluvial soils with low fertility and low water-holding capacity, and the other one by upland areas in the interfluvial zone with fertile and water-holding soils. They sampled six functional traits (leaf area, leaf thickness, specific leaf area, stem-specific density, relative bark thickness, and maximum plant height) of 101 species. They found, expectedly, that stress tolerance strategies of species depend on the water deficit and fire regime of the habitat. An interesting aspect of their result was that the same response patterns were found for both between communities and within species analysis – indicating that if local conditions are specific enough, they can act as dominating selective agents at multiple levels of biological organization simultaneously. This knowledge provides us another potential angle for synthesizing together the two traditionally contrary approaches (trade-offs vs. trait correlations) used in understanding the stress tolerance of plants.

At the same time, another study in our VSI (Goud and Roddy, 2022 this issue) showed that the trait–trait and trait–environmental patterns can also depend on the considered level of biological organization. This research was carried out in a Pine barrens (rare temperate forest ecoregion in coastal areas of northeastern North America) gradient from lowland bog to upland forest, where the authors studied leaf functional traits (SLA, LDMC and leaf thickness) on three dominant shrub species. Their results suggest that the between- and within-species trait variations along environmental gradients form a complex set between adaptations, acclimatization and micro-environmental variations. This knowledge brings forth a somewhat forgotten concept in functional ecology according to which plants, and especially woody plants, are structurally modular organisms (Watson, 1986; de Kroon et al., 2009; Herrera, 2017), and that different parts of the same plant, which can range in size from leaves to whole branches or root systems, can respond differently to variation in abiotic and biotic conditions. There are so far very few studies that have analyzed how environmental factors specifically affect the intraspecific variability of different plant parts of the same organism (see Herrera, 2017, for review). Thus, the approach by Goud and Roddy (2022 this issue) is an important step toward disentangling the reactions and mechanisms at work along complex environmental gradients.

3. Ecophysiological perspective on woody plant multi-stress tolerance

A plant's ability to survive stressful environments strongly relates to a number of tolerance mechanisms, ranging from molecular to physiological and ecological level. Understanding plant stress responses and associated tolerance mechanisms is crucial to both basic biology as well as to improve predictions of plant impacts of climate change, thus enabling greater societal awareness and mitigation planning.

In this VSI, we host five ecophysiological-oriented review articles that survey a series of studies covering the main responses of woody plants to a multitude of abiotic stressors. Briefly, these reviews focus on:

- (i) The main stressors of two relevant woody species in their native environments – i.e. *Quercus ilex* L. (an evergreen oak that dominates the landscape of several Mediterranean forests) and *Polylepis tarapacana* Phil. (a tree characteristic of the Altiplano, one of the highest elevation forest stands on Earth) (Martín-Sánchez et al., 2022 this issue; Rojas et al., 2022 this issue).
- (ii) The morpho-anatomical and physiological adjustments against combined abiotic stressors (López et al., 2022 this issue; Nardini, 2022 this issue).

Woody plant adaptations to multiple abiotic stressors: where are we?

