Hard and tough: the coordination between leaf mechanical resistance and drought tolerance

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Keywords:
Leaf mass per area
Leaf density
Cell wall
Major veins
Turgor loss point
Leaf hydraulic conductance
Drought

ABSTRACT

Leaves of terrestrial plants vary tremendously in size, shape, and stiffness. Hard leaves with high mass per unit area (LMA) occur more frequently in water- and nutrient-limited habitats, where stress-tolerance is key to survival. Coordination between leaf mechanical properties and drought tolerance can arise because some (but not all) of the anatomical modifications leading to high LMA are mechanistically correlated to physiological traits conferring tolerance to dehydration. Thick cell walls are frequently coupled with low turgor loss point values, and also prevent cell shrinkage and collapse after turgor loss has occurred. This also protects the leaf against shrinking-induced loss of water transport capacity in the extra-vascular pathway. In turn, vascular water transport in the leaf veins is at risk of embolism-induced disruption under drought, but higher length of major veins per unit area can provide alternative pathways for water delivery to the mesophyll, while contributing to increased leaf stiffness. Water shortage in dry and warm habitats implies the risk of reduced photosynthetic rates, apparently favouring species that produce hard and drought-tolerant leaves, to warrant long leaf life span and to maintain gas exchange and positive carbon gain when conditions become harsh.

Leaf size and toughness are amongst the most heterogeneous features of terrestrial plants, and both traits show several consistent biogeographical patterns in their global variation. As an example, leaf area shows clear latitudinal and altitudinal trends on a global scale (Wright et al., 2017), with smaller leaves typically found in drier sites of warmer regions, especially when characterized by high temperature and irradiance. Similarly, high leaf toughness expressed as leaf mass per unit area (LMA), is a common functional trait in dry and warm habitats (de la Riva et al., 2016; Dong et al., 2020) and more generally in nutrient-limited ecosystems (Poorter et al., 2009; Read et al., 2016; Wright et al., 2002). In turn, high LMA is correlated to leaf structural resistance (Onoda et al., 2011). This association between leaf traits favouring mechanical stiffness and challenging environmental conditions limiting gas exchange and photosynthetic rates, possibly reflects the adaptive advantage of increased leaf life span under such conditions, to assure adequate compensation and pay-back of carbon costs incurred by the plant in leaf construction (Chabot and Hicks, 1982; Onoda et al., 2017; Alonso-Forn et al., 2020).

Hard leaves can be defined as leaves with high toughness, strength and stiffness (Edwards et al., 2000), and typically display high LMA values. 'Hard' leaves confer clear adaptive advantages in terms of resistance to herbivores and physical agents potentially leading to mechanical damage, like wind and precipitation (Choong et al., 1992; Turner, 1994; Caldwell et al., 2016). A recurrent question in the scientific literature is whether leaves with high LMA are also more tolerant toward other abiotic stress factors, with special reference to drought stress (Oertli et al., 1990; Salleo and Nardini, 2000). A survey of classical and recent literature on this topic reveals that answers to this question are somehow contrasting, with studies reporting no correlation between LMA and metrics of drought tolerance (e.g. Medina et al., 1990; Salleo et al., 1997; Blackman et al., 2010), and others supporting the hypothesis that hard leaves are also more resistant to water shortage (e.g. Nardini et al., 2012; Savi et al., 2017; Méndez-Alonzo et al., 2019). These discrepancies between studies likely reflect different phylogenetic trajectories in the different species' assemblages considered, but also the fact that variations in LMA can arise from different anatomical traits influencing leaf thickness and/or density. Each of these traits can have (or not) different mechanistic correlations with physiological traits underlying leaf drought tolerance. Hence, answering questions on the link between leaf mechanical resistance and drought tolerance requires an understanding of which traits can confer to leaves their capacity to cope with water shortage on one hand, and their stiffness on the other hand,

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

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and how these traits are eventually correlated.

