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Revisiting the functional basis of sclerophylly within the leaf economics spectrum of oaks: different roads to Rome

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Revisiting the functional basis of sclerophylly within the leaf economics spectrum of oaks: different roads to Rome

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Key words: Sclerophylly, *Quercus*, stress factors, drought, nutrient scarcity, hervibory, col tolerance, leaf live-span.

Abstract

Sclerophylly has evolved independently in different woody plant genera, and has been traditionally considered as a stress-tolerance trait. However, the underlying drivers for this functional trait are still a matter of debate; it has been proposed as an adaptive response to miscellaneous stress factors, such as nutrient scarcity, drought stress, herbivory, cold tolerance and due to the large investment costs of sclerophylly, it is generally associated with a longer leaf life-span. Defining the mechanisms behind and the leaf-economic consequences of the development of sclerophylly in woody plants will allow us to understand its ecological implications, anticipate the potential for adaptation of different tree species to global change and to define new woody plant ideotypes for stress tolerance. For this purpose, the genus *Quercus* constitutes a unique living laboratory to understand global adaptive patterns along the leaf economic spectrum in trees. With more than 400 species, oaks are distributed along six zonobiomes and its versatility has resulted in a wide range of variation in leaf functional traits and contrasting adaptive strategies. However, this wide variability cannot be explained alone by any of the ecological factors considered neither any of them could be fully discarded. Noteworthy, our study also suggests that these constrains may have a synergistic effect and from a functional point of view, we can conclude that in oaks leaf habit largely modulates the physiological implications of sclerophylly.

1. General introduction

The term sclerophylly comes from the Greek *skleros* (hard) and *phyllon* (leaf) literally meaning "hard-leaved." According to Schimper [1], sclerophyllous species have common characteristics, such as; leaves with entire margins, oriented obliquely or parallel to the incidence of sun rays, thick cell walls, abundance of sclerenchyma and highly developed cuticle. Thus, Schimper concluded that "these qualities in the aggregate give the leaf its characteristic, stiff, leathery consistency."

Thus, as the concept of sclerophylly is an impression it is difficult to obtain an accurate measure,different methods and proxies have appeared for estimating this characteristic, such as the Loveless Sclerophylly Index [2,3] or Leaf Mass per Area (LMA) [4–7] and others that will be explained more in depth.

However, the underlying drivers for this functional trait are still a matter of debate; it has been proposed as an adaptive response to miscellaneous stress factors, such as drought [8,9], nutrient scarcity [2,3,10], low temperatures during vegetative period [11,12] and physical damage [13,14]. On the other hand, it has been argued that the higher construction costs of sclerophyllous leaves tend to be compensated by a longer leaf life-span, although the mechanisms behind are controversial [15].

In this review, we expose the main factors that promote sclerophylly and its functional implications using the genus *Quercus* as a living model. This genus comprises more than 400 species, is widely distributed along six well-differentiated zonobiomes, and its versatility and diversity has resulted in a wide range of variation in leaf functional traits and adaptive strategies [16].

2. How to measure sclerophylly?

2.1 Direct measurement of leaf strength: mechanical approaches

As sclerophylly means "hard-leaved", it is crucial to quantify mechanical properties of leaves in order to understand this trait. There are a number of methods available to evaluate mechanical properties of leaves (Table 1). According to the concepts, "strength" and "toughness" of a material refers to its ability to resist applied force and applied work, respectively that could lead to fracture or permanent failure , while "elasticity" refers to its ability to deform (without fracture or permanent failure) under applied force. On the one hand, fracture properties, including strength and toughness, are indicators of the ability to protect leaves against the risks of fracture caused by piercing, chewing and browsing herbivores, wind tear, etc. On the other hand, elastic properties become important when leaves are exposed to deformation, such as bending under gravitational force, rotating around the petiole and streamlining under dynamic load such as wind or avoidance of strong solar radiation under water stress (e.g. wilting) etc.

There are four major types of tests that are frequently used to measure leaf mechanical properties (Table 1; [17,18]): (1) Shearing tests (also called scissoring, cutting tests) measure how much work is required to cut across a leaf with a single blade (against an anvil) or with a pair of blades (i.e. instrumented scissors) [19–21]. (2) Punch tests, including punch-and-die and penetrometer tests, measure the maximum load required for the punch rod to penetrate a leaf [22–25]; (3) tensile tests (also called tearing tests) measure the force required to stretch and eventually tear a strip of leaf lamina [26–28]; and (4) bending tests (or flexural tests) measure the force required to bend a strip of leaf lamina that is placed on two supports [17,29] or entire leaf lamina with attached petiole [30,31]These tests can measure mechanical properties of a leaf specimen (often rectangular strip) in different directions (vertical or horizontal to the lamina surface) and different tissue types (e.g. the major leaf veins or the lamina between veins).

Leaf mechanical properties can be expressed on a different basis of expression depending on purpose (Table 1; [18]). Structural properties are affected by both chemical properties and lamina thickness, whereas chemical properties are normalized to cross-sectional area (thickness x width) of the test specimen [32]. It is also possible to evaluate how efficiently leaf mass is exploited for fracture strength or toughness from strength or toughness divided by tissue density of the specimen [18,33].

Although sclerophylly has been recognized as a key functional trait for many years [1], direct quantification of mechanical properties of sclerophylly had rarely achieved until 1990s. Turner et al. [34] measured and compared fracture toughness of several plant communities, including three sclerophyllous communities, by the cutting test. They found that the mean fracture toughness of the sclerophyllous communities were 2.1 to 4.6 times greater than the soft-leaved pioneer communities. Read & Sanson [32] made a detailed investigation of leaf chemical as well as mechanical traits using the punch, shear, tensile and bending tests for a diverse set of 33 plant species grown in a botanical garden. On average, sclerophyllous leaves were stronger, tougher and stiffer than non-sclerophyllous leaves in any mechanical tests, but more importantly, they found that structural properties (such as structural strength or bending stiffness) correlated more strongly with sclerophylly than material properties. This means that sclerophylly is characterized by not only high material strength or toughness but also lamina thickness. As discussed later, plant cuticle plays an essential role in preventing passive water loss. While less appreciated, cuticles are also important for mechanical defense and stability

[14]. Cuticle layers are composed by cutin, polysaccharides and waxes, and their Young's moduli (material stiffness) can be an order of magnitude higher than the corresponding values of the leaf lamina [35]. Furthermore, the farther is the leaf material located from the neutral axis, the more it contributes to bending stiffness (second moment of area).Therefore leaves with thicker cuticles often have higher lamina strength and stiffness [29]. Thicker and stiff cuticles are conducive to long leaf lifespan by protecting leaves from external mechanical stresses, and may contribute to keeping the leaf surface intact and sustaining high desiccation tolerance over longer lifespans.

2.2 Chemical proxies

An increase in sclerophylly is associated with a decrease in the percentage of protein content and with an increase in the percentage of fiber content [3]. Loveless [2,3] proposed a method for estimating sclerophylly based on fiber content that "should be expressed as a function of some measure of foliar tissue." He argued that fiber content could not be expressed in terms of dry mass, as it would ignore the absolute content of dry matter, nor could it be expressed as a function of fresh content due to diurnal variation, and owing to the fact that leaf fresh mass already implicitly contains the fiber content. Therefore, the estimation method of sclerophylly should be expressed as the crude protein content (calculated as nitrogen content multiplied by 6.25) per unit of leaf tissue.

$$(\text{Crude fiber dry mass} \times 100)/\ (\text{Crude protein dry mass})$$

Loveless [2,3] suggested that the use of crude protein content has some advantages since it is a useful indicator to measure functionally active leaf tissue (protoplasm), does not vary throughout the day and is an indicator that does not define fiber content in terms of another measure that already includes the fiber in it. However, the estimation of sclerophylly using the method proposed by Loveless has some drawbacks. Firstly, the Sclerophylly Index (SI) cannot be used to correlate the degree of sclerophylly with the fiber or protein content, since these components are already part of the ratio. Secondly, it seems that the increase in SI is mainly due to a decrease in the denominator (protein content, not related to sclerophylly), rather than to an increase in fiber content (related to sclerophylly)[36]. Furthermore, there is an increasing body of evidence that a large fraction of leaf nitrogen can be incorporated in cell wall proteins, especially in more sclerophyllous species [37,38] suggesting that the “crude protein” content is not a good measure of the protoplasm.

2.3 Leaf mass per area as a global proxy for sclerophylly

Leaf mass per area (LMA), is the most widely used proxy for sclerophylly in ecology (see e.g. [4–7,18,39,40]). The main advantage of LMA is that it can be easily determined and stands as a good indicator of the investment per unit of leaf area. Hence, it is a reflection of the cost-benefit between light interception and plant carbon balance, and hence of the leaf economic spectrum (LES; [6,40]). At least on a global scale, LMA shows a good correlation with mechanical measures of sclerophylly [18] and, to a lesser extent, with chemical proxies [3,41]. LMA is indeed a composite of leaf thickness (LT) and leaf density (LD), which can vary independently along environmental gradients [5,41,42] . Although the relative contribution of LT and LD to sclerophylly depends on the underlying strategy, both factors are known to contribute to leaf toughness [18]. When we consider oaks within a global context, deciduous oaks (DEC, those losing all leaves during the unfavorable season) did not differ significantly in LMA from other DEC plant species, whereas evergreen oaks (EVE, those retaining their leaves during the whole year) showed higher LMA than EVE plant species (Figure 1a). Oaks in general seem to have relatively thin leaves (low LT, Figure 1b), and dense tissues (high LD, Figure 1c), with EVE falling within the uppermost range of LD (Figure 1c). As we will discuss later in detail in section 4.1, large LMA values may have contrasting physiological implications, depending on the relative contribution of LT and LD. In particular, we will see how the high LD of EVE constitutes a major physiological constraint by restricting CO_2 diffusion.

Despite a general association between LMA and leaf structural strength, the two variables may vary independently. For example, oaks tend to have particularly strong leaves, going beyond differences in LMA (Figure 1). On the one hand, leaves with higher concentrations of fibers can have higher leaf structural strength without affecting LMA (i.e. higher specific strength) [18]. On the other hand, sclerophyllous leaves often have thicker cuticles, which also contribute to leaf strength and stiffness [29,35], but have a comparatively small effect on LMA (for further discussion about the association between LMA and cuticles see section 4.2). While we aware of these constraints, throughout this review we will focus on LMA as the most general proxy for sclerophylly, and the only one that has been determined in a wide range of oak species.

2.4 Botanists' Sclerophylly Index

Schimper [1] noted that sclerophyllous leaves have a "characteristic stiff and leathery consistency", thus, the concept of sclerophylly is an impression or a textural concept in botanical terms. Therefore, another way to determine the comparative degree of sclerophylly among several species would be to ask a group of botanists. Edwards et al. [43] proposed the Botanists' Sclerophylly Index (BSI) "to provide a direct assessment of sclerophylly, i.e. an index based on leaf texture". They asked a group of seven botanists who independently ranked by feel a set of 19 species from lowest to highest degree of sclerophylly. Although this index is useful to characterize sclerophylly and to rank species according to their degree of sclerophylly, it does not give absolute values and there is a possibility that botanists make mistakes due to their prior knowledge of the species.

3. Key factors promoting sclerophylly

3.1 Sclerophylly as a xeromorphic trait to cope with drought

3.1.1 The "evidence" given by Mediterranean woody plants

The development of hard leaves as a response to drought is one of the earlier interpretations of sclerophylly [14,44,45], still current [46–49] but under debate ([50] and references therein). The association between sclerophylly (the development of specially hard or tough leaves) and xeromorphism (all the anatomical and morphological traits common in plants living in dry or physiologically dry habitats) partially depends on phytogeographical evidence. The predominance of sclerophyllous shrubs and trees in all five Mediterranean regions of the world, with dry and hot summers [1,14,51–54]. In fact, many oak species are dominant constituent of such vegetation type in Mediterranean basin and in California. LMA values of Mediterranean evergreen oaks are higher than other phytogeographical groups of distribution within *Quercus* genus [55]. The negative influence of this summer drought period in the physiology of Mediterranean plants [56–58] or even survival [59,60] has led to a functional link between hard and/or tough leaves and the ability to withstand water stress.

Schimper [1] described the features of a typical xeromorphic leaf, as a way of coping with limited water-supply in their habitats. Among several adaptations, he included the presence of sclerenchyma although an explicit function of it is not defined. Schimper also suggested that the increase in "physiological dryness" (a term indicating the lack of available water for plants) should induce some concomitant changes in the leaf anatomy or morphology. Among others, the development of smaller, thicker and sclerophyllous leaves was reported in his analysis. This response, common of many plant species of dry habitats, was put at the same level as leaf-succulence or aphylly by Schimper [1], among the different plant responses to drought. He argued that the regions of Earth with "prolonged summer-drought" (or Mediterranean-type areas in other words) are the habitat of "evergreen xerophyllous" woody plants that show sclerophyllous leaves. Oppenheimer [61] gave a list of anatomical features that were common in xeromorphous leaves, and included the increase in mechanical tissues as "a general principle" in those plants from dry habitats. Moreover, the leaf thickening – or the reduction of surface to volume, as literally expressed by this author – was also proposed as a key trait in plants living in dry conditions. Both characteristics should imply a higher LMA, linking xeromorphism and sclerophylly. In fact, he included the Mediterranean evergreen sclerophyllous plants among the six main xerophyte types according to their physiognomy or phytogeography. Kummerow [52] insisted that regions with Mediterranean-type climates show a vegetation with a similar physiognomy, which could be interpreted as xerophytic – plants of dry habitats – and, specifically, "sclerophyllous xerophytes". Those plants were again the evergreen hard-leaved trees and shrubs previously described by Schimper [1] or Mooney & Dunn [51]. Both studies clearly supported the idea that the leaf anatomy of these sclerophyllous plants was responsible for the adaptation for withstanding water stress during the summer. The anatomical modifications suggested by Kummerow [52] coincide with those proposed by Oppenheimer [61], including reduction in the external leaf area and presence of group of traits inducing high leaf density, such as smaller cell size with thick cell walls, a high vein density or the presence of a reinforcement tissues. The presence of sclerenchyma among the leaf tissues in these leaves was proposed to serve as a protection when subjected to intense water deficit. Mooney [62] recognized similar features in the leaves of different species of shrubs from the areas under Mediterranean-type climate of California as a response to water stress. The development of dense mesophyll tissue – constituted by small cells with relatively thick walls and low presence of intercellular spaces and a higher proportion of palisade to spongy mesophyll thickness – is still proposed as an anatomical responses to water shortage [63].

3.1.2 *What can be concluded from other phytogeographical data? Sclerophyllous oaks under non-Mediterranean conditions*

However, this association between the Mediterranean-type climates and sclerophylly conflicted with other phytogeographical evidence, namely the presence of sclerophyllous woody plants in wet climatic regions of the Earth [14,61,64]. In fact, their massive presence in areas with wet tropical climatic regimes is well-established [45,65], with some areas clearly dominated by evergreen, sclerophyllous oak species [66]. Palaeobotanical studies would suggest that the possible ancestors of Mediterranean species of holly oaks (*Quercus* Group Ilex) lived in fully-humid conditions [67], confirmating the pre adaptive conditions of a high LMA in present Mediterranean woody plants [68].

Gil-Pelegrín et al. [50] concluded that evergreen oaks from tropical (zonobiome II), arid (zonobiome III), Mediterranean (zonobiome IV), and temperate (zonobiome VI) showed significantly equal values for LMA, in spite of the extreme differences in their respective phytoclimates in origin when growing in a common garden. On the contrary, the two groups of winter-deciduous species, namely Mediterranean (zonobiome IV) and temperate (zonobiome VI) did not show differences in LMA values between them but did show significantly lower values than all the evergreen oaks. These data confirm i) the existence of sclerophyllous *Quercus* species in contrasting phytoclimates and ii) the existance of both sclerophyllous and malacophyllous species in the same phytoclimatic conditions (zonobiomes IV and VI specially). In order to take into account the possible relationship between aridity and LMA, the values of any of these groups have been plotted against an index of aridity for oak species of all of the considered groups (Figure 2). We used the Lang aridity index (AI_{Lang}) – the ratio of the mean annual precipitation (MAP) and the mean annual temperature (MAT) [69] — in several native locations as confirmed by herbarium data (see [50]). On the one hand, evergreen oak species from zonobiome III and IV – i.e., Arid or Mediterranean phytoclimates respectively- showed the lowest values for AI_{Lang}, confirming that both inhabit dry to very dry areas. The AI_{Lang} for other evergreen oaks reaches ranges classified as clearly humid and even perhumid when some species of temperate deciduous (TEM-DEC) are considered, in spite of the similarity in LMA (see above). Otherwise, deciduous species, which do not differ statistically in LMA, do differ in terms of AI_{Lang}. This is because LMA values of Mediterranean deciduous species (MED-DEC) overlap to some extent with the values of MED-EVE species in xeric locations and with those of deciduous temperate (TEM-DEC) species found in wetter locations. Obviously, a simple phytogeographical association between the overall climatic aridity and sclerophylly cannot be immediately derived.

Concerning sclerophyllous oaks in tropical environments, several different studies have ruled out the influence of water deficit as the main factor explaining their abundance in these humid habitats [70–72]. Grubb [14], in fact, the term sclerophyllous to be quite ambiguous, in contrast to leaf anatomical characters that can be described for the so-called ‘hard-leaves’. He proposed the distinction between “pycnophylls” (from the ancient Greek *puknós*, dense, compact) for the Mediterranean plants with dense mesophylls, and “pachyphylls” (from ancient greek *pakhús*, thick) for the tropical sclerophyllous plants, with thick but lacunous mesophylls. Grubb [14] attributed to the Mediterranean pycnophylls a higher ability to withstand water deficit than tropical pachyphylls, breaking an uniequivocal link between developing hard-leaves and coping with drought. However, the suspicion of a possible influence of water shortage in the development of these tropical sclerophyllous leaves has also been considered [73]. The possibility of leaf water shortage in tropical climates could arise from low soil water retention and strong radiation in some of these habitats [14,73,74], or from severe physiological stress imposed on the canopy by root anoxia during long lasting inundation periods [75,76]. Unfortunately, the lack of sufficient functional studies related to this topic, and especially concerning oaks under tropical climates, precludes our ability to reach unambiguous conclusions.