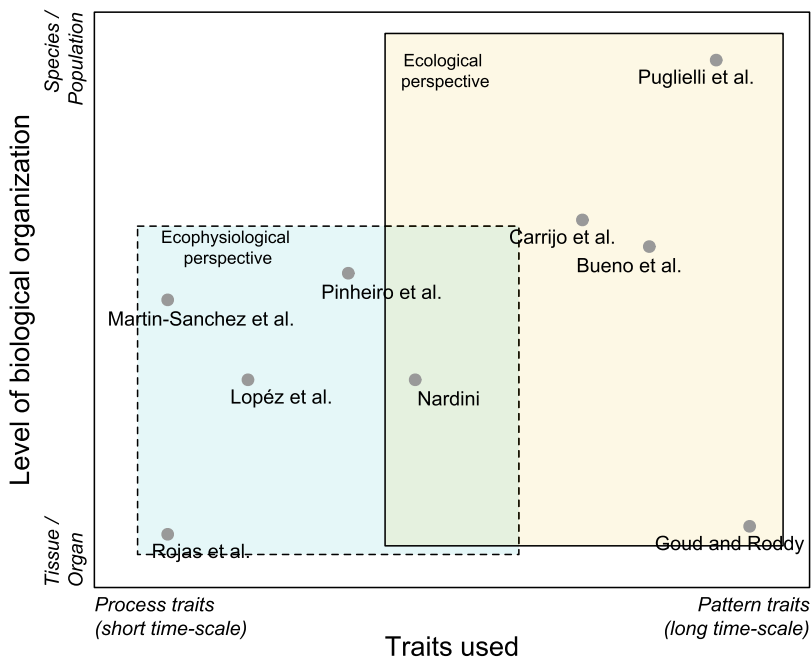


Fig. 5. Mapping the contributions included in this Virtual Special Issue within the conceptual framework provided by Volaire (2018) aimed to summarize the conceptual differences between ecological or ecophysiological perspective on plant adaptations to tolerate multiple stressors. The available ecological and ecophysiological evidence on the topic, reviewed here and summarized by the contributions to our Virtual Issue, spans shaded areas, with some overlaps between ecological and ecophysiological perspectives. Empty areas of the space identify major research gaps.

these stressors arises because some anatomical modifications observed in hard leaves (i.e., leaves with high LMA) – including thick cell walls, high major vein density, and narrow xylem conduits – are mechanistically correlated to physiological traits conferring tolerance to dehydration – such as low turgor loss point and high xylem resistance to embolism (Nardini, 2022 this issue). In fact, increases in drought tolerance (lower turgor loss point and higher xylem resistance to embolism), paralleled by increases in LMA (indicating higher leaf mechanical resistance), have been observed for sunflower plants exposed to drought conditions during growth (Cardoso et al., 2018). Further studies assessing variations in both drought tolerance and leaf mechanical resistance within woody species (e.g., da Silva Brito et al., 2022) and genotypes are thus necessary for a better understanding of whether trees can exhibit the same adaptive patterns as observed in herbaceous plants.

Uncertainties about the vulnerability of woody species in different ecosystems to multiple abiotic stressors are still large. Therefore, assessing how plants of different ecosystems respond to extreme abiotic stress factors is much needed, as acclimation and adaptation mechanisms can be then exploited to sustain agroecosystems and conserve biodiversity in the context of climatic change (Pinheiro et al., 2022 this issue).

4. Conclusion

With our VSI, we wanted to focus on the main advancements in the ecological and ecophysiological research on plant adaptations to tolerate multiple abiotic stresses to finally understand *where are we?* To better highlight how the contributions of this VSI locate in the broader context of current knowledge on abiotic stress tolerance, we mapped them within the conceptual framework proposed by Volaire (2018) (Fig. 5). It becomes evident that there remains a huge gap of knowledge on how patterns and process traits can be integrated to disentangle species/population level plant adaptations to multiple abiotic stresses (empty area in Fig. 5). Reaching such an integration requires combining extensive databases of process traits, first principles models, remote sensing/eddy covariance techniques, pattern traits and biotic interactions to finally bridge the scope of ecological and ecophysiological

research on woody plant multi-stress tolerance. However, this matter is evidently complicated by the inherent difficulty of combining traits that reflect patterns and processes at different levels of biological organization and operating at different temporal and spatial scales. Unifying these approaches into a single framework is, therefore, the next challenge for (eco)physiological research.

We sincerely hope that the present VSI will provide part of the map to identify new routes toward new questions and tools to build a so much needed general predictive framework for woody plant adaptations to tolerate multiple stressors. We also hope that relatively few dimensions can be used to describe tolerance strategies toward all stressors because, quoting Field (1991): ‘if species respond uniquely to every stress, and if every stress must be evaluated from a different perspective, the scaling problem is greatly complicated, perhaps beyond all hope of practical solution’.

Declaration of Competing Interest

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.

Data availability

No data was used for the research described in the article.

Acknowledgment

The authors thank two anonymous reviewers and Hermann Heilmeyer for insightful comments. GP was supported by the grant IJC2020-043331-I funded by MCIN/AEI /10.13039/501100011033, the grant PID2021-122214NA-I00 funded by MCIN/AEI/ 10.13039/501100011033 and by FEDER “ESF Investing in your future”. LL is supported by the Estonian Academy of Sciences - Research professor for Arctic studies. AAC was supported by the USDA National Institute of Food and Agriculture, Hatch Project 7003279.