Anatomical determinants of leaf hardness

High LMA can derive from increased leaf thickness, increased leaf density, or both (Villar et al., 2013; Griffith et al., 2016; Xiong et al., 2016). Leaf thickness in an expression of leaf volume to area ratio, which depends on the amount of mesophyll cells per unit area rather than on specific anatomical modifications of individual cells or groups of cells (de la Riva et al., 2016). On the other hand, leaf density expresses the amount of dry mass per unit volume and strongly depends on structural and anatomical features of cells and tissues (John et al., 2017). Leaf density correlates to cell wall thickness and composition that can contribute up to 70% of LMA variation (Poorter et al., 2009; Onoda et al., 2017). Another important driver of leaf density and, hence, of LMA is the vein length per unit leaf surface area (VLA), with special reference to major veins (1st to 2nd order, VLA_{maj}) (Kawai and Okada, 2016; John et al., 2017; Kawai and Okada, 2018; Zhang et al., 2019). In fact, major veins also play important structural roles, as they contain many cells with thick secondary walls and occupy a large share of leaf space (Poorter et al., 2009; Westbrook et al., 2011; Sack et al., 2013), overall increasing the amount of dry matter per unit leaf volume. On this basis, the eventual linkage between LMA and leaf drought tolerance needs to be investigated by looking at the mechanistic correlations between anatomical drivers of leaf density and sound physiological metrics of drought tolerance.

Physiological determinants of leaf drought tolerance and possible correlation with LMA: turgor loss point

Leaf drought tolerance strongly depends on two physiological traits, i.e. the leaf water potential (Ψ_{leaf}) at turgor loss point (Ψ_{tlp}) (Bartlett et al., 2012) and the hydraulic vulnerability, generally expressed as the Ψ_{leaf} value inducing 50% loss (Ψ_{50}) of leaf hydraulic conductance (K_{leaf}) (Casolo et al., 2015). Ψ_{tlp} sets the water potential value below which leaf cells lose turgor, with consequent stomatal closure and rising risks of plasmolysis, cell collapse and death (Lenz et al., 2006; Binks et al., 2016; Mantova et al., 2021). Hence, species with lower Ψ_{tlp} can better tolerate water shortage (Nardini et al., 2003b; Savi et al., 2017; Zhu et al., 2018) and are preferentially distributed in water-limited biomes and habitats (Gortan et al., 2009; Bartlett et al., 2012; Nardini et al., 2012; Petruzzellis et al., 2021). Species-specific differences in Ψ_{tlp} are mostly driven by changes in cell osmotic potential (π_0) (Turner, 2017; Bartlett et al., 2012) and partially by modifications of cell wall elastic modulus (ε) (Bartlett et al., 2012), which in turn depends on cell wall thickness and composition (Balsamo et al., 2015; Peguero-Pina et al., 2017). While the mechanistic link between Ψ_{tlp} and π_0 is well understood (Turner, 2017), negative relationships between Ψ_{tlp} and ε (Mitchell et al., 2008; Savi et al., 2017) might simply reflect a coordination between traits, in that cells with low π_0 develop high turgor pressure when fully hydrated, possibly requiring mechanical reinforcement of cell walls. Increased thickness and mechanical resistance of cell walls, coupled to reduced cell dimensions, might also favour cell survival at water potentials below Ψ_{tlp}. In fact, it is known that leaf cells of some species can avoid post-plasmolysis collapse and cytorrhisis by sustaining negative turgor pressure (Oertli et al., 1990), and small and thick-walled cells would sustain more negative turgor before undergoing collapse (Ding et al., 2014). Because both increased cell number per unit volume and thickness of individual cell walls have an impact on LMA, it is not surprising that significant correlations can emerge in some studies between LMA, Ψ_{tlp}, and cell resistance to collapse and death, supporting the view that leaf stiffness can be coordinated with drought tolerance (Niinemets, 2001).