However, several studies about the ecology and ecophysiology of a group of evergreen and sclerophyllous oak species of the *Ilex* group, also known as section *Heterobalanus* (Oerst.) Menitsky [67], provide an insight into the development of hard leaves with high LMA under climates that differ from those in arid or Mediterranean zonobiomes. These oaks can be dominant species in many forest of the Himalaya-Hengduan Mountains [77,78], at an altitudinal range roughly from 1000 to 3500 m a.s.l. [79]. In spite of the genetic proximity with their circum-Mediterranean relatives (e.g. *Q. ilex*), with evident leaf morphological similarities [80], the species of Himalaya-Hengduan inhabit areas within climates that differ substantially from the summer drought period of the Mediterranean-type climates [81]. In fact, their wide altitudinal range results in a high temperature gradient, such that climates range from subtropical at the base to warm or cool temperate at mid altitudes and to cold subalpine climates at the upper distribution limit of these species [77,82–84].

The whole area is influenced by the monsoon rhythm, which implies the existence of a clear seasonality and a warm rainy season from mid-June to September, preceded by a cold and dry season (from October to February) and a pre monsoon dry summer (March to May) [82,83]. More than 80% of the annual rainfall - between 1000 and 3000 mm [85,86] - can be accounted during the warm rainy season [82,83,85,87]. Compared to this situation, the precipitation in most areas under Mediterranean-type climates register annual values around 300 mm in average, with a minimum account during the summer [50]. Therefore, these two contrasting phytoclimatic conditions for the circum-Mediterranean and the Himalayan-Hengduan oak species of the *Ilex* group can apparently question the seminal idea of a link between sclerophylly and xeromorphy in these species. In other words, are these sclerophyllous oaks of the Himalaya-Hengduan affected by drought to a similar extent as their circum-Mediterranean relatives? In fact, the extreme seasonality mentioned above induces a long dry period in the monsoonal climates where these sclerophyllous oaks predominate [84,87]. The combination of a temperature rising with scarce precipitations during the pre-monsoon months induces a specially critical period for the vegetation in terms of water deficit [88,89], when the minimal values of water potential reported in these sclerophyllous species have been registered [78,83,87]. Moreover, the intra-annual variation in water deficit due to the inherent seasonality of the climates affected by the monsoon runs parallel to an inter-annual incidence of severe drought that induces periodic extreme water deficit in these oak species.

Poudyal et al [87], reported mean values for the predawn (ψ_{pd}) and midday water potential (ψ_{md}) in *Q. semecarpifolia* and *Q. lanata* obtained from December 1998 to April 2001 in Phulchowki Hill, Nepal. The two oak species were living at middle altitudes (2000-2100 m a.s.l.) of the whole range (1400-2715 m a.s.l.). This extensive study reported minimum values for ψ_{pd} around -1.7 MPa for both species, reached exclusively in March 1999, coinciding with the driest moment during this year. However, the value for this variable remained close to 0.3-0.4 MPa during the rest of the period studied, including the dry pre-monsoon months of 2000 and 2001. Concerning ψ_{md}, this trait showed minimum values during the driest moments of the 3 years under study (months of March and April), but never below -2.5 MPa for *Q. semecarpifolia* or -1.8 MPa for *Q. lanata*, with mean values of -1.18 MPa and 0.82 respectively. All the values reported would be above the osmotic potential at zero turgor in *Q. lanata* during the same period and geographical area [83], indicating the maintenance of positive turgor even in the driest periods [83,89]. In fact, Singh et al (2000) reported that such intense droughts affect the Central Himalaya in 5-6 year cycles. Such periodicity in the incidence of severe droughts have been associated to the influence of global phenomena, as El Niño [90], justifying the periodicity of the inter-annual variability. The incidence of such variability in the ecophysiology of different sclerophyllous oaks of the *Ilex* group is confirmed in different studies. However, during 1999 Singh et al (2000) studied the effect of a severe drought in other two oak species of the *Ilex* group, *Q. floribunda* and *Q. leucotrichophora* in Kumaun, the Central Indian Himalaya. During the peak of drought, they registered mean values of predawn water potential of -4.4 MPa, but the value fell to -5.5 MPa in the specimens more severely affected (showing dead leaves). Leaf shedding is interpreted as an ultimate mechanism that could allow the preservation of buds for future leaf production, as also reported in a Mediterranean deciduous oak by Peguero-Pina et al [91] during a severe drought in northern Spain.

These extreme values are close to the lowest values reported for *Q. ilex* (around -5 or even -6MPa; [92,93]. The ability to survive after reaching these low water potential values, preserving their buds to produce leaves again, would imply that these species show a high resistance to drought, establishing a direct correspondence with other circum-Mediterranean oaks of the *Ilex* group [94,95].

3.1.3 *The co-occurrence of sclerophyllous and malacophyllous oaks in Mediterranean-type climates: Any difference to cope with drought?*

As above suggested, another phytogeographical fact that can question the role of a high LMA as a direct functional mechanism to cope with drought is the presence of winter-deciduous oak with relatively low LMA values in many areas under Mediterranean-type climates of the Northern Hemisphere [96]. Some of these winter-deciduous species occupy dry habitats of the Eastern Mediterranean Basin [60] or coexist with evergreen congeneric oaks in the western Mediterranean Basin [97].

The co-existence of these winter-deciduous oaks (MED-DEC) with evergreen oaks, although being the aim of different ecophysiological studies [91,98] is not easily explained from an ecophysiological perspective [54] and further research is needed to fully understand this fact.

On the one hand, MED-DEC species have been considered elements of a different geobotanical group, the so-called “sub-Mediterranean” vegetation [99,100], being characteristic of those areas – most of them associated to mountain ranges - where the influence of the Mediterranean summer aridity is mitigated by a higher annual precipitation and a lower mean temperature [50,101]. This fact is supported by the intermediate values of AI_{Lang}, which does not show significant differences both with those for MED-EVE and TEM-DEC. Such sub-Mediterranean areas have been assumed as transitional stages or ecotone between the genuine temperate and Mediterranean climatic types [100,102]. Comparative ecophysiological studies concerning both types of Mediterranean oaks have reflected different strategies to cope with water limitations [96,98], and some of them concluded that evergreen species are able to resist higher level of extreme water stress [54,91,103,104]. The co-occurrence of these sub-Mediterranean oaks with the sclerophyllous and evergreen congeneric species in many areas of the western Mediterranean Basin should be the consequence of the alteration of the habitat affecting the water storage capability of the degraded soils [105].

Corcuera et al. [96] compared different species of oaks growing in a common garden taking into account the leaf area, LMA and different characteristics derived from the analysis of PV-curves. In this study, species were *a priori* grouped according to phytogeographical criteria into i) evergreen sclerophyllous from genuine Mediterranean areas ii) deciduous malacophyllous from Mediterranean areas or nemoro-Mediterranean oaks and iii) deciduous malacophyllous from temperate areas or genuine nemoral oaks. These groups clearly coincide with the MED-EVE, MED-DEC and TEM-DEC classification in this paper. In terms of LMA, the three groups showed statistically different means, but MED-DEC and TEM-DEC showed lower differences between them than with the mean value for MED-EVE, with LMA values nearly twice in average than reported for their deciduous congenerics. On the contrary, MED-EVE showed much smaller leaves in terms of leaf area than the deciduous species. So, MED-EVE showed common morphological attributes, corresponding to the archetypal image of sclerophyllous and small leaved trees commonly associated to the Mediterranean type climates. TEM-DEC can be considered the other extreme for both morphological traits, as expected for malacophyllous and broadleaved tree species of temperate climates. MED-DEC showed intermediate values for both morphological traits, but clearly closer to the values of TEM-DEC. However, in terms of the variables derived from the PV curves analysis, a clear coincidence in the value of osmotic potential at full turgor (π_0) between Mediterranean species, independently of their leaf habit were reported, against the lower value found for with TEM-DEC. Concerning oaks, the finding of higher π_0 in oaks living in dry habitats have been previously reported (see [96] and references therein). MED-DEC showed the higher values for leaf water potential at turgor loss (π_{tlp}), slightly but significantly higher than the mean value for MED-EVE and much higher than the one for TEM-MED. According to the result of a global meta-analysis, incorporating data from different biomes, Bartlett et al. [106] concluded that π_{tlp} was the trait more closely related to drought tolerance, with π_0 as the main characteristic influencing π_{tlp}. As suggested Bartlett et al. [106], π_{tlp} is related with i) the minimum soil water potential for water uptake and ii) with the ability for maintaining gas exchange at lower soil water potential. Both facts can be crucial for surviving and grow under Mediterranean climates, especially when leaf life span is limited to the dry summer in MED-DEC. So, with this proposal in mind, MED-DEC could be interpreted as clearly able of coping with the summer drought as well as the genuine Mediterranean MED-EVE, which should be in accordance with the results of Damesin et al [54] when compared the responses of co-occurring *Q. ilex* and *Q. pubescens* under Mediterranean conditions in southern France.

Corcuera et al [96] also found a clear statistical difference concerning the maximum bulk modulus of elasticity (ε_{max}) when the three phytogeographical groups of oaks were compared. MED-EVE had higher values of ε_{max} , clearly above the value for MED-DEC and, specially, for TEM-DEC. The role of this trait, the rigidity of the cell walls, has been studied by several authors in terms of coping with drought (see [50] and references therein). Bartlett et al [106] did not attribute any relevance in terms of coping with drought to ε_{max} , but a low cell-wall elasticity plays a role in water conservation, as a large change in turgor can be achieved with a minor change in symplasmic water [107,108]. This may constitute a mechanism to reduce water loss, through the effect of turgor loss in stomatal closure [109], reducing the diurnal and seasonal water loss [108]. A high ε_{max} in MED-EVE would be interpreted as a conservative mechanism [110], allowing them to avoid a rapid soil water consume in extremely dry areas or in location with poor developed soils or degraded soils. The lower ε_{max} found in MED-DEC would allow the maintenance of positive turgor and, consequently, plant gas exchange and growth at the expense of a higher water consume through the summer, with the risk of developing water potential values inducing xylem cavitation, as was observed in *Q. subpyrenaica*, a MED-DEC oak species of northwestern Spain by Peguero-Pina et al [91].

Woody plants from dry areas seems to develop a higher resistance to water stress-induced cavitation than those native from mesic habitats [111]. So, the comparison of the specific vulnerability to drought-induced xylem cavitation may serve as a way to compare the relative tolerance to climatic drought between MED-EVE and MED-DEC.
The quantification of this resistance can be done using different traits derived from the so-called cavitation curve, with P_{50} and P_{88} (water potential values inducing the loss of 50% and 88% of hydraulic conductivity loss respectively) as the most common characteristics in comparative studies (e.g. [112,113]). Although a direct functional relationship between LMA and the xylem vulnerability to cavitation in the stems should not be expected, we can use such resistance to cavitation as an indicator of the ability of the species to cope with water deficit. We also note that oaks are long-vesseled species and thus subject to artefacts in the production of vulnerability curves. The relative P_{50} and P_{88} values are still likely meaningful, but this is an area of continued debate within the literature.
There is a tendency of P_{50} and P_{88} to increase as the aridity increases (lower AI_{Lang} values) is evident, with an exponential decay for higher AI_{Lang} where TEM-DEC predominate (Figure 3). Nevertheless, although the higher values for aridity and cavitation thresholds have been reported for some species of the MED-EVE (e.g. [94]), other representative species of this group that inhabit areas with high aridity do not show high P_{50} and P_{88} values (see high dispersion in y axis). Notably, very negative values for P_{50} and, specially, for P_{88} are reported for species of the MED-DEC group. In fact, when the values for both cavitation thresholds are compared among groups, P_{50} and P_{88} values do not differ among Mediterranean oaks with contrasting leaf habits. Urli et al. [113] proposed that P_{88} more clearly reflects the irreversible damage associated with drought in angiosperms. Thus, based on their resistance to cavitation, species living in more arid areas (with high LMA values) are probably not more highly resistant to xylem cavitation,

and deciduous species (with low LMA values) are not necessarily more vulnerable to losses in hydraulic conductivity induced by drought (Figure 3). Therefore, assuming P_{88} is a reasonable proxy for an overall ability of coping with aridity in *Quercus* species, sclerophyllous oaks do not have more drought resistant stem xylem than other oaks.

3.2 Sclerophylly in response to limited nutrient resources

Since the first studies of Schimper in 1903 [1] in which a relationship between sclerophylly and xeromorphism was proposed, numerous studies have arisen questioning this relationship, such as those carried out by Beadle [114,115]. This author, observing the Australian flora, showed that sclerophylly was not necessarily a xerophytic adaptation, since he perceived the existence of the humid sclerophyllous forest. Moreover, he concluded that in the Sydney district, the community structure was explained directly or indirectly by the phosphate content of the soil. In this area, rainforest composed of plants with laureate leaves occurs in the most fertile soils, whereas dry-looking sclerophyllous forests, composed of highly xeromorphic plants, occur in less fertile soil but, according to Beadle, this is not as a response to lack of water. Furthermore, Beadle [10] also studied the number of tropical and subtropical rainforest genera and observed that it correlates with the level of phosphate in the soil, independently of precipitation. He also found that the adaptation to low fertile soils accentuates xeromorphic characters through a reduction in leaf size, and his experiments indicated that the degree of xeromorphy could be reduced in many cases by the addition of phosphorus and nitrate.

Although these early studies were based on Australia, where the presence of soils with low nutrient content, mainly phosphorus, is common [116], other authors have also observed the existence of sclerophyllous species in nutrient-limited tropical rainforests [45,70].

Loveless [2], also found that there was a high correlation between phosphorus content in leaves and the fibre/protein ratio. In addition, he showed that below a phosphorus content of 0.3%, the fiber/protein ratio increases with the decrease in phosphorus and suggested that “phosphate deficiency of the soil might be an important factor in sclerophylly”. Moreover, in later studies it has been observed that sclerophylly is a response to nutrient-poor soils [65,117], and especially to phosphorus deficiency [118] or nitrogen stress [39,119]. However, Sereneski-de Lima *et al*. [120], studying the highly sclerophyllous mangrove tree species from South Brazil, concluded that mangrove trees were not limited by soil nitrogen nor phosphorus, thus, the high LMA observed was not determined by soil oligotrophy.

Focusing on genus *Quercus*, there are studies that support Beadle's postulates, since they find sclerophyllous species inhabiting oligotrophic conditions. Cork-oak (*Q. suber*) forests that inhabit in Northeast Iberian Peninsula had a mineral content of the litter fall composition with low macronutrients such as nitrogen and phosphorus [121]. Furthermore, Castro & Fernandez-Nuñez [122] showed that in three monospecific *Quercus* forests of Northeastern Portugal there is a soil-fertility gradient among the three ecosystems, coinciding with the degree of sclerophylly. From the malacophyllous *Q. pyrenaica*, found in more favored areas, to the highly sclerophyllous *Q. ilex* subsp. *ballota*, developed in oligotrophic conditions, going through *Q. suber* in intermediate zones.

Conversely, other studies found no significant relationships between the degree of sclerophylly and low nutrient content. Cavender-Bares *et al.* [123] studied 17 *Quercus* species growing in Florida across different habitats, and found only weak associations between LMA and nutrient-related soil traits (inorganic nitrogen, soil pH, phosphorus and calcium). García *et al*. [124] found mixed forests of *Q. suber* (sclerophyllous) with *Q. faginea* or *Q. canariensis* (malacophyllous) in areas of southern Spain and Portugal, where phosphorus availability was very low. Similarly, Aranda & Comino [125] found poor-nutrient soils in the oak forests of Sierra Nevada National Park (southern Spain), where *Q. pyrenaica* (malacophyllous) and *Q. ilex* subsp. *ballota* (highly sclerophyllous) coexist. However, in Cazorla-Segura-Las Villas Natural Park, also dominated by mixed forests (*Q. faginea* and *Q. ilex* subsp. *ballota*), soils with high levels of nutrients were found.

Furthermore, sclerophyllous oaks are not the only group found in environments with Mediterranean climate and high nutrient content [125,126]; malacophyllous oaks, such as *Q. robur*, *Q. infectoria*, *Q.* brantii or *Q. saii*, also persist with low phosphorus availability [127]. Moreover, it has even been observed that this element can control the primary production of these forests [127,128]. Zhang et al. [129] found a wide range of variation in LMA (ca. 40-80 $g{\cdot}m^{-2}$) across provenances of *Q. acutissima*, a malacophyllous species distributed along a wide range of soil conditions in China [130]. However, the LMA range was kept constant across the three provenance trials included in the study, despite contrasting soil conditions.

Overall, the potential link between sclerophylly and soil nutrient availability still remains controversial, due to the interrelation among soil traits (e.g. water availability and nitrogen content may be both affected by soil depth and texture) and with other environmental drivers (e.g. the concomitant increase in nutrient and water availability in deep valley soils).

As a proof of concept for the potential association between soil nutrients and the prevalence of sclerophylly, we took advantage of the information on species occurrence and soil traits, available from the US Forest Inventory and Analysis (FIA) database (http://www.fia.fs.fed.us/; accessed march 2019). Following a similar approach to that described by Rueda et al. [131] we first compiled information on soil conditions and species occurrence from all plots with presence of oaks, and assigned to each species a typical LMA value, based on literature data (for further details on the methodology see Supplementary Material). This resulted in 124687 sites across the USA, with information on 36 oak species. With these data, we could determine average values per species for all soil and site variables, in order to perform correlation analysis between LMA and the prevailing site conditions across the distribution range of each species (Figure 4).