References

- Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Cobb, N., 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *For. Ecol. Manag.* 259, 660–684.
- Bueno, C.G., Meng, Y., Neukenkamp, L., 2022. How can mycorrhizal symbiosis mediate multiple abiotic stresses in woody plants? *Flora* 295, 152146. <https://doi.org/10.1016/j.flora.2022.152146>.
- Cardoso, A.A., Brodribb, T.J., Kane, C.N., DaMatta, F.M., McAdam, S.A., 2020. Osmotic adjustment and hormonal regulation of stomatal responses to vapour pressure deficit in sunflower. *AoB Plants* 12.
- Cardoso, A.A., Brodribb, T.J., Lucani, C.J., DaMatta, F.M., McAdam, S.A., 2018. Coordinated plasticity maintains hydraulic safety in sunflower leaves. *Plant Cell Environ.* 41, 2567–2576.
- Carmona, C.P., Bueno, C.G., Toussaint, A., Träger, S., Díaz, S., Moora, M., Tamme, R., 2021. Fine-root traits in the global spectrum of plant form and function. *Nature* 597, 683–687. <https://doi.org/10.1038/s41586-021-03871-y>.
- Chapin, F.S., 1991. Integrated responses of plants to stress: a centralized system of physiological responses. *Bioscience* 41, 29–36. <https://doi.org/10.2307/1311538>.
- Chapin, F.S., Autumn, K., Pugnaire, F., 1993. Evolution of suites of traits in response to environmental stress. *Am. Nat.* 142, S78–S92.
- Choat, B., Brodribb, T.J., Brodersen, C.R., Duursma, R.A., López, R., Medlyn, B.E., 2018. Triggers of tree mortality under drought. *Nature* 558, 531–539.
- Craine, J., Engelbrecht, B., Lusk, C., McDowell, N., Poorter, H., 2012. Resource limitation, tolerance, and the future of ecological plant classification. *Front. Plant Sci.* 3, 246.
- Creek, D., Lamarque, L.J., Torres-Ruiz, J.M., Parise, C., Burlett, R., Tissue, D.T., Delzon, S., 2020. Xylem embolism in leaves does not occur with open stomata: evidence from direct observations using the optical visualization technique. *J. Exp. Bot.* 71, 1151–1159.
- da Silva Brito, N.D., dos Santos Medeiros, M.J., de Souza, E.S., de Lima, A.L.A., 2022. Drought response strategies for deciduous species in the semiarid Caatinga derived from the interdependence of anatomical, phenological and bio-hydraulic attributes. *Flora* 288, 152009.
- De Kroon, H., Visser, E.J., Huber, H., Mommer, L., Hutchings, M.J., 2009. A modular concept of plant foraging behaviour: the interplay between local responses and systemic control. *Plant Cell Environ.* 32, 704–712.
- Delagrèze, S., Messier, C., Lechowicz, M.J., Dizengremel, P., 2004. Physiological, morphological and allocational plasticity in understory deciduous trees: importance of plant size and light availability. *Tree Physiol.* 24, 775–784. <https://doi.org/10.1093/treephys/24.7.775>.
- Díaz, S., Kattge, J., Cornelissen, J.H.C., Wright, I.J., Lavorel, S., Dray, S., Gorné, L.D., 2016. The global spectrum of plant form and function. *Nature* 529, 167–171. <https://doi.org/10.1038/nature16489>.
- Duursma, R.A., Blackman, C.J., López, R., Martin-StPaul, N.K., Cochard, H., Medlyn, B.E., 2019. On the minimum leaf conductance: its role in models of plant water use, and ecological and environmental controls. *New Phytol.* 221, 693–705.
- Field, C.B., 1991. Ecological scaling of carbon gain to stress and resource availability. In: Mooney, H.A., Winner, W.E., Pell, E.J. (Eds.), *Response of Plants to Multiple Stresses*. Academic Press, Inc, San Diego, pp. 35–65.
- Garnier, E., Navas, M.L., Grigulis, K., 2015. *Plant Functional Diversity: Organism Traits, Community Structure, and Ecosystem Properties*. Oxford University Press, Oxford. <https://doi.org/10.1093/acprof:oso/9780198757368.001.0001>.
- Givnish, T.J., 1988. Adaptation to sun and shade: a whole-plant perspective. *Funct. Plant Biol.* 15, 63–92. <https://doi.org/10.1071/pp9880063>.
- Goud, E.M., Roddy, M.J., 2022. Variation in leaf traits among and within dominant shrubs of contrasting Pine Barrens habitats. *Flora* 293, 152109.