Physiological determinants of leaf drought tolerance and possible correlation with LMA: leaf hydraulic efficiency and safety

Maintaining adequate liquid water supply to transpiring leaves is fundamental to maintain hydration and assure photosynthetic carbon gain to the plant (Nardini and Salleo, 2003; Brodribb, 2009), because CO_2 uptake from the atmosphere is unavoidably associated with large losses of water vapour. Even under water shortage and after stomatal closure has occurred, water transport is required to maintain leaf hydration thus avoiding desiccation, leaf shedding and eventually plant death by hydraulic failure (Nardini et al., 2001; Sperry et al., 2002). Hence, K_{leaf} should be ideally kept at relatively high and constant values even under water limitation.

K_{leaf} depends on hydraulic properties of the leaf vasculature (i.e. vein xylem, K_x) and of the outside-xylem compartment (K_{ox}) (Cochard et al., 2004; Gascò et al., 2004; Nardini et al., 2010). When water potential decreases under drought, K_{leaf} declines because of different physiological processes occurring in these compartments. First, cell dehydration might lead to inhibition of aquaporins, thus decreasing K_{ox} because of negative effects on membrane permeability (Nardini et al., 2005; Miniussi et al., 2015; Maurel et al., 2016). Moreover, turgor loss can induce cell and leaf shrinkage (Canny et al., 2012), disrupting another important determinant of K_{ox}, i.e. apoplastic water flow in the mesophyll (Scoffoni et al., 2014; Trifilò et al., 2016; Abate et al., 2021). Hence, low Ψ_{tlp} and associated cell features reducing the risk of collapse and shrinking help leaves maintaining relatively constant K_{ox} even under drought. In fact, it is not surprising that some studies have found significant correlations between Ψ_{tlp} and Ψ_{50} in different species' assemblages across habitats differing in long-term water availability (Blackman et al., 2010; Nardini et al., 2012; Nardini and Luglio, 2014), thus leading to an indirect linkage between LMA and Ψ_{50}.

Another important determinant of K_{leaf} drop under water stress is xylem embolism accumulating in the vein system, leading to blockage of vascular water transport and hence to decreased K_x (Nardini et al., 2001; Scoffoni et al., 2017; Trifilò et al., 2021). Drought stress induces the progressive drop of xylem pressure, which can eventually surpass the critical threshold for embolism formation and spread, as observed in several different species (Nardini et al., 2003a; Salleo et al., 2003; Brodribb et al., 2016). Species more resistant to embolism generally display more abundant but narrower conduits in their leaf veins compared to more vulnerable species (Scoffoni et al., 2017). Xylem conduits of tolerant species also have thicker cell walls, possibly to reduce the risk of conduit collapse under very negative xylem pressure (Blackman et al., 2010). Hence, modifications of the vascular system to improve embolism resistance might translate into higher leaf tissue density, with direct impact on LMA.

Species-specific differences in vulnerability to embolism are also correlated to leaf size and to the length of major veins (1st to 2nd order) per unit leaf surface area (VLA_{maj}). Species with higher VLA_{maj} typically display more negative Ψ_{50}, because more major veins provide more alternative pathways for water flow over the leaf in case of partial blockage of some veins by xylem embolism, thus mitigating the negative impacts of drought on K_x (Nardini and Salleo, 2003; Scoffoni et al., 2011). VLA_{maj} is negatively related to leaf area (Scoffoni et al., 2011; Mauri et al., 2020), and because veins represent the leaf structure with the higher density (John et al., 2017), these leaves also tend to have high LMA values (Blonder et al., 2011; Nardini et al., 2012), even though correlations between these traits are not always striking (Sack et al., 2013).

Leaves of different species typically show different values of Ψ_{50}, inherently associated with different plant adaptive strategies, so that Ψ_{50} tends to be more negative for plants adapted to grow in water-limited habitats compared to mesic ones (Blackman et al., 2014; Nardini and Luglio, 2014). Because of the mechanistic correlation between cell and vein features and maintenance of both K_{ox} and K_x, it is not