Across the USA, soil quality showed an effect on LMA, although it came associated with other geographic gradients. We found higher LMA values in shallower and more mineral, dense soils (Figure 4a), with lower soil water content (Figure 4b) and lower total nitrogen content (Figure 4c). However, this could be linked to the high LMA prevailing in the dry mountain regions (ARID-EVE, MED-EVE in Figure 4), as opposed to the low LMA prevailing in the cold-temperate planes (TEM-EVE), leading to a positive association with elevation (Figure 4d). The altitudinal trend was partly disrupted by the low LMA of the winter-deciduous (TEM-DEC) *Q. gambelii*, which shows the highest mean elevation, and the moderately high LMA of the southern-temperate evergreens (TEM-EVE; e.g. *Q. virginiana*, *Q. minima*. Overall, we found the largest LMA values in the arid and Mediterranean mountain ranges in the Southwest and the Pacific coast, largely dominated by evergreen and sub-evergreen sclerophyllous oaks (e.g. *Q. agrifolia*, *Q. chrysolepis*, *Q. rugosa*; ARID-EVE and MED-EVE). Conversely, the lowest values were found in the North Central and Northeastern cold-temperate regions, dominated by temperate deciduous oaks (TEM-DEC), such as *Q. muehlenbergii*, *Q. macrocarpa*, *Q. rubra*. or *Q. alba*..

Notably, phosphorous availability did not show any association with LMA (Figure 4e), opposing the postulates by Beadle [10,114,115]. Furthermore, although a weak association with pH (Figure 4f) was found, the highest LMA were found within the less nutrient-limiting range of pH (6-7). LMA also showed a negative association with some exchangeable cations (r^2=0.32, p<0.001 for magnesium, r^2=0.23, p<0.01 for aluminum), but was not significantly correlated with neither calcium nor potassium. A similarly weak, negative trend was found for other metals, such as iron (r2=0.22, p<0.01) or zinc (r2=0.22, p<0.01), but none of them appear to be particularly limiting. Conversely, nitrogen content emerges as the soil trait most strongly associated with LMA in our survey (Figure 4e), confirming the negative association between soil nitrogen content and LMA reported in previous studies [39,119]. In this regard, despite the emphasis put on Phosphorus since the early studies of Beadle [114,115], nitrogen may have a more critical role than phosphorus in shaping plant adaptive responses [126]. A recent study on model plants highlighted that phosphate starvation genes are largely controlled by nitrogen availability, but not vice versa [132].

Despite the apparent response of LMA to Nitrogen availability, at least in our case this trend cannot be isolated from the large-scale geographic gradients in environmental and soil physical traits. Eroded, shallow soils prevail in the dry mountain areas in the West (MED-EVE, ARID-EVE), contrasting with the deep, fertile and wet soils in Central and Northeastern plains (TEM-DEC). Besides, the association between LMA and soil nitrogen could be further enhanced by the higher decomposability (and eventually faster turnover) in deciduous trees, as compared with the evergreens [133,134]. Furthermore, LMA tend to be negatively correlated with both leaf nitrogen content and leaf digestibility, and positively correlated with fiber content ([2,6,133]; see also section 4.1). Hence, low nitrogen content in the soils might be partly an indirect consequence of sclerophylly, rather than a driving force for the selection for this trait. In support of the influence of tree litter on soil nitrogen, the negative association between LMA and nitrogen was less consistent in the deeper soil horizons (r^2=0.35, p<0.001) than in the forest floor (r^2=0.45, p<0.001; Figure 4). Although this point is hard to disentangle based on standard field surveys, it may deserve further assessment through experimental, manipulative approaches.

3.3 Sclerophylly to increase leaf longevity by reducing mechanical damage

From a global plant perspective, increases in leaf sclerophylly can be associated with increases in leaf longevity, as several authors have reported positive relationships between LMA or physical properties with leaf lifespan (LL) (e.g. [4,6,18,21,135,136]. Focusing on the genus *Quercus*, a relationship between LL and LMA obtained from literature and personal measurements follows the same positive trend (Figure 5). In this genus and independently of the species leaf habit and climate, an increase in LL from 5 to 15 months is associated with a strong increase in LMA from 85 to 170 g m^{-2}. However, a further increase in oak LL to 50 months is not related to a significant increase in LMA, indicating the existence of an oak LMA threshold (c.a. 185 g m^{-2}) towards higher values of LL. Additionally, within leaf habit and climate, we only found a significant correlation (r^2=0.39 p<0.001) for the temperate deciduous (TEM-DEC) group (Figure 5).

The higher LMA found in longer-lived leaves has been explained through a greater leaf reinforcement by the accumulation of structural carbohydrates, mainly due to the increase in cellulose (CC) and hemicellulose (HC) content [32,136] (Figure 6). By contrast, lignin and cutin content (LCC) does not seem to have a direct correlation with LMA and leaf duration, suggesting other explanations for the LCC interspecific differences such as water transport functions associated with the venation system of the leaf [136].

The accumulation of structural carbohydrates might enhance leaf persistence through the increase enhanced leaf protection [15,37,137]. This would help to resist the tear and wear due to physical [87,138] and biotical [139,140] interactions with the environment [15]. In this sense, leaf herbivory by insects has been the most common mechanical stress factor studied in the literature [139,141,142]. Generally, insects avoid eating sclerophyllous (high-LMA) leaves, both under laboratory [41] and field experiments [143,144]. Accordingly, *Quercus* species with lower LMA suffer a higher percentage of leaf area lost per branch due to insect herbivory (see supplementary material Figure 1). The influence of mechanical leaf properties on insect herbivory can also determine the organization of the community composition of herbivores, including their diversity and density [140,145]. However, in other studies the relationship between the level of sclerophylly and herbivory is not so evident [117]. Some species with low LMA values can be eaten as little as species with high values of LMA [41]. In those cases, small concentrations of secondary defense compounds such as tannins [146], may significantly curb the set of herbivores able to feed on given leaves without hardly depending on the level of sclerophylly [137], although the degree of herbivory in relation to LMA and secondary chemical content has not been studied across oak species.

3.4 Sclerophylly as a cold protection mechanism in evergreen oaks

In evergreen species, winter is a season that can constitute stressful conditions due to low temperatures and other interacting stresses. Low temperatures occurring on bright days can lead to photoinhibition [147,148]. Frost can damage plant cells and, consequently, reduce the physiological activity of the leaf [11]. Frost can also freeze the water of the xylem and can produce xylem embolism, stopping water circulation to foliage leading to a physiological desiccation stress. Moreover, cuticular abrasion damage produced by snow and ice can enhance cuticular transpiration, increasing also the potential desiccation stress [12].

To mitigate cold stress effects, plants may adjust several structural and physiological traits related to LMA. According to González-Zurdo et al. [149], *Q. ilex* and *Q. suber*, two evergreen Mediterranean oaks, presented higher leaf thickness in those sites with lower values of mean annual temperature. Increasing leaf thickness both by increasing the number of cell layers or by increasing individual cell layer, reduces the average intensity of light reaching the interior of the leaf, thereby reducing the probability for photodamage [150,151]. Being thicker also results in a greater water content per unit leaf area [152,153]. Due to the higher heat capacitance of water, the increase in water content per area may reduce the rates of leaf freezing [154] and leaf thawing [155], reducing the physiological damage by frost, especially in leaves exposed to multiple freeze-thaw cycles [151]. Frost acclimation may also lead to increases in cell wall thickness and cell wall rigidity [156]. This acclimation may help to avoid the collapse of cells under low water potentials that may occur when frozen soils prevent water delivery to transpiring leaves. A higher cell wall rigidity also implies that for a given change in water potential, there is a lower degree of water migration from cells to extracellular spaces in comparison to more elastic cell walls [151]. Intracellular water can remain supercooled during low temperatures, whereas extracellular water freezes faster, therefore a higher rigidity would delay water freezing [157]. The higher cell wall rigidity may be due to an increase in fiber contents [158,159]. In fact, González-Zurdo et al. [149] observed higher contents of cellulose + hemicellulose in individuals of *Q. ilex* and *Q. suber* inhabiting sites with higher number of days with frost per year.

These adjustments in leaf traits in response to low temperatures might promote an increase in the LMA of evergreen oaks, at least within species [149,160]. However, among species, it is still unclear whether the main driver of changes in LMA is severity of cold itself (e.g. characterized by mean annual temperature, MAT) or it is related to the length of the cold season. Most of the studies only focus on MAT and other temperature indicators, not analyzing the effect of the length of the unfavorable cold season. In this sense, Kikuzawa *et al.* [7] found a strong positive relationship between MAT and the portion of the year for favorable growth. Furthermore, taking into account the temperature in natural conditions of 30 oak species [50], we have found a strong correlation ($R^2=0.84$, $P<0.0001$) between MAT and the number of months with mean temperature below 5ºC (Figure 7), i.e. the unfavorable season for growth, according to Wypych et al [161]. These correlations suggest that LMA variations among species attributed to MAT, could be also attributed and explained by the length of the unfavorable season. Therefore, further research is needed in order to clarify whether variations in LMA among oak species actually respond to the intensity of low temperatures or, by contrast, to the length of the cold season.

4. Functional implications of sclerophylly

4.1. Sclerophylly as a key factor modulating oak photosynthesis in the context of the leaf economics spectrum (LES)

LMA – the most widespread quantitative proxy for sclerophylly – is one of the major traits in the leaf economics spectrum (LES), which globally describes the coordinated variations in leaf structural, chemical and photosynthetic characteristics [6]. Fundamentally, LES runs from the high return end, characterized by low investment per unit area (i.e. low LMA), low leaf longevity, high nitrogen content per dry mass (N_{mass}) and high photosynthetic rates per unit mass (A_{mass}), to the low return end characterized by opposite variation in these key leaf traits [6]. The negative association between LMA and A_{mass} at a global scale has been linked to a higher investment in non-photosynthetic structural tissues and/or a lower efficiency of the photosynthetically active mesophyll [162].

However, when considered globally, the relationships among area-based net CO_2 assimilation (A_{area}), area-based nitrogen (N_{area}) and LMA are less clear, and could be modulated by the influence of different physiological and anatomical traits [38]. Bearing in mind this general framework, these authors put in evidence the role of different mechanistic traits in these area-based relationships, such as the mass fraction in cell walls, nitrogen allocation to Rubisco versus cell walls, the mesophyll conductance to CO_2 (g_m) and related anatomical characteristics, considering the existence of possible opposite effects on A_{area} associated to changes in LMA. Thus, Onoda *et al.* [38] concluded that, globally, diffusive and biochemical limitations to photosynthesis associated to thicker cell walls (i.e. lower g_m and lower N allocation to Rubisco, respectively) can be complemented by greater N_{area} in species with large LMA, thereby largely equalizing A_{area} across species with contrasting LMA.

Besides global variation across all species, meaningful variations among species in foliage traits have also been reported within a single genus. This is the case of *Quercus*, which exhibits a strong intra- [163] and interspecific [50] variability in LMA. In this regard, the meta-analysis performed by Peguero-Pina *et al.* [164] demonstrated that the genus *Quercus* shows a broad range of variation in several major traits in LES (i.e. LMA, N_{mass} and A_{mass}), covering a high span within the full LES. In this section, we have extended this meta-analysis up to 71 oak species with the dataset available from the TRY Plant Trait Database ([40]; see Supplementary Material for details), which also included additional traits such as N_{area}, A_{area} and stomatal conductance for H_2O (g_s). Moreover, we have classified the species according with their climate origin and leaf habit in one of the following groups: temperate deciduous (TEM-DEC), temperate evergreen (TEM-EVE), Mediterranean deciduous (MED-DEC), Mediterranean evergreen (MED-EVE), tropical deciduous (TRO-DEC) and tropical evergreen (TRO-EVE).

Overall, the results obtained confirm that the genus *Quercus* follows the general trends described in the LES, as LMA was negatively related with N_{mass} and A_{mass} ($P<0.0001$, Figure 8). However, this pattern was not observed when considering area-based relationships. Thus, the relationship between LMA and A_{area} was not statistically significant ($P=0.095$, Figure 8), although it was positive when considering only DEC species ($P=0.002$, Figure 8). Moreover, LMA and N_{area} showed a strong positive relationship ($P<0.0001$, Figure 8), which is in line with the results found by Yang *et al*. [165], who reported a strong correlation between N_{area} and LMA when analyzed the variation in LES traits in 483 species at 48 sites across China. Taken together, our findings could indicate the existence of additional factors modulating these relationships in oak species. Thus, an increase in mesophyll thickness concomitant to higher foliage robustness [41,42] would explain the increase in N_{area}, probably because of overall greater number of cell layers and greater leaf volume [57,163,166]. In consequence, this phenomenon counteracts the negative influence of higher LMA values on photosynthetic capacity of oaks. By contrast, we have not found any significant relationship between LMA and g_s, mostly due to the occurrence of species with the lower g_s values in the groups with lower and higher LMA values (TEM-DEC and MED-EVE, respectively) (see in supplementary material figure 2). Otherwise, MED-DEC species with relatively low LMA values had the higher g_s values among all the oak species analyzed (see in supplementary material figure 2). This reflects the fact that transpiration rate should be independent of the amount of photosynthetic machinery per unit area [50].

It is interesting that DEC and EVE oak species were grouped, respectively, towards the high and low return end, irrespective of their climatic origin. In fact, LMA is one of the most important functional traits that clearly separates EVE and DEC [50,96]. That is, within *Quercus*, these relationships seem to be more influenced by the leaf habit than by the climatic/ecological conditions of each species, indicating the co-existence of multiple trait values in the same climate [167]. In line with this, Kappelle and Leal [168] found a high span in LMA and nitrogen when studied several leaf traits in 41 tree species in a montane forest of Costa Rica (Figure 9), and very similar to that described here for oaks (Figure 9). It is noteworthy that the relationship between LMA and N_{area} with the dataset from Kappelle and Leal [168] showed a positive relationship in spite of include very diverse species. Otherwise, Yang *et al*. [165] suggested that climate influences trait variation in part by selection for different life forms and families. In spite of this, these authors found a positive correlation between LMA and N_{area} and photosynthetic capacities after removal of climate effects, and concluded that it is still necessary to collect more systematic trait data across all climates and biomes. For instance, available data about tropical *Quercus* species are very limited, in spite of the great number of oak species occurring under these climatic conditions [66].

Both higher g_s and N_{area} yield higher A_{area} values in oaks, and the best fit for these correlations was a curve describing an exponential rise to a maximum assimilation rate of 17.5 and 19.1 µmol CO_2 m^{-2} s^{-1}, respectively (Figure 10). In other words, there was a decreasing sensitivity of maximum CO_2 uptake per leaf area when g_s and N_{area} reached threshold values, which indicated that other factors could also constrain A_{area}, especially in species with higher g_s (i.e. MED-DEC) and N_{area} (i.e. MED-EVE and MED-DEC). In this regard, the diffusion of CO_2 from the sub-stomatal cavities to the sites of carboxylation (i.e. the mesophyll conductance, g_m) plays a key role in the photosynthetic process of *Quercus* species, being in many cases the most limiting factor for carbon assimilation, as reviewed by Peguero-Pina *et al.* [164]. This seems to be the case of MED-EVE from Europe and California [169], but also for MED-DEC species such as *Q. faginea* [170]. It should be noted that several studies have revealed that g_m is negatively related to LMA [38,171,172]. Specifically, the fact that g_m is limited by large LMA values has been mostly related to several leaf anatomical traits (i.e. mesophyll and cell wall thickness), and has been demonstrated for different species [162,173–175] including MED oaks [169]. Besides the increases in N_{area} associated to higher LMA values, Peguero-Pina *et al.* [169] demonstrated the existence of other anatomical adaptations at the cell level (increased mesophyll and chloroplast surface area exposed to intercellular air space) that allow MED-EVE to reach A_N values comparable to congeneric deciduous species despite their higher leaf thickness and LMA.

In line with this, other authors have analyzed the role of other anatomical structures that contribute to high LMA in plant photosynthetic performance. This is the case of the bundle sheath extensions (BSE), which are strips of parenchyma, collenchyma or sclerenchyma cells connecting the vascular bundles with the epidermis that can influence photosynthetic light-use efficiency of leaves [176]. Nikolopoulos *et al.* [177] suggested that the inherent reduction of A_N due to the occurrence of non-photosynthetic tissues such as BSE may be compensated from higher photosynthetic rates per areole, due to a higher light availability within mesophyll. These authors also stated that BSE enables light transmission to deeper leaf layers, so its optical role might only be essential in species with thick leaves (i.e. with high LMA), as previously shown by Karabourniotis *et al*. [178] for *Q. coccifera*.

Nevertheless, more research is needed in order to confirm the widespread occurrence (or not) of these mechanisms, as the number of studies concerning the role of such structural traits in determining A_N is still limited.

4.2 Functional mechanisms associating sclerophylly and drought tolerance

The predominance of sclerophyllous oaks in habitats prone to induce water limitations, such as those under Mediterranean climate, has not been adequately explained in a functional way, so the role of a hard leaf for withstanding water shortage remains unclear. In this sense, different ecophysiological studies have revealed that Mediterranean sclerophyllous woody species show different, and even contrasted, strategies to cope with water stress [108,179,180] which question the existence of a single role of sclerophylly in terms of water relation [96,104].

One possible reason for the lack of a clear functional correspondence between sclerophylly and coping with water deficit is the use of LMA as the most common functional proxy. Effectively, a leaf can reach a high LMA through an increase in thickness (LT), a higher leaf density (LD) density tissues, or the combination of both factors [5,18,41,42], with very different functional consequences.

Does an increase in LMA through a higher LD have a role in water relations? Oertli [181] proposed that leaves can withstand negative turgor pressure without being subjected to cell collapse, or cytorrhysis, if their tissue are constituted by small cells with thick walls. The extreme buckling of mesophyll cells at low water potentials (see [182]) will induce physical and irreversible damages in the plasmalemma. Oertli et al. [183] proposed that this mechanism of avoiding cytorrhysis by developing thick cell walls is especially important for plants living in dry habitats but with access to water along the year, as is the case of Mediterranean plants. However, this ability was not able to cope with extreme water deficit. The seminal idea of Oertli has been recently revisited [184], but further research is need to accept this mechanism as an explanation for the abundance of sclerophyllous in dry areas, such those under Mediterranean-type climates.