- Grime, J.P., 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *Am. Nat.* 111, 1169–1194.
- Grossiord, C., Buckley, T.N., Cernusak, L.A., Novick, K.A., Poulter, B., Siegwolf, R.T., McDowell, N.G., 2020. Plant responses to rising vapor pressure deficit. *New Phytol.* 226, 1550–1566.
- Grubb, P.J., 1998. A reassessment of the strategies of plants which cope with shortages of resources. *Perspect. Plant Ecol. Evol. Syst.* 1, 3–31. <https://doi.org/10.1078/1433-8319-00049>.
- Grubb, P.J., 2016. Trade-offs in interspecific comparisons in plant ecology and how plants overcome proposed constraints. *Plant Ecol. Divers* 9, 3–33.
- Gupta, A., Rico-Medina, A., Caño-Delgado, A.I., 2020. The physiology of plant responses to drought. *Science* 368, 266–269.
- Hallik, L., Niinemets, Ü., Wright, I.J., 2009. Are species shade and drought tolerance reflected in leaf-level structural and functional differentiation in Northern Hemisphere temperate woody flora? *New Phytol.* 184, 257–274. <https://doi.org/10.1111/j.1469-8137.2009.02918.x>.
- Herrera, C.M., 2017. The ecology of subindividual variability in plants: patterns, processes, and prospects. *Web Ecol.* 17, 51–64.
- Hutchinson, G.E., 1957. Concluding remarks. In: *Proceedings of the Cold Spring Harbor Symposium on Quantitative Biology*, 22, pp. 415–427. <https://doi.org/10.1101/SQB.1957.022.01.039>.
- Kitajima, K., 1994. Relative importance of photosynthetic traits and allocation patterns as correlates of seedling shade tolerance of 13 tropical trees. *Oecologia* 98, 419–428.
- Laanisto, L., Niinemets, Ü., 2015. Polytolerance to abiotic stresses: how universal is the shade–drought tolerance trade-off in woody species? *Glob. Ecol. Biogeogr.* 24, 571–580.
- Larcher, W., 1987. *Streu bei pflanzen*. *Naturwissenschaften* 74, 158–167.
- Laughlin, D.C., 2014. The intrinsic dimensionality of plant traits and its relevance to community assembly. *J. Ecol.* 102, 186–193. <https://doi.org/10.1111/1365-2745.12187>.
- Levitt, J., 1972. *Responses of Plants to Environmental Stresses*, Physiological Ecology. Academic Press, New York.
- Li, L., McCormack, M.L., Ma, C., Kong, D., Zhang, Q., Chen, X., Zeng, H., Niinemets, Ü., Guo, D., 2015. Leaf economics and hydraulic traits are decoupled in five species-rich tropical-subtropical forests. *Ecol. Lett.* 18, 899–906. <https://doi.org/10.1111/ele.12466>.
- Lichtenthaler, H.K., 1996. Vegetation stress: an introduction to the stress concept in plants. *J. Plant Physiol.* 148, 4–14.
- López, R., Ramírez-Valiente, J.A., Pita, P., 2022. How plants cope with heatwaves in a drier environment. *Flora* 295, 152148. <https://doi.org/10.1016/j.flora.2022.152148>.
- Lusk, C.H., Pérez-Millaqueo, M.M., Piper, F.I., Saldaña, A., 2011. Ontogeny, understorey light interception and simulated carbon gain of juvenile rainforest evergreens differing in shade tolerance. *Ann. Bot.* 108, 419–428. <https://doi.org/10.1093/aob/mcr166>.
- Lusk, C.H., Reich, P.B., Montgomery, R.A., Ackerly, D.D., Cavender-Bares, J., 2008. Why are evergreen leaves so contrary about shade? *Trends Ecol. Evol.* 23, 299–303. <https://doi.org/10.1016/j.tree.2008.02.006>.
- Marksteijn, L., Poorter, L., 2009. Seedling root morphology and biomass allocation of 62 tropical tree species in relation to drought- and shade-tolerance. *J. Ecol.* 97, 311–325. <https://doi.org/10.1111/j.1365-2745.2008.01466.x>.
- Martin-Sánchez, R., Peguero-Pina, J.J., Alonso-Forn, D.A., Ferrio, J.P., Sancho-Knapik, D., Gil-Pelegrín, E., 2022. Summer and winter can equally stress holm oak (*Quercus ilex* L.) in Mediterranean areas: a physiological view. *Flora* 290, 152058.
- McAdam, S.A., Cardoso, A.A., 2019. The recurrent evolution of extremely resistant xylem. *Ann. For. Sci.* 76, 1–4.
- McDowell, N.G., Michaletz, S.T., Bennett, K.E., Solander, K.C., Xu, C., Maxwell, R.M., Middleton, R.S., 2018. Predicting chronic climate-driven disturbances and their mitigation. *Trends Ecol. Evol.* 33, 15–27.