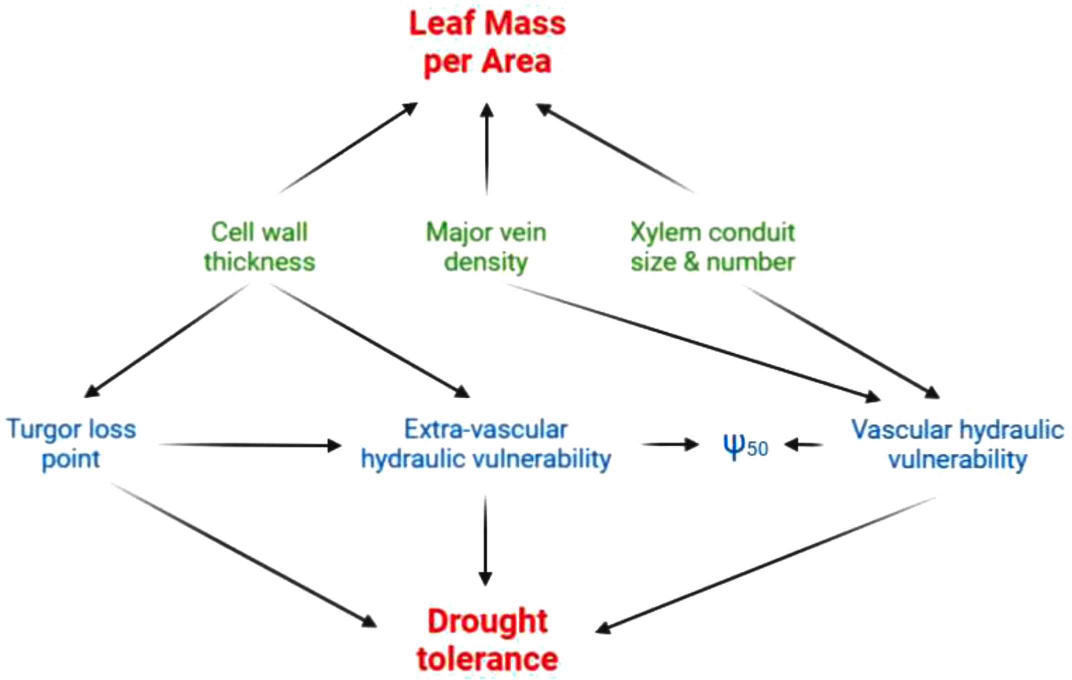

Fig. 1. Possible functional basis of coordination between leaf mass per area and drought tolerance, as mediated by mechanistic correlations between anatomical features (green) and physiological traits (blue).

surprising that some studies have reported significant correlations between Ψ_{50} and LMA (Scoffoni et al., 2011; Nardini et al., 2012; Villagra et al., 2013; Nardini et al., 2014), although others suggested the lack of correlation or coordination between these traits (Chen et al., 2009; Blackman et al., 2010; Nardini and Luglio, 2014; Blackman et al., 2018).

Want to endure adversities? Be hard and tough

Considerations listed above lead to suggesting that some of the anatomical modifications associated with high LMA and leaf mechanical stiffness, like thick cells walls (Lees, 1984), high major vein length per unit area (Kawai and Okada, 2016), and size/density of vein xylem conduits (Scoffoni et al., 2017), might be also coupled to species-specific drought tolerance, via mechanistic relationships between these structural features and the capability to better maintain turgor and leaf hydraulics during progressive leaf dehydration (Fig. 1). Combining leaf mechanical resistance with high drought tolerance confers adaptive advantages to plants growing in water-limited environment, which are also often nutrient-limited. In fact, both these limiting factors imply reduced photosynthetic rates at leaf level, possibly favouring species that produce leaves hard enough to warrant long leaf life span, and enough drought tolerant to maintain some gas exchange and positive carbon gain when conditions become harsh. Climate-change induced modifications of precipitation regimes, and related increased frequency/intensity of drought episodes in several biomes (Spinoni et al., 2014; Naumann et al., 2018) have the potential to induced vegetation shifts that might favour expansion of hard-leaved and drought-tolerant species or genotypes (Martínez-Vilalta and Lloret, 2016). Because, at the very end, when the going gest tough, the tough get going.

Credit author statement

This is a single-authored paper.

Declaration of Competing Interest

The author declares that he has no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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