Closely related to this ability for avoiding cell collapse by thicker cell walls, the relation between LD and the cell rigidity (ε_{max}) has been considered for explaining sclerophylly in water-limited habitats [5,104]. As above discussed, it is not clear that the higher ε_{max} the higher the resistance to water deficit, although more rigid cells would be an effective mechanism for symplastic water conservation [96] and an efficient mechanism for withstanding drought in sclerophylls [5,104,185] as it would allow higher water potential gradients between leaf and soil for a given symplastic water loss.

However, few authors have reported a positive correlation between LMA and ε_{max} [46,186–188], whereas others suggested a lack of correlation between both traits [108,179]. In this regard, we have found a non-linear positive relationship between LMA and ε_{max} from the data provided by Corcuera et al. [96] for different *Quercus* species growing in a common garden (Figure 11). We obtained a similar result when this meta-analysis was extended up to 25 oak species, including the dataset available from the TRY Plant Trait Database [40] (data not shown).

A caution is needed when relating LMA and ε_{max}, as the former is dependent on all the dry matter accumulated per area while the rigidity of the mesophyll cell walls should explain the later [46,108]. So, only the establishment of a closer relation between the morphological properties of the cell walls (thickness and rigidity) of these cells and their contribution to the overall LD could satisfy the idea that a higher LMA by denser leaf tissues could constitute an adaptive mechanism to cope with water deficit.

Salleo et al. [185] proposed another adaptive advantage of sclerophyll in terms of water deficit, when he suggested that the water contained in the mechanical tissues of some sclerophyllous woody plant species would positively contributes to the recovery of the water deficit and its consequences [185]. Further studies should confirmate this interesting idea.

Another way for increasing LD with a further increase in LT may be the increment in vein density, due to the anatomy of the vascular bundles and, eventually, of the bundle sheath extensions. A functional advantage, in terms of water limitations, of a higher vein density was proposed by Scoffoni et al. [189] and confirmed by Nardini et al [190], when found that the higher the density of major vein – first, second and third order- the higher the resistance to water stress-induced xylem cavitation. Further evidence of an increase of major veins density in oaks with increasing the aridity of their distribution range was found by Peguero-Pina et al. [95].

Implications of sclerophylly on water conservation

An intense summer drought period imposes harsh ecological constraints to the plant life in Mediterranean climates [58,59,191] and it has led to the controversial hypothesis that hard leaves of Mediterranean woody plants, including representatives of the genus *Quercus*, might be a functional adaptation to cope with the water stress [51,62,192].

It is well known that drought-stressed plants close their stomata to minimize the water loss, and under such conditions, diffusion across the cuticle is the only route of water loss. So, the cuticular water permeability has been used as an indicator of the efficiency of the cuticular transpiration barrier. The genus *Quercus*, presenting both deciduous and evergreen species, is ideal for testing whether sclerophylly can be considered as a functional adaptation to withstand drought at the leaf cuticular level. To address this question, we compiled cuticular water permeability and leaf mass per area (LMA) values in the literature and checked how these traits were related. The cuticular conductance (g_{min}) represents the lowest conductance a leaf can reach when stomata are maximally closed as a consequence of desiccation stress (Körner, 1995). Therefore, it is a proxy for cuticular permeability [187,193,194]. Both g_{min} and p were included in this analysis under the assumption that the influence of leaky stomata is very small or absent [187,193,194] and, therefore, they play the same ecological role. To the best of our knowledge, only seven publications reported concomitantly values of cuticular permeability and LMA of *Quercus* species (Supplementary Table S1). Cuticular permeability given in mmol m^{-2} s^{-1} were converted to m s^{-1} according to Kerstiens (1996), where 0.41 mmol m^{-2} s^{-1} equals 1×10^{-5} m s^{-1}. In total, 21 individual data for permeability and 19 for LMA, including in some cases multiple data for a single plant species, were evaluated. LMA and permeability data ranged from 33.0 g m^{-2} (*Q. petraea*) to 245.7 g m^{-2} (*Q. coccifera*), and in the alternative dimension from 2.1×10^{-5} m s^{-1} (*Q. agrifolia*) to 17.9×10^{-5} m s^{-1} in (*Q. faginea*), respectively. Both plant traits had normal distributed data and, therefore *t*-tests could be used to investigate differences among group of species.

Pairs of LMA and cuticular water permeability were found for eight evergreen and five deciduous species of oaks. In contrast to the common notion, the barrier properties of the leaf cuticle are not correlated to LMA (see in supplementary material figure 3). This agrees with previous studies on xerophytic plant species [195,196]. Therefore, LMA is not a predictor for cuticular transpiration.

Data for eight deciduous and six evergreen oak species were subjected to further analyses. LMA of deciduous oaks (77.4 ± 18.7 g m^{-2}) was over 2-fold lower than that found for evergreen oaks (179 ± 29.3 g m^{-2}; Figure 12A). In contrast to LMA, the cuticular permeability of deciduous oaks ($9.0 \pm 5.0 \times 10^{-5}$ m s^{-1} or 21.93 ± 12.18 mmol m^{-2} s^{-1}; mean ± standard deviation) and evergreen oaks ($8.4 \pm 3.4 \times 10^{-5}$ m s^{-1} or 20.40 ± 8.41 mmol m^{-2} s^{-1}) was very similar. Thus, no statistically significant difference was found between deciduous and evergreen oaks (Figure 12B).

These findings demonstrate that high LMA does not affect the efficacy of the cuticular transpiration barrier and, therefore, does not support the hypothesis that the stiff leaves of *Quercus* would be a functional adaptation to cope with the summer drought through a decrease in cuticular transpiration. It has been widely accepted that waxes mainly make up the plant cuticular barrier against passive water loss [197,198]. However, this relation is not yet well understood. Cuticular waxes are complex mixtures of up to 150 components distributed into compound classes with different properties. Previous studies on several plant species have shown that cuticular permeability neither correlates with the cuticular wax loads nor cuticle thickness [195,196,199,200]. Recently, Bueno et al. (accepted [201]) showed that *Q. coccifera* plants produce different leaf wax loads when grown either under arid or humid conditions, but that the cuticular transpiration barrier properties were not affected by the growing conditions. While the plants under arid conditions had a higher wax load, the relative compositions of the waxes were identical for both habitats.

5. Concluding remarks

Our critical review of the different proposed explanations for sclerophylly indicates that there is ‘no single way to Rome’. The wide variability found for this trait within the genus *Quercus* cannot be explained alone by any of the ecological factors considered (water, nutrients, leaf longevity, herbivory, temperature), neither any of them could be fully discarded. Noteworthy, our study also suggests that these constrains may have a synergistic effect. Hence, habitats combining several ecological limitations are the ones where sclerophylly is more prevalent, as exemplified by the case of Mediterranean evergreens (see Figure 13). Mediterranean habitats are unique in combining summer drought and a relatively cold winter, splitting the growing season in two isolated periods (spring and autumn). This has generally promoted leaf longevity, as a mechanism to take advantage of spring and autumn optimal conditions. As discussed above, these long-living leaves must be also hard enough to overcome accumulated (both abiotic and biotic) stressors. We could also identify a substantial knowledge gap regarding oak species in tropical biomes, despite being a major biodiversity hotspot for the genus. The few studies available so far suggest that evergreen oaks in tropical dry highlands may show converging physiological adaptations with Mediterranean oaks, a point that deserves further assessment. From a functional point of view, we can conclude that in oaks leaf habit largely modulates the physiological implications of sclerophylly. We have highlighted that, among evergreens, sclerophylly has a cost not only in terms of carbon investment, but also limits carbon uptake capacity, mainly through diffusional limitations. Conversely, the increase in LMA among deciduous oaks is associated with larger photosynthetic capacity, reflecting the strategy of Mediterranean deciduous oaks to maximize carbon gain during optimal periods, as an adaptation to the splitting of the growing season.

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Fig. 1 Measurements of mechanical strength (force to punch, force to tear, work to shear) and leaf attributes (leaf mass per area (LMA), leaf thickness and leaf density) in deciduous (DEC) and evergreen (EVE) oak species, as compared with species from other genera. Data from the Leaf Biomechanics Dataset [10]

Fig. 2 Relation between Lang aridity index (AILang) and leaf mass area (LMA) for oak species belonged to different groups. AILang calculated as the ratio between mean annual precipitation (MAP) and mean annual temperature (MAT). DEC: deciduous, EVE: evergreen, TEM: temperate, MED: mediterranean, TRO: tropical, ARID: arid. Data as mean ± se values of 73 oak species obtained from Gil-Pelegrín et al.[43]. Letters indicate significant differences (Tukey test, $p<0.05$) in AILang between groups of species

Fig. 3 Relationship between Lang aridity index (AILang) and the stem water potential inducing a loss of 50% (P50) and 88% (P88) of xylem hydraulic conductivity for oak species belonged to different groups. AILang calculated as the ratio between mean annual precipitation (MAP) and mean annual temperature (MAT). Group abbreviations as in Figure 2. Data as mean ±se. ** means a p-value < 0.01. P50 and P88 values obtained from literature (see Supplementary. MAP and MAT obtained from WorldCLim data base according to Gil-Pelegrín et al 2017 [43]. Mean group values ±se of these parameters are plotted in the upper right side of each figure. Letters indicate statistically significant differences (Tukey test, $P < 0.05$) in the mean values of P50 and P88

Fig. 4 Association between typical leaf mass per area (LMA) and average site conditions across 36 oak species found in the US Forest Inventory (see Supplementary Material). Species were classified according to their most typical biome and leaf habit, following [50]. Circles, diamonds and hexagons stand for temperate, Mediterranean and arid biomes. Light and dark colors denote deciduous and evergreen species, respectively. ELEV, elevation; SWC, soil water content. Soil characteristics in this figure refer to the forest floor, except Olsen-P and pH, which correspond to soil horizons

Fig. 5 Relationship between leaf lifespan (LL) and leaf mass per area (LMA) for species of Genus *Quercus*. Black continuous line is the correlation ($r^2=0.47$, $p<0.001$) with all species. Dash line represents the correlation ($r^2=0.39$, $p<0.001$) for temperate deciduous species. Data from literature [6,123,136,144,202,203] and personal measurements

Fig. 6 Relationship between leaf mass per area (LMA) and cellulose content (CC), hemicellulose content (HC) and cutin and lignin content (LCC) for Mediterranean evergreen and deciduous *Quercus* species. Data obtained from [136]

Fig. 7 Relationship between mean annual temperature (MAT) and length of the cold season, measured as the number of months with mean monthly temperature (Tm) below 5ºC. Each circle represents a different oak species. Data are mean values of at least 40 locations within the distribution range of each species. Geographical distribution coordinates and climatic characteristics for each oak species were obtained from herbarium data and WorldClimV2.0 database, respectively, following the methodology described in [50]. *** means a p-value < 0.001

Fig. 8 Relationships between leaf dry mass per unit area (LMA) and i/ photosynthetic capacity per leaf dry mass (A_{mass}) (upper left panel), ii/ photosynthetic capacity per leaf area (A_{area}) (down left panel), iii/ nitrogen content per dry mass (N_{mass}) (upper right panel), and iv/ nitrogen content per leaf area (N_{area}) (lower right panel) for different *Quercus* species. Data obtained from literature (see Supplementary Material). Symbols as in Figure 2

Fig. 9 Relationships between leaf dry mass per unit area (LMA) and i/ nitrogen content per dry mass (N_{mass}) (upper panel), and ii/ nitrogen content per leaf area (N_{area}) (down panel) for 41 tree species in a montane forest of Costa Rica obtained from the dataset published by Kappelle and Leal [168]

Fig. 10 Relationships between photosynthetic capacity per leaf area (A_{area}) and i/ stomatal conductance (g_s) (left panel), and ii/ nitrogen content per leaf area (N_{area}) (right panel) for different *Quercus* species. Data obtained from literature (see Supplementary Material). Symbols as in Figure Figure 2

Fig. 11 Relationship between leaf dry mass per unit area (LMA) and the maximum bulk modulus of elasticity ($\mathcal{E}_{max}$) for different *Quercus* species. Symbols as in Figure Figure 2

Fig. 12 Leaf mass per area (LMA) (A; 19 data points) and cuticular permeances or minimum conductances (A; 21 data points) of 14 *Quercus* species collected from the literature (Supplementary Table S1). Data represent eight deciduous oak species (DEC, 11 and 12 data points for LMA and permeability, respectively) and six evergreen oak species (EVE, 8 and 9 data points). The boxes stand for the lower (Q1) and upper (Q3) quartiles. The solid lines represent the median, whereas dashed lines represent the mean. The whiskers stand for the smallest and largest values that are not more than 1.5 interquartile ranges away from the box. The potential outliers falling outside the Q1 – Q3 range are represented by dots. The asterisk indicates a significant difference of LMA between DEC and EVE oaks (*t*-test, $P < 0.05$)

Fig. 13 A summary of the key factors promoting sclerophylly (circles) and the transverse section of the mesophyll leaf of Quercus robur, Q. faginea, and Q. ilex subsp. rotundifolia ranked from less to more sclerophyllous. Mesophyll bright areas mainly coincide with thick cell walls in epidermal structures, vascular bundles and bundle sheath extensions. Scale bar 100 μm. A high factors' circle size indicates a high influence of the factor on the specie

Table 1. A list of leaf mechanical properties and their units

	Fracture properties			Elastic properties	
Type of tests	**Structural level**	**Material level**	**Mass level**	**Structural level**	**Material level**
Shearing test	Work to shear (J m^{-1})	Fracture toughness (J m^{-2})	Specific toughness (J m Kg^{-1})	NA	Shear modulus
Punch test	Force to punch (N m^{-1})	Punch strength (N m^{-2})	Specific punch strength (N m Kg^{-1})	NA	NA
Tensile test	Force to tear (N m^{-1})	Tensile strength (N m^{-2})	Specific tensile strength (N m Kg^{-1})	Tensile stiffness (N)	Young's modulus (N m^{-2})
Bending test	NA	NA	NA	Bending stiffness (N m^{2})	Young's modulus (N m^{-2})

Fig. 1

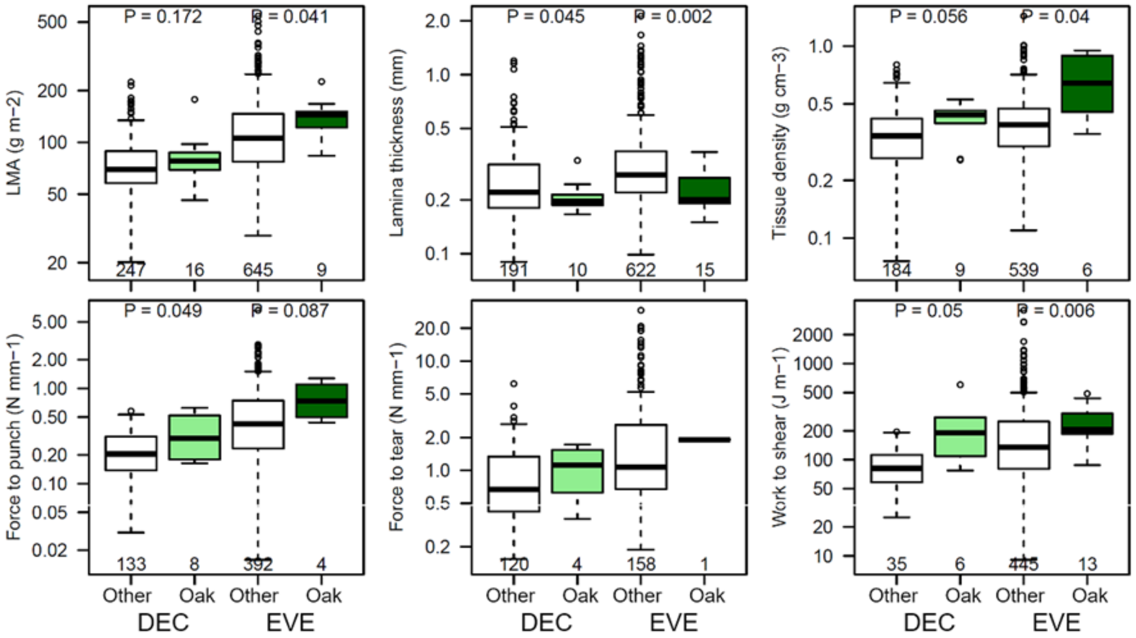

P = 0.172
P = 0.041
LMA (g m−2)
500
200
100
50
20
247
16
645
9
P = 0.045
P = 0.002
Lamina thickness (mm)
2.0
1.0
0.5
0.2
0.1
191
10
622
15
P = 0.056
P = 0.04
Tissue density (g cm−3)
1.0
0.5
0.2
0.1
184
9
539
6
P = 0.049
P = 0.087
Force to punch (N mm−1)
5.00
2.00
1.00
0.50
0.20
0.10
0.05
0.02
133
8
392
4
P = 0.045
Force to tear (N mm−1)
20.0
10.0
5.0
2.0
1.0
0.5
0.2
120
4
158
1
P = 0.05
P = 0.006
Work to shear (J m−1)
2000
1000
500
200
100
50
20
10
35
6
445
13
Other
Oak
Other
Oak
DEC
EVE

Fig. 2

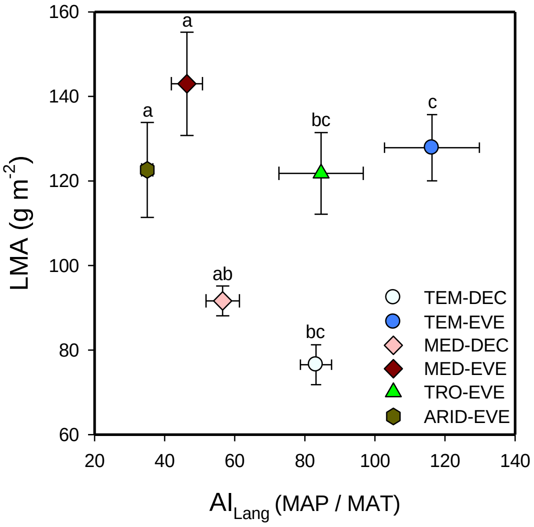

LMA (g m^{-2})
160
140
120
100
80
60
20
40
60
80
100
120
140
AI$_{Lang}$ (MAP / MAT)
a
a
bc
c
ab
bc
○ TEM-DEC
● TEM-EVE
◇ MED-DEC
◆ MED-EVE
▲ TRO-EVE
⬢ ARID-EVE