- McDowell, N.G., Sapes, G., Pivovarov, A., Adams, H.D., Allen, C.D., Anderegg, W.R., Xu, C., 2022. Mechanisms of woody-plant mortality under rising drought, CO₂ and vapour pressure deficit. *Nat. Rev. Earth Environ.* 3, 294–308.
- McDowell, N.G., Pockman, W.T., Allen, C.D., Breshears, D.D., Cobb, N., Kolb, T., Yezzer, E. A., 2008. Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? *New Phytol.* 178, 719–739.
- Moles, A.T., 2018. Being John Harper: using evolutionary ideas to improve understanding of global patterns in plant traits. *J. Ecol.* 106, 1–18. <https://doi.org/10.1111/1365-2745.12887>.
- Nardini, A., 2022. Hard and tough: the coordination between leaf mechanical resistance and drought tolerance. *Flora* 288, 152023.
- Niinemets, Ü., 2006. The controversy over traits conferring shade-tolerance in trees: ontogenetic changes revisited. *J. Ecol.* 94, 464–470. <https://doi.org/10.1111/j.1365-2745.2006.01093.x>.
- Niinemets, Ü., 2010a. Responses of forest trees to single and multiple environmental stresses from seedlings to mature plants: past stress history, stress interactions, tolerance and acclimation. *For. Ecol. Manag.* 260, 1623–1639. <https://doi.org/10.1016/j.foreco.2010.07.054>.
- Niinemets, Ü., 2010b. A review of light interception in plant stands from leaf to canopy in different plant functional types and in species with varying shade tolerance. *Ecol. Res.* 25, 693–714. <https://doi.org/10.1007/s11284-010-0712-4>.
- Niinemets, Ü., Valladares, F., 2006. Tolerance to shade, drought, and waterlogging of temperate Northern hemisphere trees and shrubs. *Ecol. Monogr.* 76, 521–547.
- Niinemets, Ü., Valladares, F., 2008. Environmental tolerance. In: Jørgensen, S.E., Fath, B. D. (Eds.), *Encyclopedia of Ecology*. Academic Press, Oxford, pp. 1370–1376.
- Nogués-Bravo, D., Pulido, F., Araújo, M.B., Diniz-Filho, J.A.F., García-Valdés, R., Kollmann, J., Svenning, J.C., Valladares, F., Zavala, M.A., 2014. Phenotypic correlates of potential range size and range filling in European trees. *Perspect. Plant Ecol.* 16, 219–227. <https://doi.org/10.1016/j.ppees.2014.05.005>.
- Pinheiro, C., David, T.S., Baptista, P., Guerra-Guimarães, L., 2022. Mediterranean woody agroecosystems in a warming and drier climate: the importance of sustainable knowledge-based management. *Flora* 291, 152070.
- Poorter, H., Niinemets, Ü., Ntagkas, N., Siebenkäs, A., Mäenpää, M., Matsubara, S., Pons, T.L., 2019. A meta-analysis of plant responses to light intensity for 70 traits ranging from molecules to whole plant performance. *New Phytol.* 223, 1073–1105. <https://doi.org/10.1111/nph.15754>.
- Poorter, H., Niinemets, Ü., Walter, A., Fiorani, F., Schurr, U., 2010. A method to construct dose–response curves for a wide range of environmental factors and plant traits by means of a meta-analysis of phenotypic data. *J. Exp. Bot.* 61, 2043–2055. <https://doi.org/10.1093/jxb/erp358>.
- Poorter, L., Marksteijn, L., 2008. Seedling traits determine drought tolerance of tropical tree species. *Biotropica* 40, 321–331. <https://doi.org/10.1111/j.1744-7429.2007.00380.x>.
- Puglielli, G., Laanisto, L., Poorter, H., Niinemets, Ü., 2021a. Global patterns of biomass allocation in woody species with different tolerances of shade and drought: evidence for multiple strategies. *New Phytol.* 229, 308–322. <https://doi.org/10.1111/nph.16879>.
- Puglielli, G., Hutchings, M.J., Laanisto, L., 2021b. The triangular space of abiotic stress tolerance in woody species: a unified trade-off model. *New Phytol.* 229, 1354–1362.
- Puglielli, G., Pavanetto, N., Laanisto, L., 2022. Towards a “periodic table” of abiotic stress tolerance strategies of woody plants. *Flora* 292, 152089.
- Reich, P.B., 2014. The world-wide ‘fast–slow’ plant economics spectrum: a traits manifesto. *J. Ecol.* 102, 275–301. <https://doi.org/10.1111/1365-2745.12211>.

- Rojas, R., Flexas, J., Coopman, R.E., 2022. The highest elevation treeline in the world: *polylepis tarapacana* Phil. as a unique opportunity to study ecophysiological adaptations to extreme conditions. *Flora* 292, 152076.
- Rueda, M., Godoy, O., Hawkins, B.A., 2018. Trait syndromes among North American trees are evolutionarily conserved and show adaptive value over broad geographic scales. *Ecography* 41, 540–550. <https://doi.org/10.1111/ecog.03008>.
- Ruehr, N.K., Grote, R., Mayr, S., Arneth, A., 2019. Beyond the extreme: recovery of carbon and water relations in woody plants following heat and drought stress. *Tree Physiol.* 39, 1285–1299.
- Sendall, K.M., Reich, P.B., 2013. Variation in leaf and twig CO₂ flux as a function of plant size: a comparison of seedlings, saplings and trees. *Tree Physiol.* 33, 713–729. <https://doi.org/10.1093/treephys/tpt048>.
- Sendall, K.M., Lusk, C.H., Reich, P.B., 2015. Becoming less tolerant with age: sugar maple, shade, and ontogeny. *Oecologia* 179, 1011–1021. <https://doi.org/10.1007/s00442-015-3428-x>.
- Shirley, H.L., 1936. Lethal high temperatures for conifers, and the cooling effect of transpiration. *J. Agric. Res.* 53, 239–258.
- Smith, T., Huston, M., 1989. A theory of the spatial and temporal dynamics of plant communities. *Vegetatio* 83, 49–69.
- Stahl, U., Kattge, J., Reu, B., Voigt, W., Ogle, K., Dickie, J., Wirth, C., 2013. Whole-plant trait spectra of North American woody plant species reflect fundamental ecological strategies. *Ecosphere* 4, art128. <https://doi.org/10.1890/ES13-00143.1>.
- Tomlinson, K.W., Poorter, L., Sterck, F.J., Borghetti, F., Ward, D., de Bie, S., van Langevelde, F., 2013a. Leaf adaptations of evergreen and deciduous trees of semi-arid and humid savannas on three continents. *J. Ecol.* 101, 430–440. <https://doi.org/10.1111/1365-2745.12056>.
- Tomlinson, K.W., van Langevelde, F., Ward, D., Bongers, F., da Silva, D.A., Prins, H.H.T., de Bie, S., Sterck, F.J., 2013b. Deciduous and evergreen trees differ in juvenile biomass allometries because of differences in allocation to root storage. *Ann. Bot.* 112, 575–587. <https://doi.org/10.1093/aob/mct132>.
- Trenberth, K.E., Dai, A., Van Der Schrier, G., Jones, P.D., Barichivich, J., Briffa, K.R., Sheffield, J., 2014. Global warming and changes in drought. *Nat. Clim. Chang.* 4, 17–22.
- Tyree, M.T., Sperry, J.S., 1989. Vulnerability of xylem to cavitation and embolism. *Annu. Rev. Plant Physiol. Plant Mol. Biol.* 40, 19–38.
- Valladares, F., Niinemets, Ü., 2008. Shade tolerance, a key plant feature of complex nature and consequences. *Annu. Rev. Ecol. Syst.* 39, 237–257. <https://doi.org/10.1146/annurev.ecolsys.39.110707.173506>.