Fig. 3

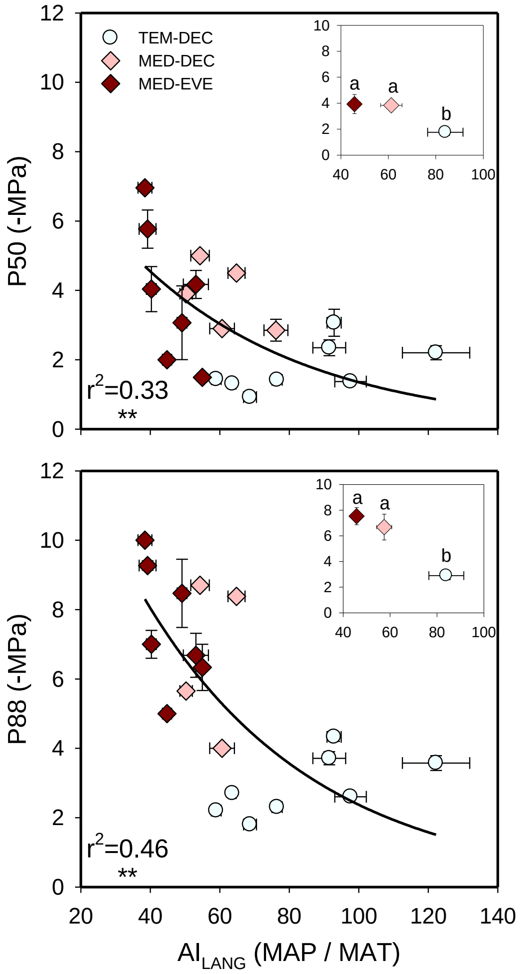

TEM-DEC
MED-DEC
MED-EVE
P50 (-MPa)
r^2=0.33
**
a
a
b
P88 (-MPa)
r^2=0.46
**
a
a
b
0
2
4
6
8
10
12
20
40
60
80
100
120
140
AI$_{LANG}$ (MAP / MAT)

Fig. 4

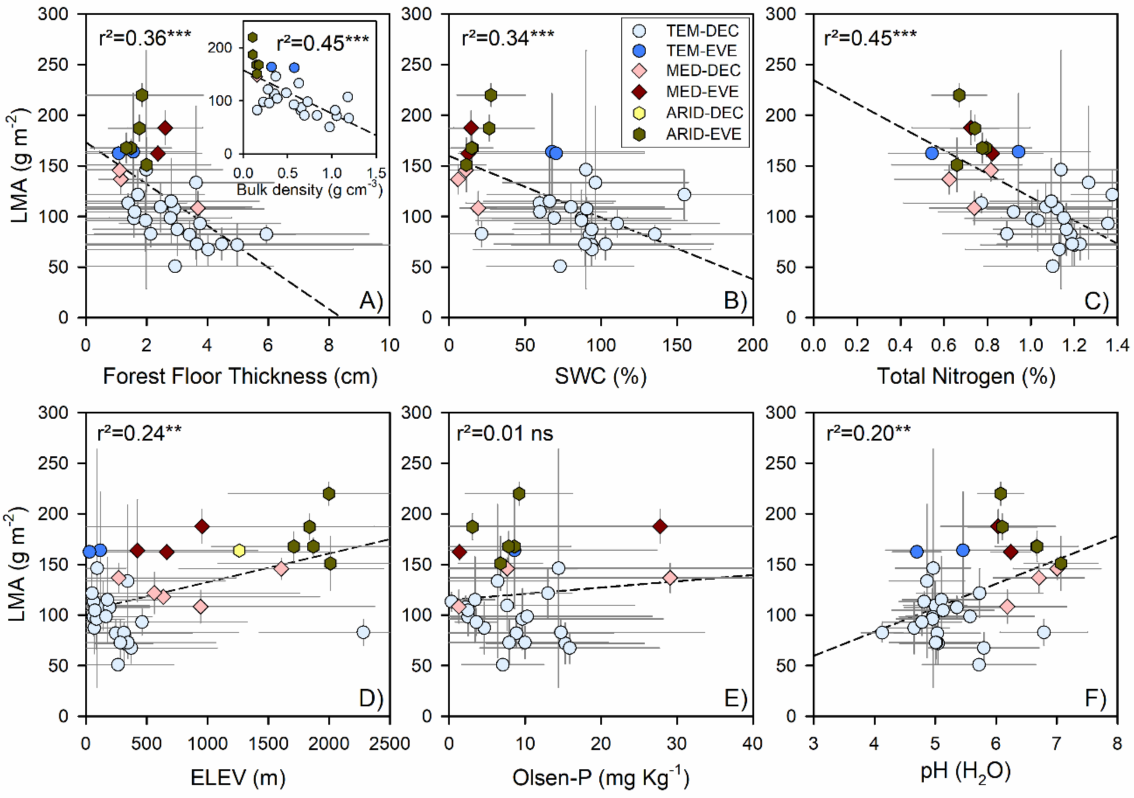

r²=0.36***
r²=0.45***
Bulk density (g cm⁻³)
A)
LMA (g m⁻²)
Forest Floor Thickness (cm)
r²=0.34***
B)
SWC (%)
TEM-DEC
TEM-EVE
MED-DEC
MED-EVE
ARID-DEC
ARID-EVE
r²=0.45***
C)
Total Nitrogen (%)
r²=0.24**
D)
ELEV (m)
r²=0.01 ns
E)
Olsen-P (mg Kg⁻¹)
r²=0.20**
F)
pH (H₂O)

Fig. 5

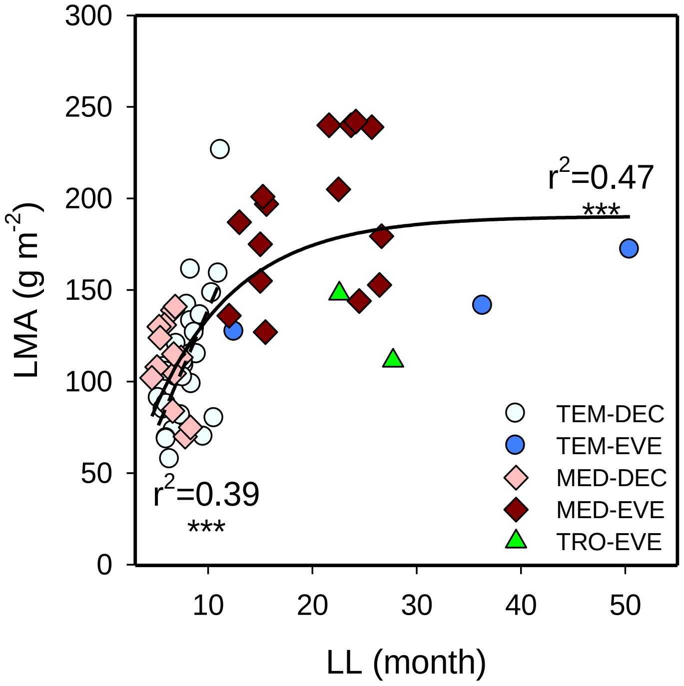

LMA (g m^{-2})
300
250
200
150
100
50
0
LL (month)
10
20
30
40
50
r^2=0.47
***
r^2=0.39
***
TEM-DEC
TEM-EVE
MED-DEC
MED-EVE
TRO-EVE

Fig. 6

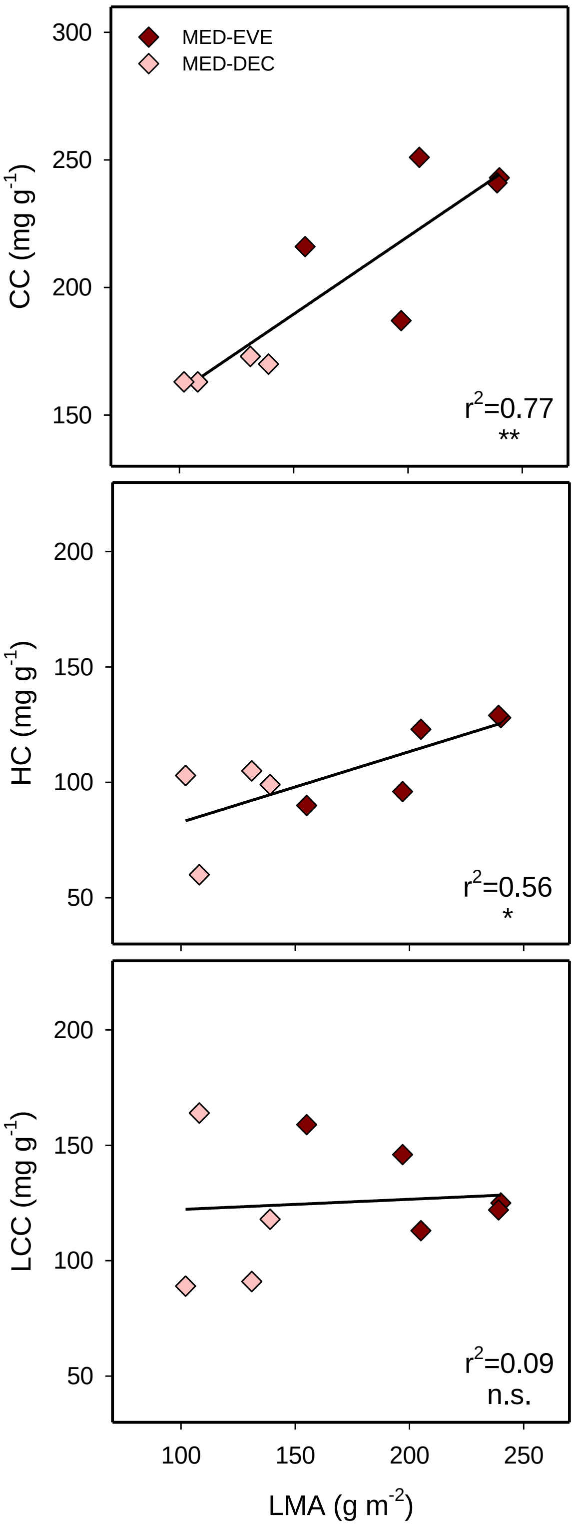
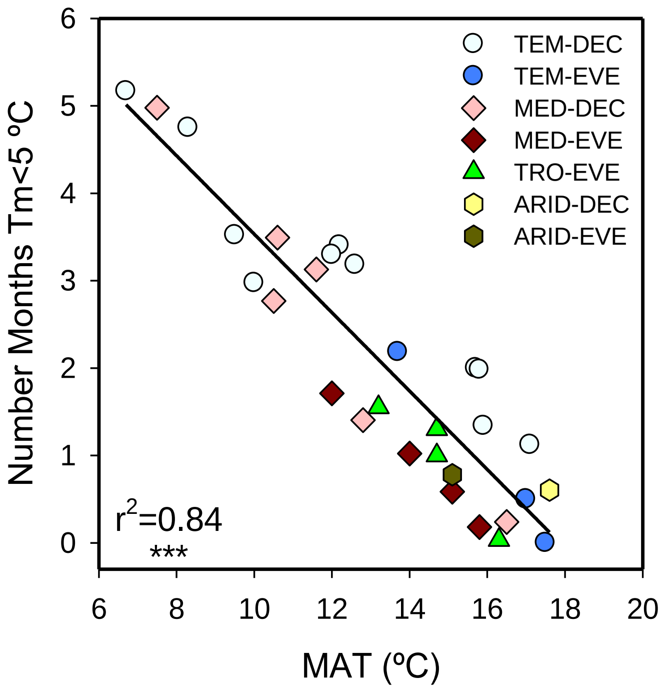

MED-EVE
MED-DEC
CC (mg g^{-1})
300
250
200
150
r^2=0.77
**
HC (mg g^{-1})
200
150
100
50
r^2=0.56
*
LCC (mg g^{-1})
200
150
100
50
r^2=0.09
n.s.
100
150
200
250
LMA (g m^{-2})

Fig. 7



Number Months Tm<5 ºC
MAT (ºC)
0
1
2
3
4
5
6
6
8
10
12
14
16
18
20
TEM-DEC
TEM-EVE
MED-DEC
MED-EVE
TRO-EVE
ARID-DEC
ARID-EVE
r2=0.84
***

Fig. 8

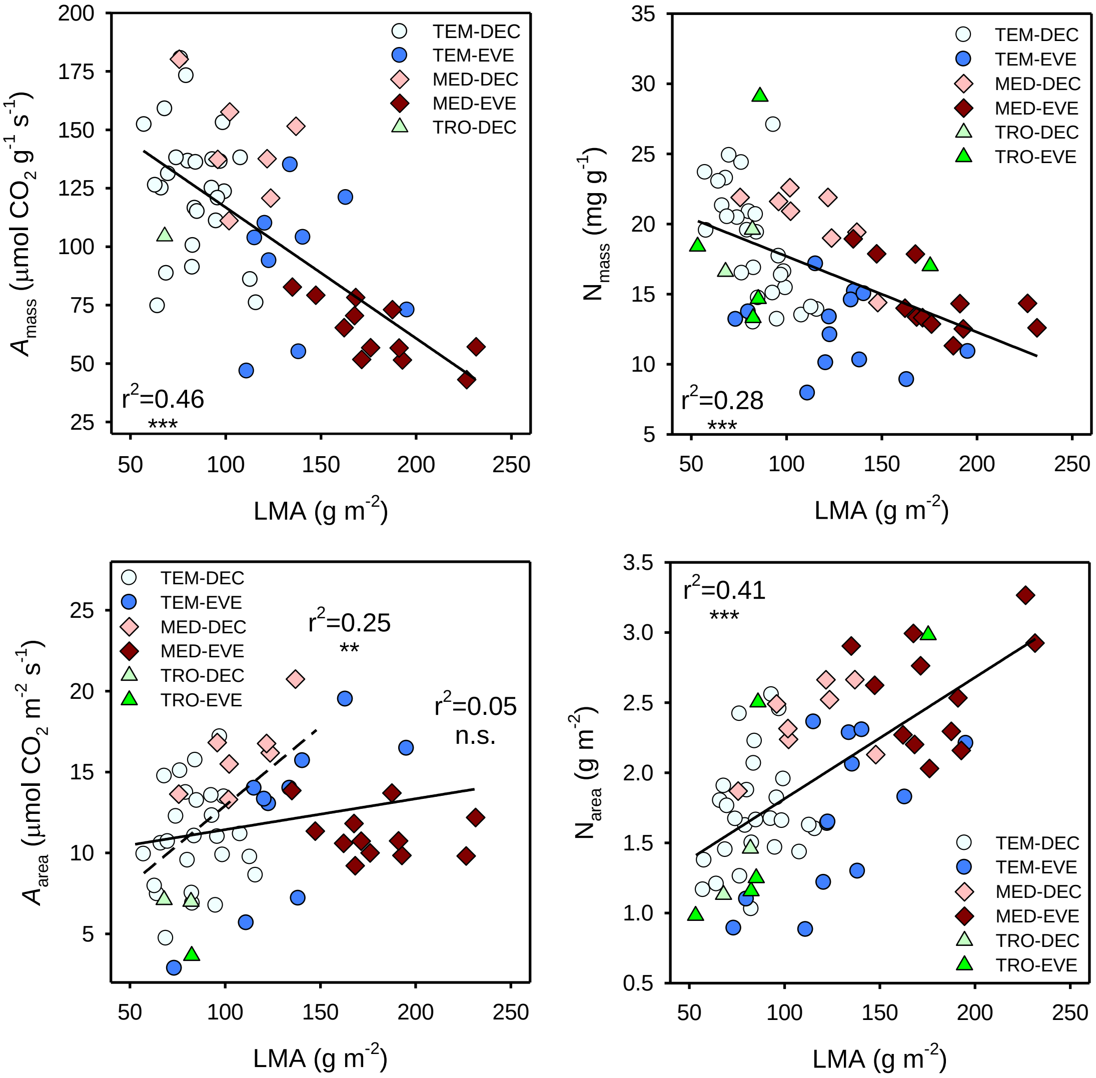

A_mass (µmol CO2 g-1 s-1)
200
175
150
125
100
75
50
25
r2=0.46
***
TEM-DEC
TEM-EVE
MED-DEC
MED-EVE
TRO-DEC
50
100
150
200
250
LMA (g m-2)
N_mass (mg g-1)
35
30
25
20
15
10
5
r2=0.28
***
TEM-DEC
TEM-EVE
MED-DEC
MED-EVE
TRO-DEC
TRO-EVE
LMA (g m-2)
A_area (µmol CO2 m-2 s-1)
25
20
15
10
5
TEM-DEC
TEM-EVE
MED-DEC
MED-EVE
TRO-DEC
TRO-EVE
r2=0.25
**
r2=0.05
n.s.
LMA (g m-2)
N_area (g m-2)
3.5
3.0
2.5
2.0
1.5
1.0
0.5
r2=0.41
***
TEM-DEC
TEM-EVE
MED-DEC
MED-EVE
TRO-DEC
TRO-EVE
LMA (g m-2)

Fig. 9

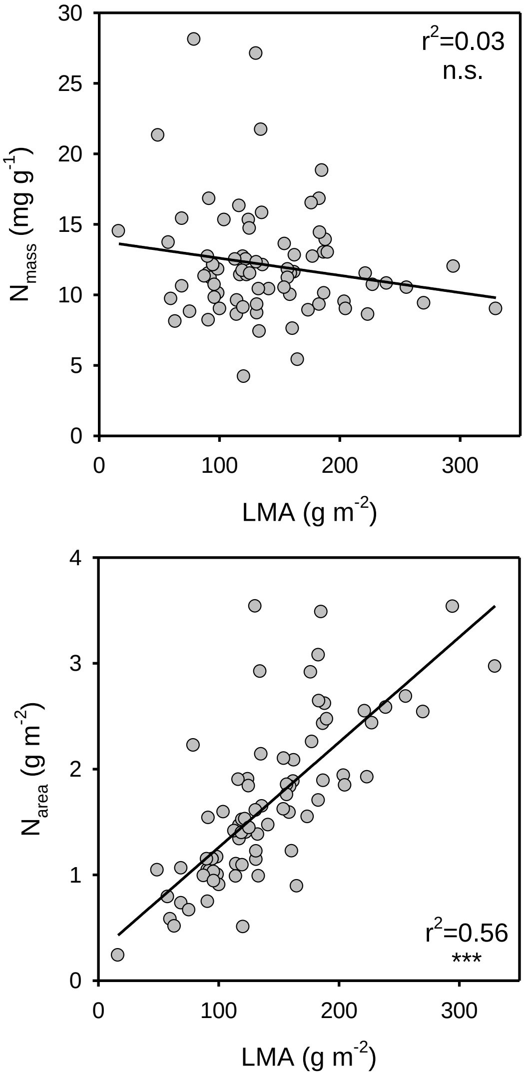

30
25
20
15
10
5
0
N_{mass} (mg g^{-1})
r^2=0.03
n.s.
0
100
200
300
LMA (g m^{-2})
4
3
2
1
0
N_{area} (g m^{-2})
r^2=0.56
***
0
100
200
300
LMA (g m^{-2})

Fig. 10

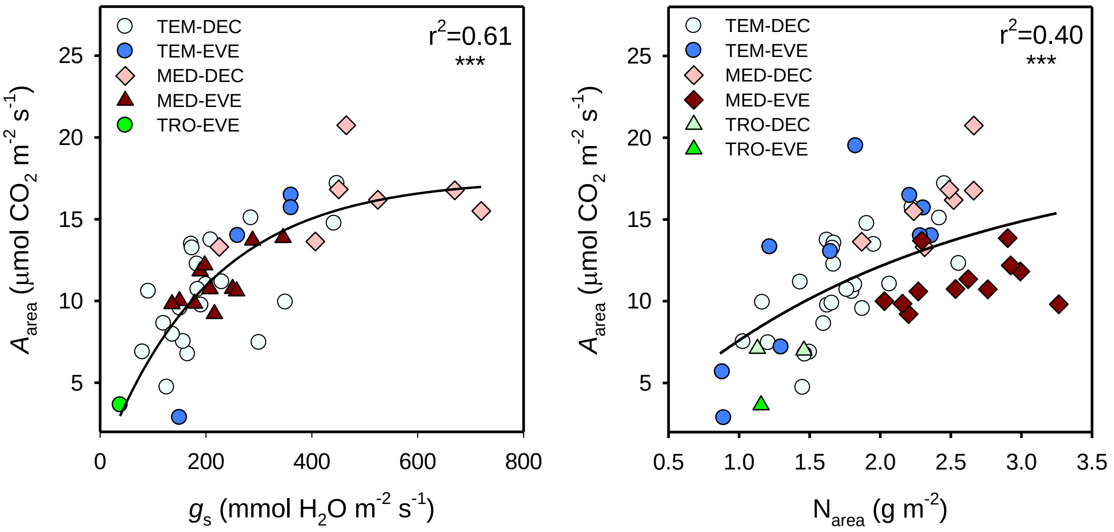

TEM-DEC
TEM-EVE
MED-DEC
MED-EVE
TRO-EVE
r²=0.61
***
25
20
15
10
5
0
200
400
600
800
A_area (µmol CO₂ m⁻² s⁻¹)
g_s (mmol H₂O m⁻² s⁻¹)
TEM-DEC
TEM-EVE
MED-DEC
MED-EVE
TRO-DEC
TRO-EVE
r²=0.40
***
0.5
1.0
1.5
2.0
2.5
3.0
3.5
N_area (g m⁻²)

Fig. 11

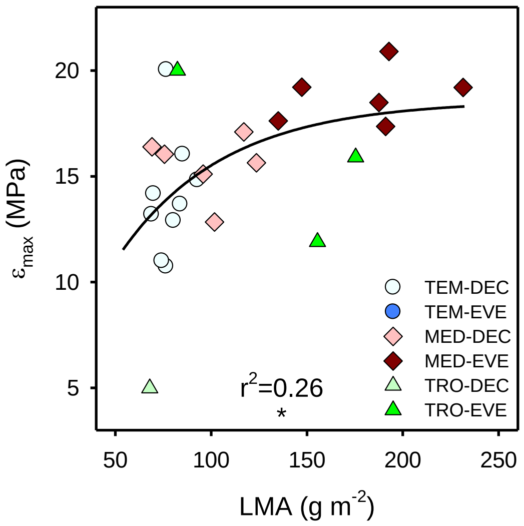
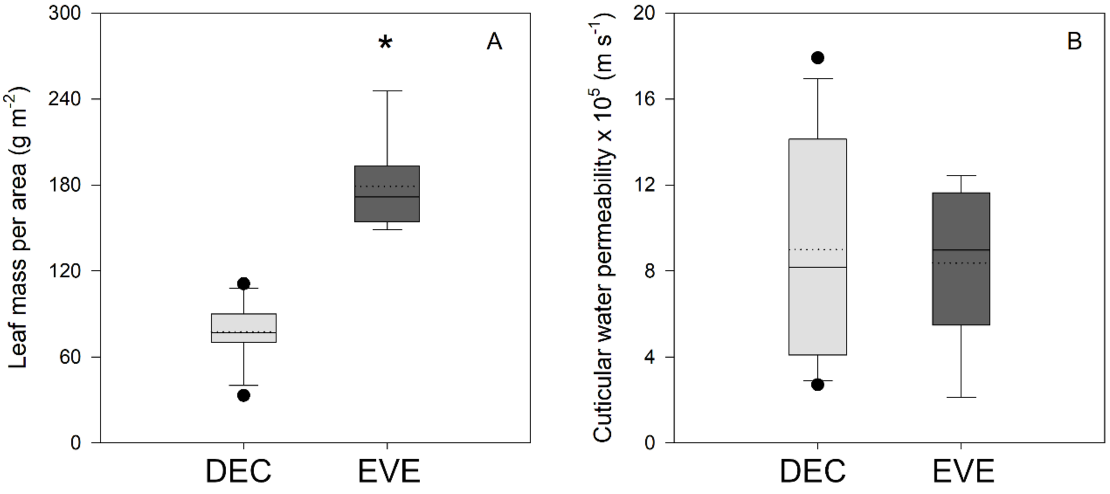
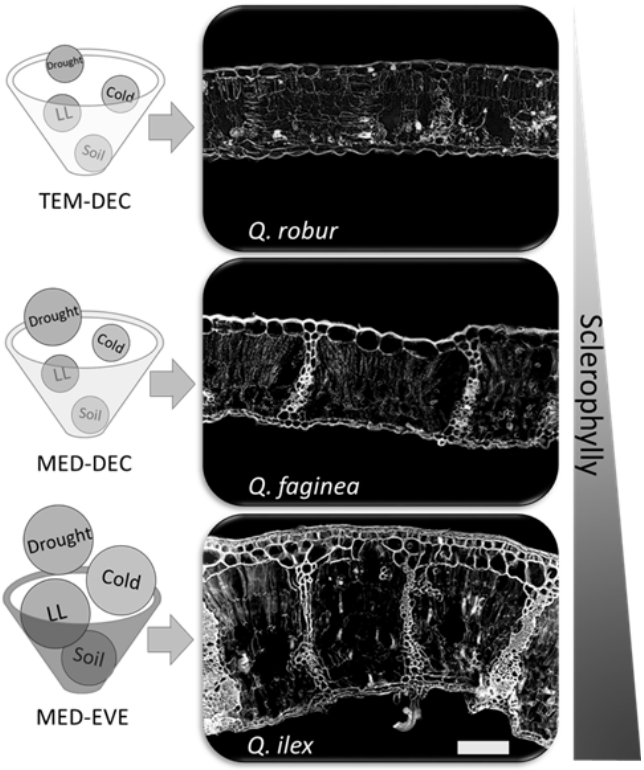

20
15
10
5
ε_max (MPa)
50
100
150
200
250
LMA (g m^-2)
r²=0.26
*
○ TEM-DEC
● TEM-EVE
◇ MED-DEC
◆ MED-EVE
△ TRO-DEC
▲ TRO-EVE

Fig. 12



Leaf mass per area (g m-2)
300
240
180
120
60
0
*
A
DEC
EVE
Cuticular water permeability x 105 (m s-1)
20
16
12
8
4
0
B
DEC
EVE