- Valladares, F., Laanisto, L., Niinemets, Ü., Zavala, M.A., 2016. Shedding light on shade: ecological perspectives of understorey plant life. *Plant Ecol. Divers.* 9, 237–251. <https://doi.org/10.1080/17550874.2016.1210262>.
- Volaire, F., 2018. A unified framework of plant adaptive strategies to drought: crossing scales and disciplines. *Glob. Chang. Biol.* 24, 2929–2938.
- Volaire, F., Gleason, S.M., Delzon, S., 2020. What do you mean “functional” in ecology? Patterns versus processes. *Ecol. Evol.* 10, 11875–11885.
- Wang, Z., Wang, C., 2023. Individual and interactive responses of woody plants' biomass and leaf traits to drought and shade. *Glob. Ecol. Biogeogr.* 32, 35–48.
- Watson, M.A., 1986. Integrated physiological units in plants. *Trends Ecol. Evol.* 1, 119–123.
- Weigelt, A., Mommer, L., Andraczek, K., Iversen, C.M., Bergmann, J., Bruehlheide, H., McCormack, M.L., 2021. An integrated framework of plant form and function: the belowground perspective. *New Phytol.* 232, 42–59.
- Westoby, M., Wright, I.J., 2006. Land-plant ecology on the basis of functional traits. *Trends Ecol. Evol.* 21, 261–268. <https://doi.org/10.1016/j.tree.2006.02.004>.
- Winemiller, K.O., Fitzgerald, D.B., Bower, L.M., Pianka, E.R., 2015. Functional traits, convergent evolution, and periodic tables of niches. *Ecol. Lett.* 18, 737–751.
- Wright, I.J., Reich, P.B., Cornelissen, J.H.C., Falster, D.S., Groom, P.K., Hikosaka, K., Westoby, M., 2005. Modulation of leaf economic traits and trait relationships by climate. *Global Ecol. Biogeogr.* 14, 411–421.
- Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F., Villar, R., 2004. The worldwide leaf economics spectrum. *Nature* 428, 821–827. <https://doi.org/10.1038/nature02403>.
- Yang, Y., Wang, H., Harrison, S.P., Prentice, I.C., Wright, I.J., Peng, C., Lin, G., 2019. Quantifying leaf-trait covariation and its controls across climates and biomes. *New Phytol.* 221, 155–168. <https://doi.org/10.1111/nph.15422>.
- Zanne, A.E., Pearse, W.D., Cornwell, W.K., McGlenn, D.J., Wright, I.J., Uyeda, J.C., 2018. Functional biogeography of angiosperms: life at the extremes. *New Phytol.* 218, 1697–1709. <https://doi.org/10.1111/nph.15114>.
- Zanne, A.E., Tank, D.C., Cornwell, W.K., Eastman, J.M., Smith, S.A., FitzJohn, R.G., Beaulieu, J.M., 2014. Three keys to the radiation of angiosperms into freezing environments. *Nature* 506, 89–92. <https://doi.org/10.1038/nature12872>.
- Carrijo, J.N., Maracahipes, L., Scalon, M.C., Silvério, D.V., Arthur, V.F., Verissimo, A., Fagundes, M.V., Abadia, A.C., Lenza, E., 2021. Functional traits as indicators of ecological strategies of savanna woody species under contrasting substrate conditions. *Flora* 284, 151925.