Fig. 13


Drought
Cold
LL
Soil
TEM-DEC
Q. robur
Drought
Cold
LL
Soil
MED-DEC
Q. faginea
Drought
Cold
LL
Soil
MED-EVE
Q. ilex
Sclerophylly

```
Your image file "Fig1.tif" cannot be opened and processed.  Please see
the common list of problems, and suggested resolutions below.

Reason:  The image file is corrupt or invalid.  Please check and
resubmit.

Other Common Problems When Creating a PDF from an image file
-----------------------------------------------------------------

You will need to convert your image file to another format or fix the
current image, then re-submit it.
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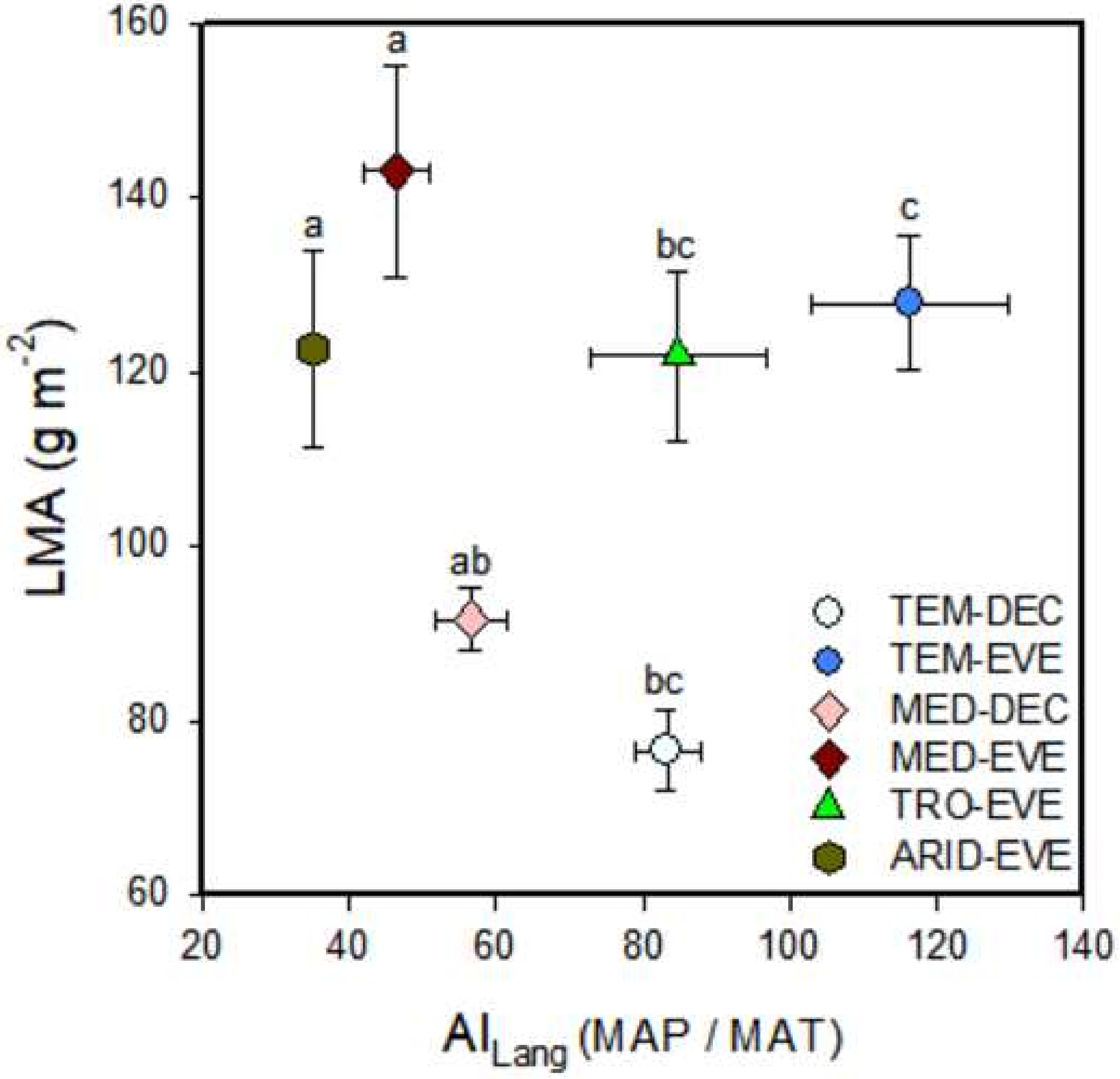
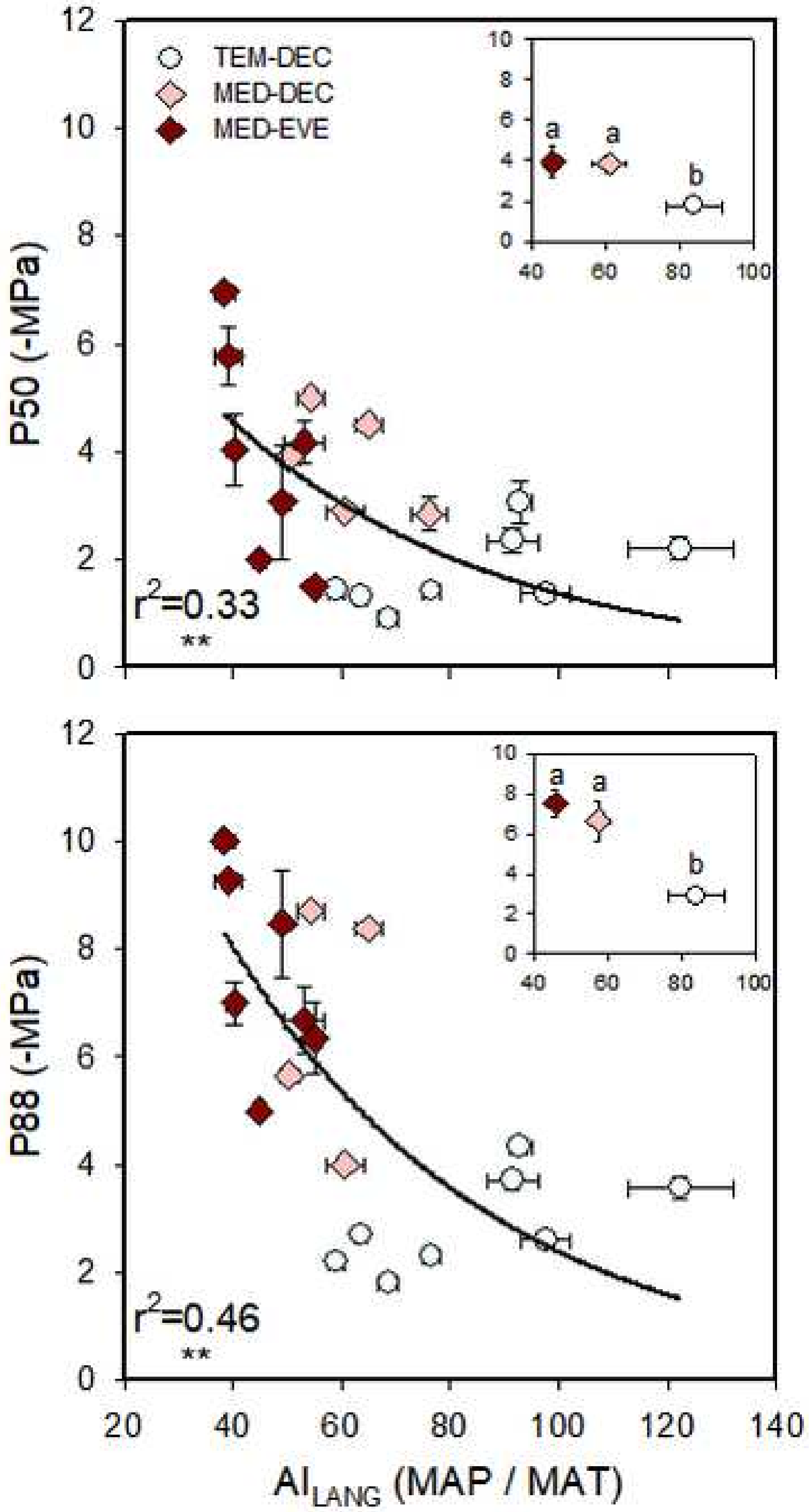
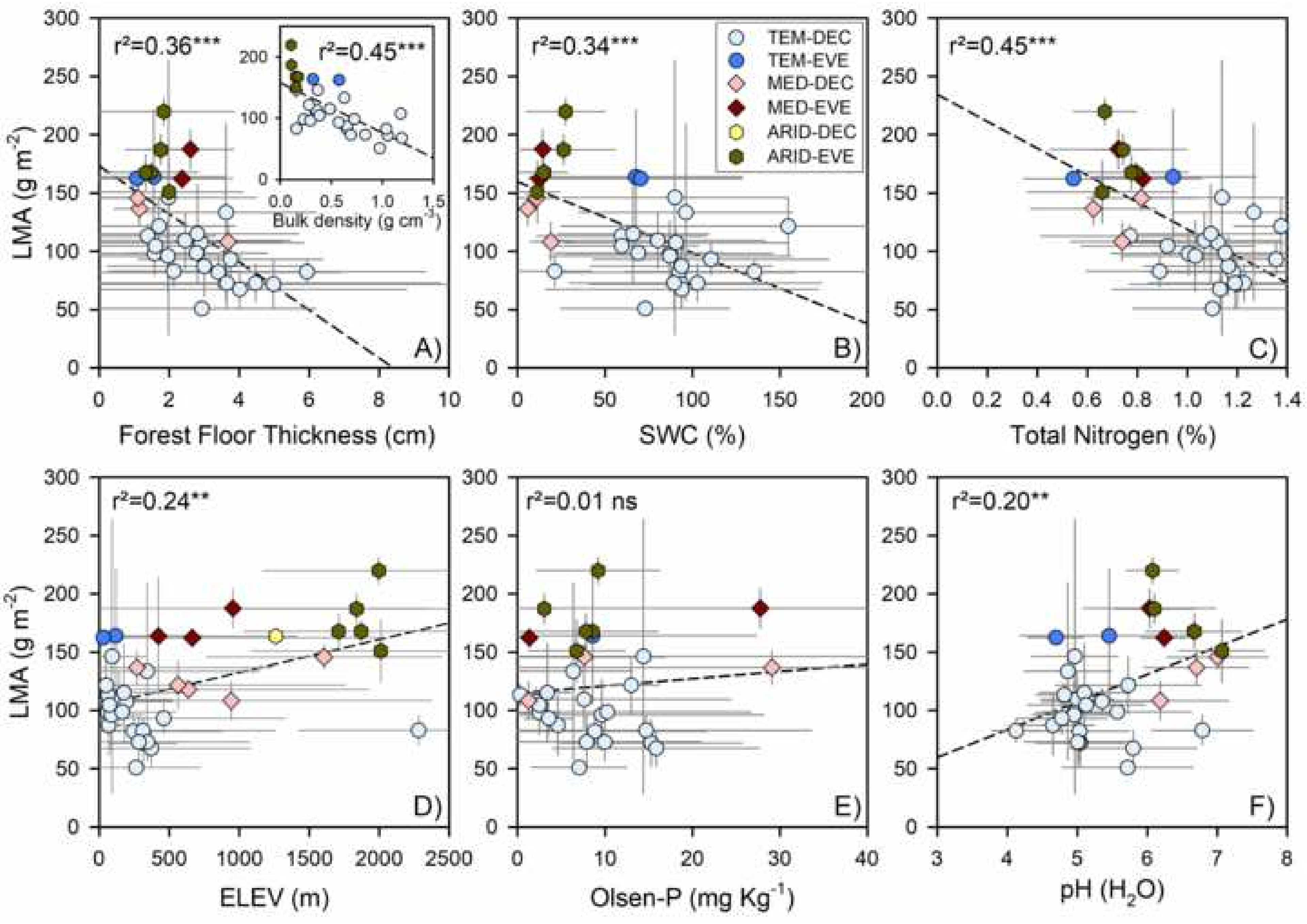
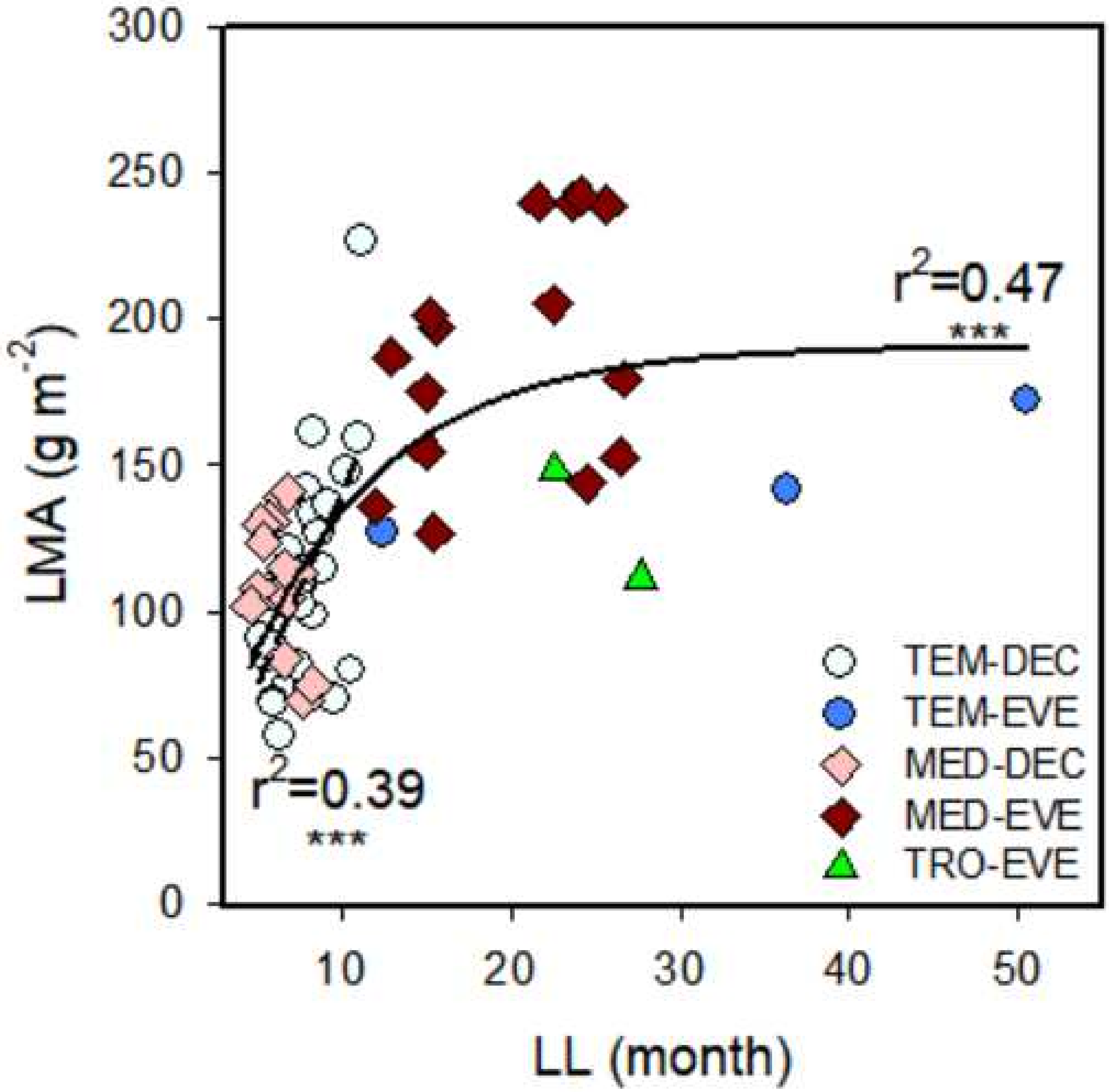

LMA (g m^{-2})
160
140
120
100
80
60
20
40
60
80
100
120
140
AI$_{Lang}$ (MAP / MAT)
a
a
bc
c
ab
bc
○ TEM-DEC
● TEM-EVE
◇ MED-DEC
◆ MED-EVE
▲ TRO-EVE
⬢ ARID-EVE

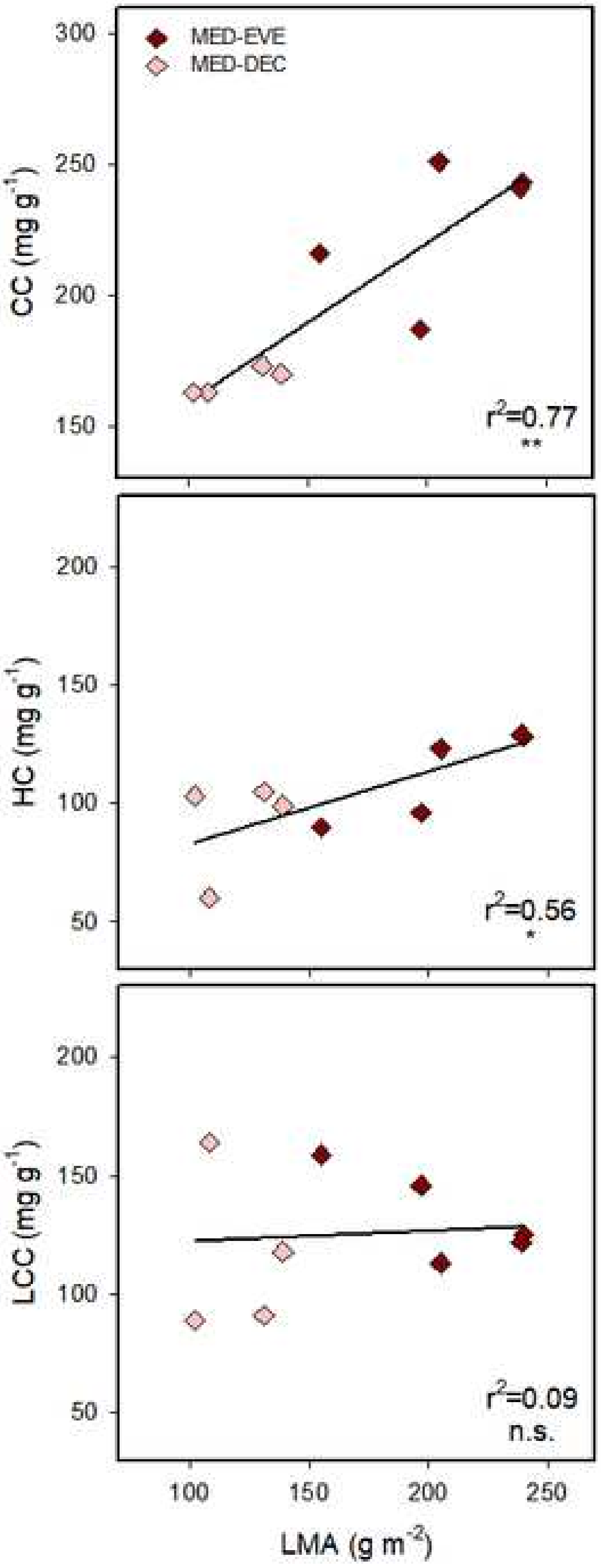

P50 (-MPa)
12
10
8
6
4
2
0
○ TEM-DEC
◇ MED-DEC
◆ MED-EVE
r²=0.33
**
10
8
6
4
2
0
40
60
80
100
a
a
b
P88 (-MPa)
r²=0.46
**
a
a
b
20
40
60
80
100
120
140
AI_LANG (MAP / MAT)

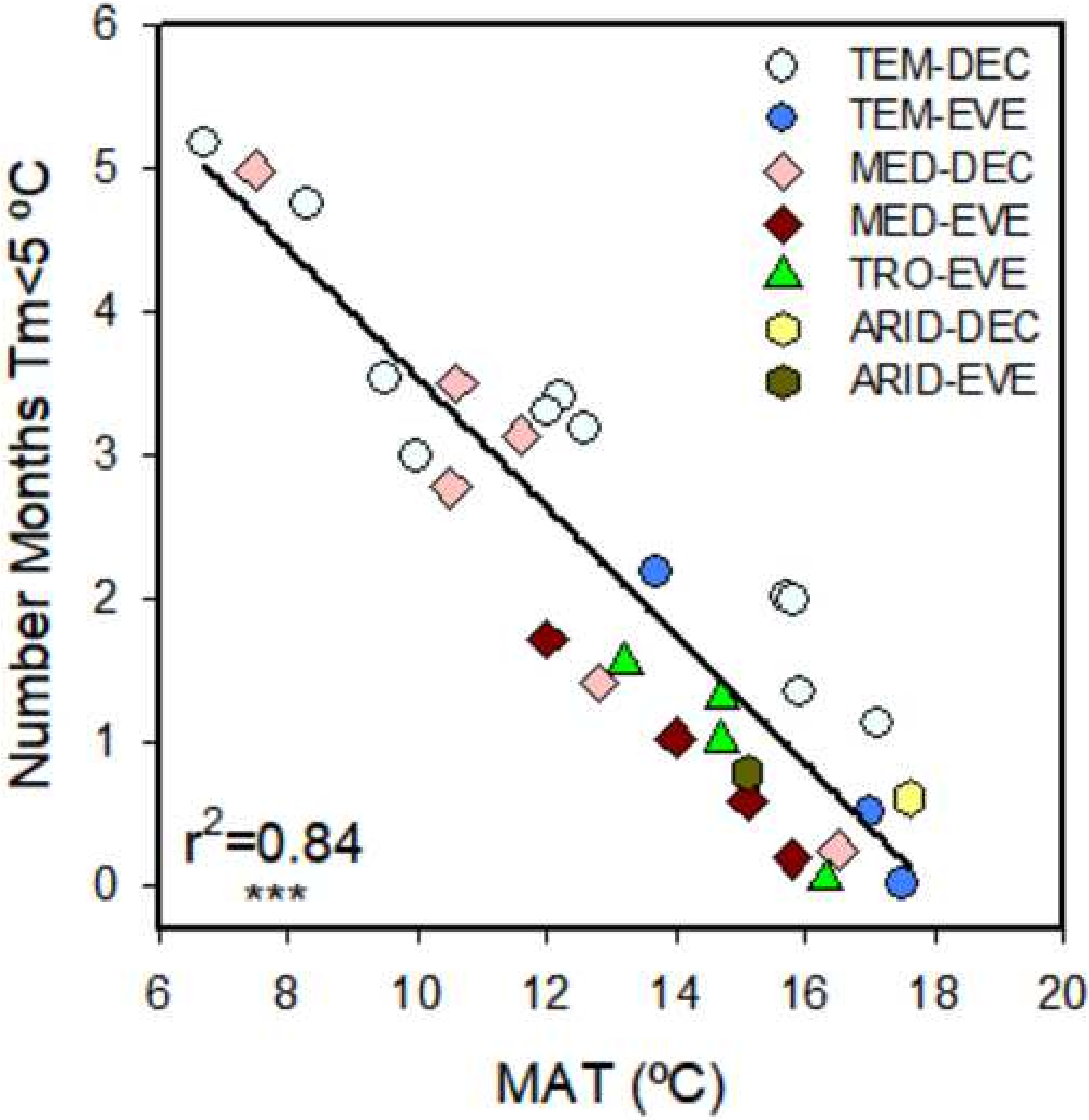


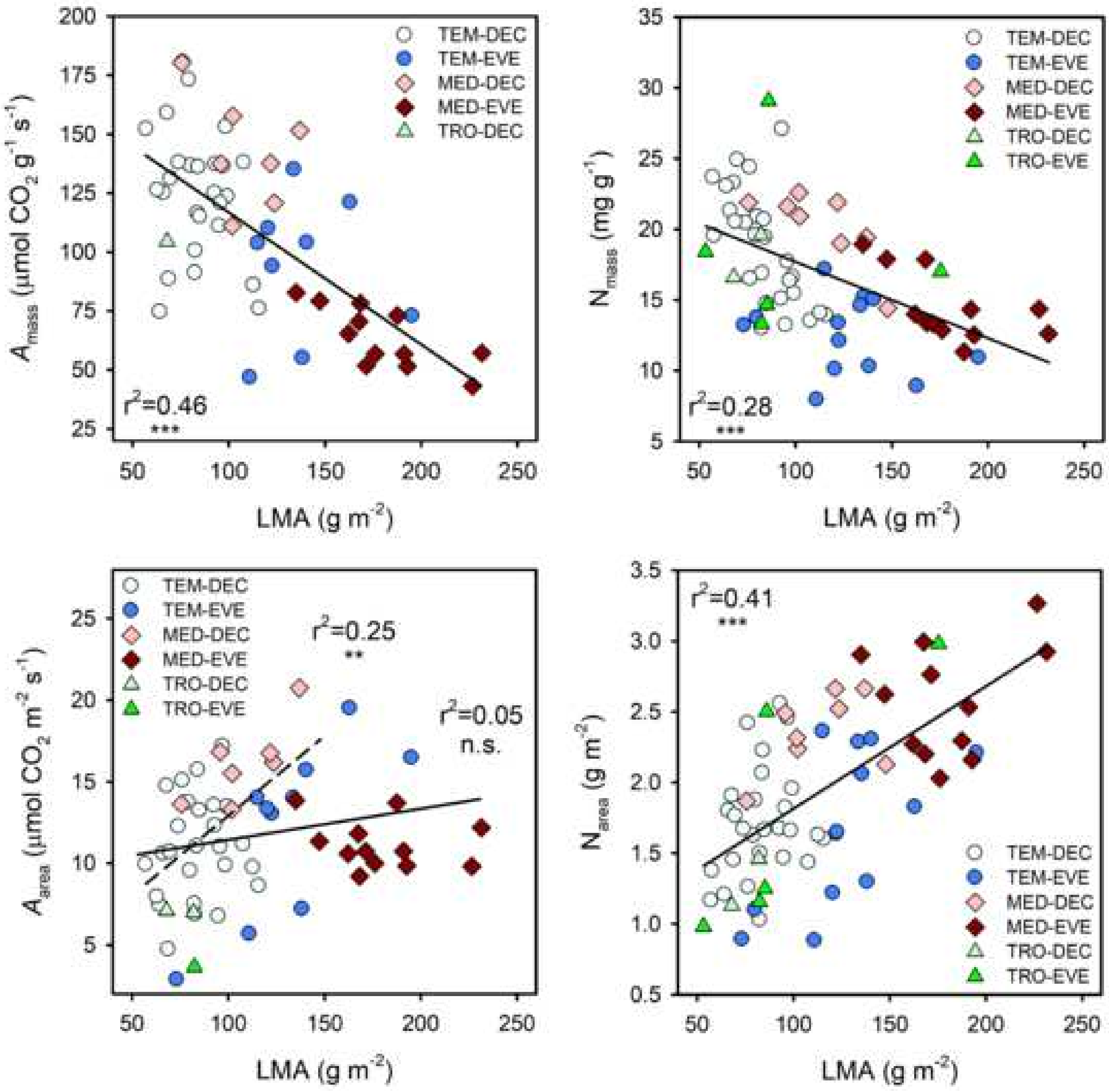
LMA (g m-2)
300
250
200
150
100
50
0
r²=0.36***
r²=0.45***
200
100
0
0.0 0.5 1.0 1.5
Bulk density (g cm-3)
A)
0 2 4 6 8 10
Forest Floor Thickness (cm)
r²=0.34***
TEM-DEC
TEM-EVE
MED-DEC
MED-EVE
ARID-DEC
ARID-EVE
B)
0 50 100 150 200
SWC (%)
r²=0.45***
C)
0.0 0.2 0.4 0.6 0.8 1.0 1.2 1.4
Total Nitrogen (%)
r²=0.24**
D)
0 500 1000 1500 2000 2500
ELEV (m)
r²=0.01 ns
E)
0 10 20 30 40
Olsen-P (mg Kg-1)
r²=0.20**
F)
3 4 5 6 7 8
pH (H2O)

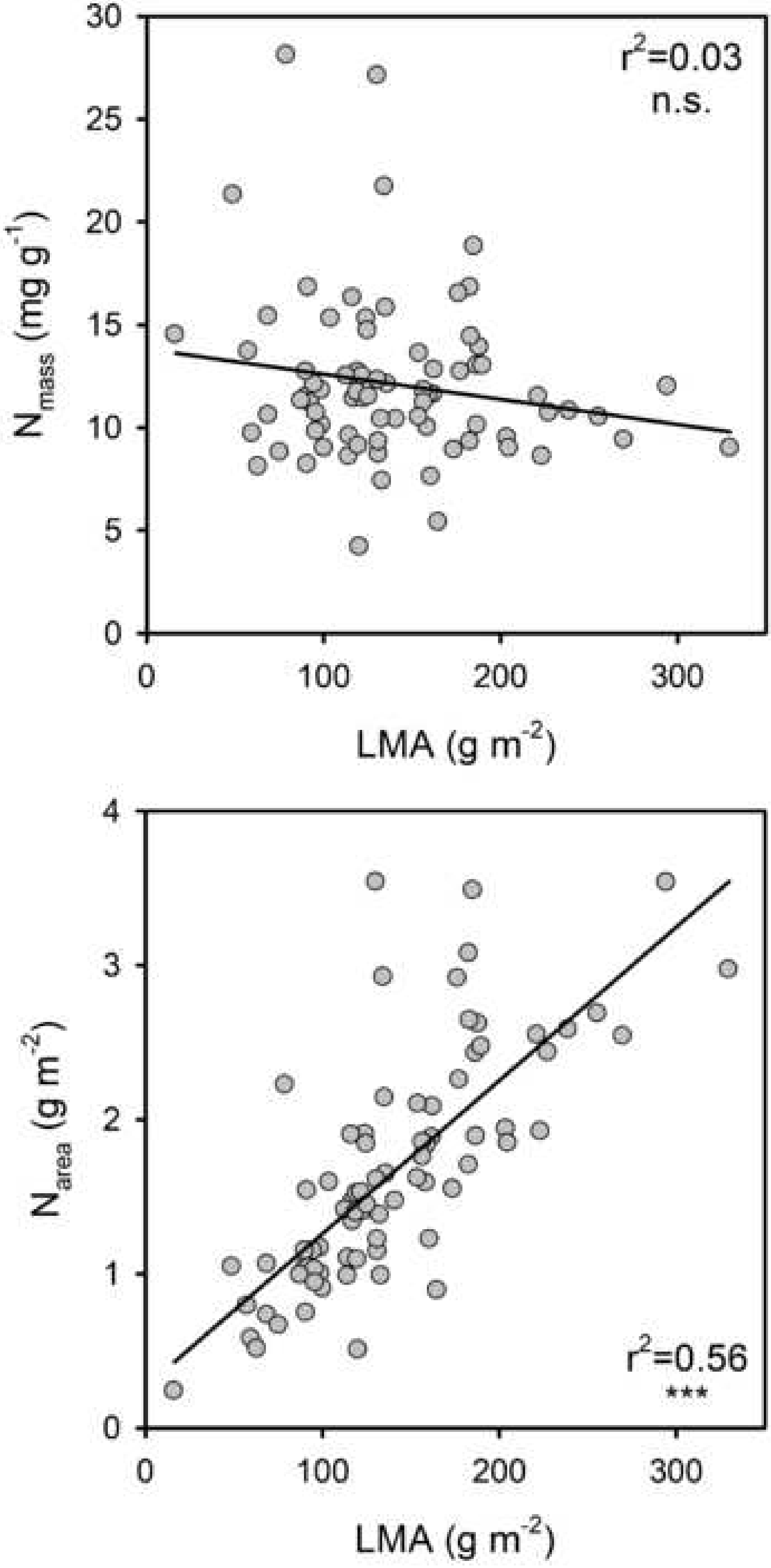

300
250
200
150
100
50
0
LMA (g m^{-2})
10
20
30
40
50
LL (month)
r^2=0.47
***
r^2=0.39
***
○ TEM-DEC
● TEM-EVE
◇ MED-DEC
◆ MED-EVE
▲ TRO-EVE

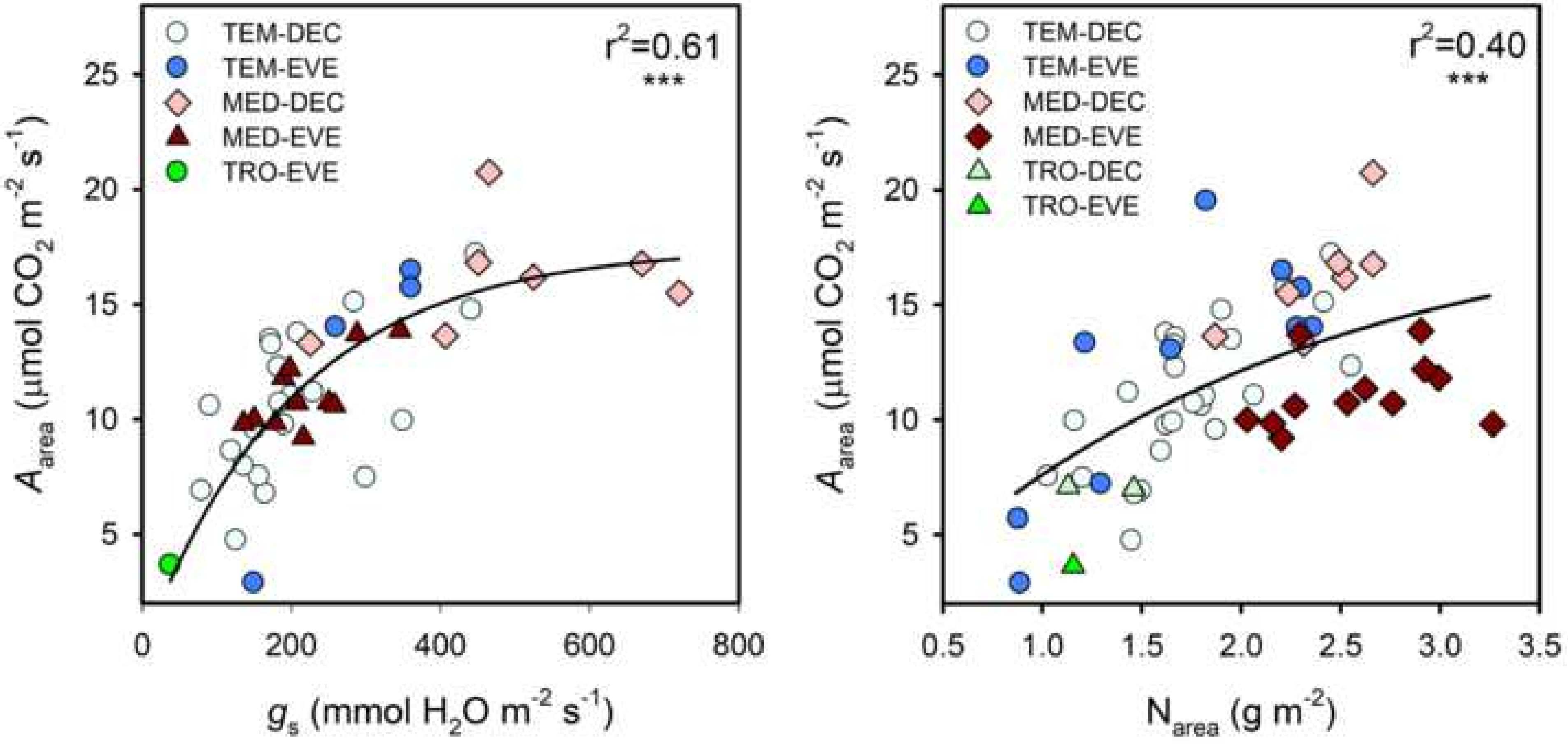
Click here to access/download;Figure;Fig6.tif

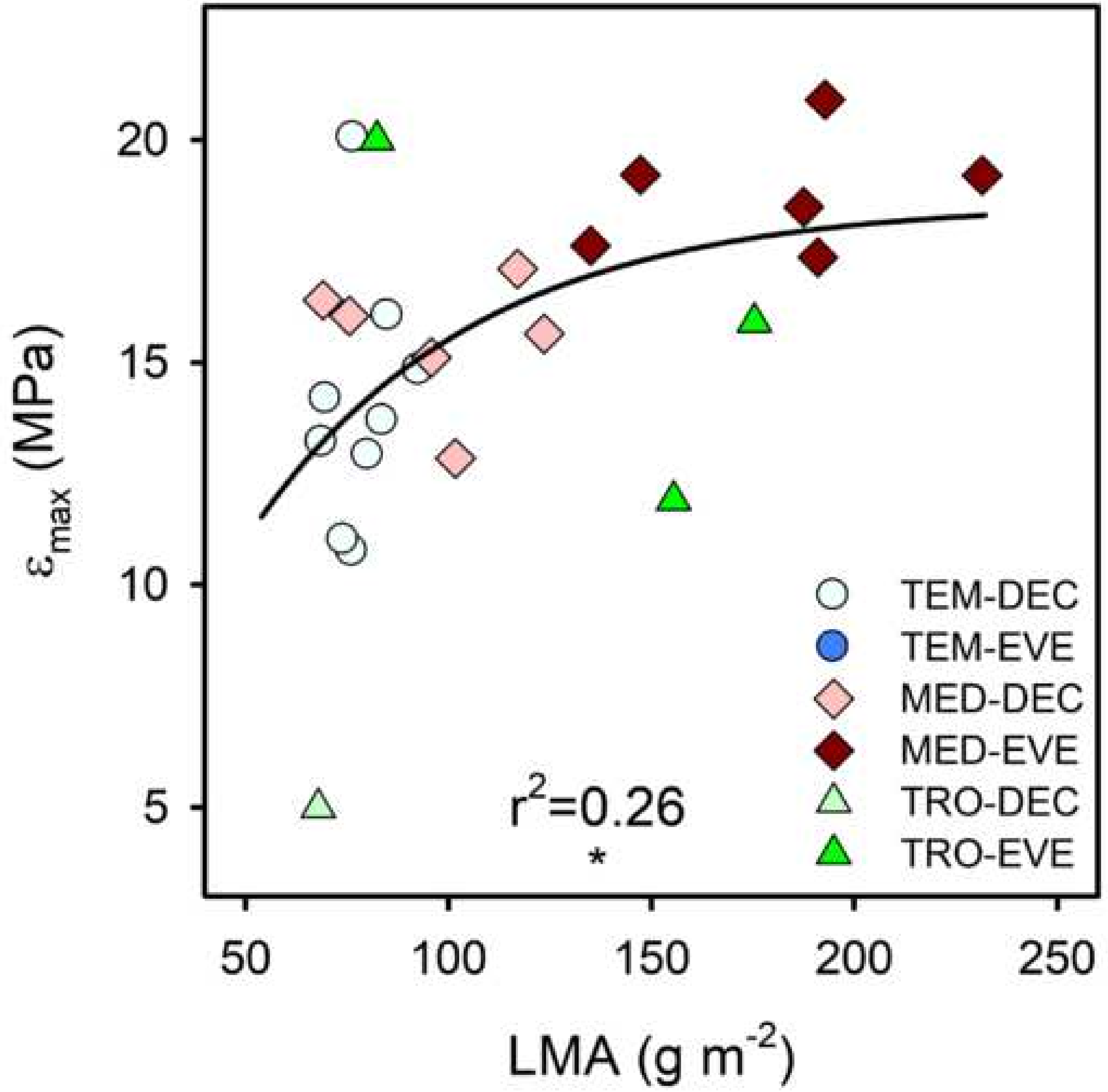



Number Months Tm<5 °C
6
5
4
3
2
1
0
6
8
10
12
14
16
18
20
MAT (ºC)
TEM-DEC
TEM-EVE
MED-DEC
MED-EVE
TRO-EVE
ARID-DEC
ARID-EVE
r²=0.84
***

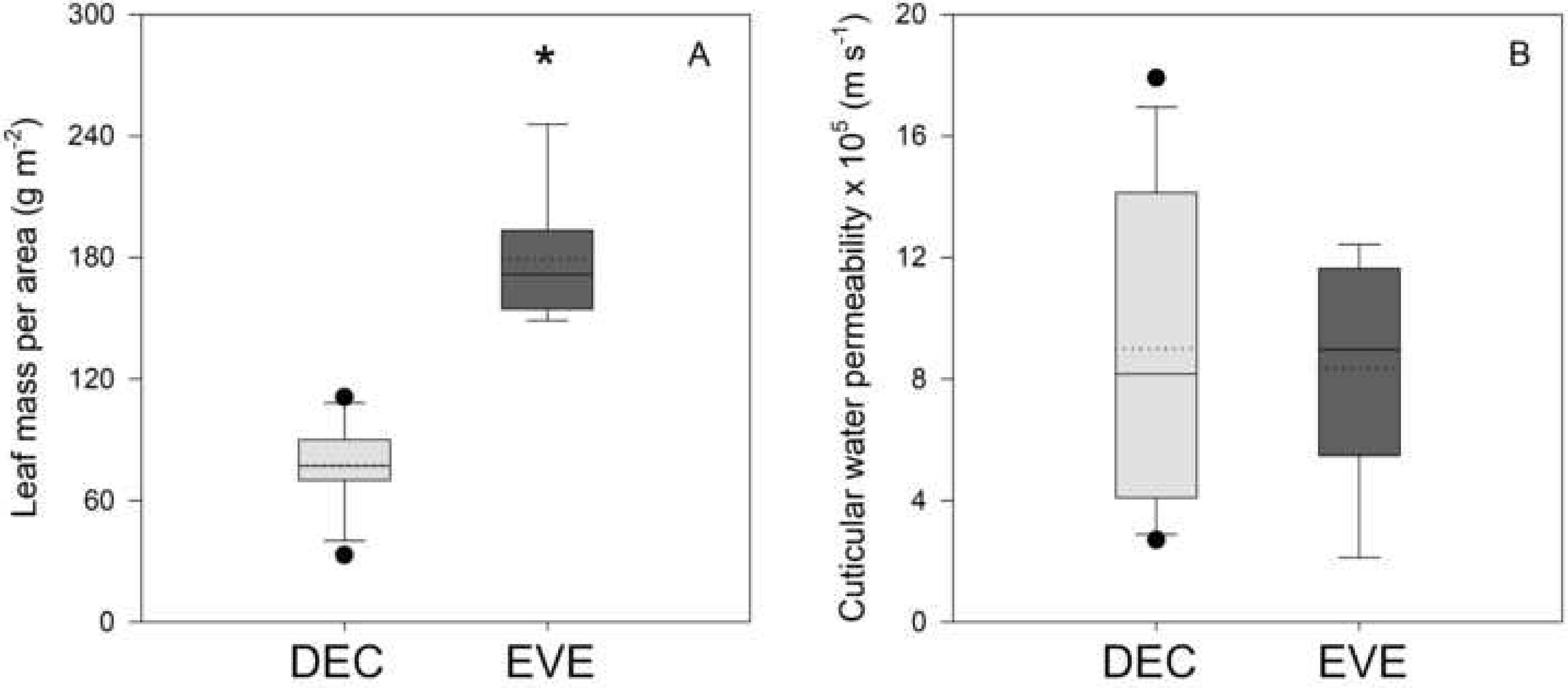

A_mass (μmol CO2 g-1 s-1)
200
175
150
125
100
75
50
25
TEM-DEC
TEM-EVE
MED-DEC
MED-EVE
TRO-DEC
r2=0.46
***
50
100
150
200
250
LMA (g m-2)
N_mass (mg g-1)
35
30
25
20
15
10
5
TEM-DEC
TEM-EVE
MED-DEC
MED-EVE
TRO-DEC
TRO-EVE
r2=0.28
***
50
100
150
200
250
LMA (g m-2)
A_area (μmol CO2 m-2 s-1)
25
20
15
10
5
TEM-DEC
TEM-EVE
MED-DEC
MED-EVE
TRO-DEC
TRO-EVE
r2=0.25
**
r2=0.05
n.s.
50
100
150
200
250
LMA (g m-2)
N_area (g m-2)
3.5
3.0
2.5
2.0
1.5
1.0
0.5
r2=0.41
***
TEM-DEC
TEM-EVE
MED-DEC
MED-EVE
TRO-DEC
TRO-EVE
50
100
150
200
250
LMA (g m-2)


30
25
20
15
10
5
0
N_{mass} (mg g^{-1})
r^2=0.03
n.s.
0
100
200
300
LMA (g m^{-2})
4
3
2
1
0
N_{area} (g m^{-2})
r^2=0.56
***
0
100
200
300
LMA (g m^{-2})


○ TEM-DEC
● TEM-EVE
◇ MED-DEC
▲ MED-EVE
● TRO-EVE
r^2=0.61
***
A_{area} (µmol CO$_2$ m^{-2} s^{-1})
25
20
15
10
5
0
200
400
600
800
g_s (mmol H$_2$O m^{-2} s^{-1})
○ TEM-DEC
● TEM-EVE
◇ MED-DEC
◆ MED-EVE
△ TRO-DEC
▲ TRO-EVE
r^2=0.40
***
A_{area} (µmol CO$_2$ m^{-2} s^{-1})
25
20
15
10
5
0.5
1.0
1.5
2.0
2.5
3.0
3.5
N$_{area}$ (g m^{-2})



ε_{max} (MPa)
20
15
10
5
50
100
150
200
250
LMA (g m^{-2})
r^2=0.26
*
TEM-DEC
TEM-EVE
MED-DEC
MED-EVE
TRO-DEC
TRO-EVE


Leaf mass per area (g m-2)
300
240
180
120
60
0
*
A
DEC
EVE
Cuticular water permeability x 105 (m s-1)
20
16
12
8
4
0
B
DEC
EVE

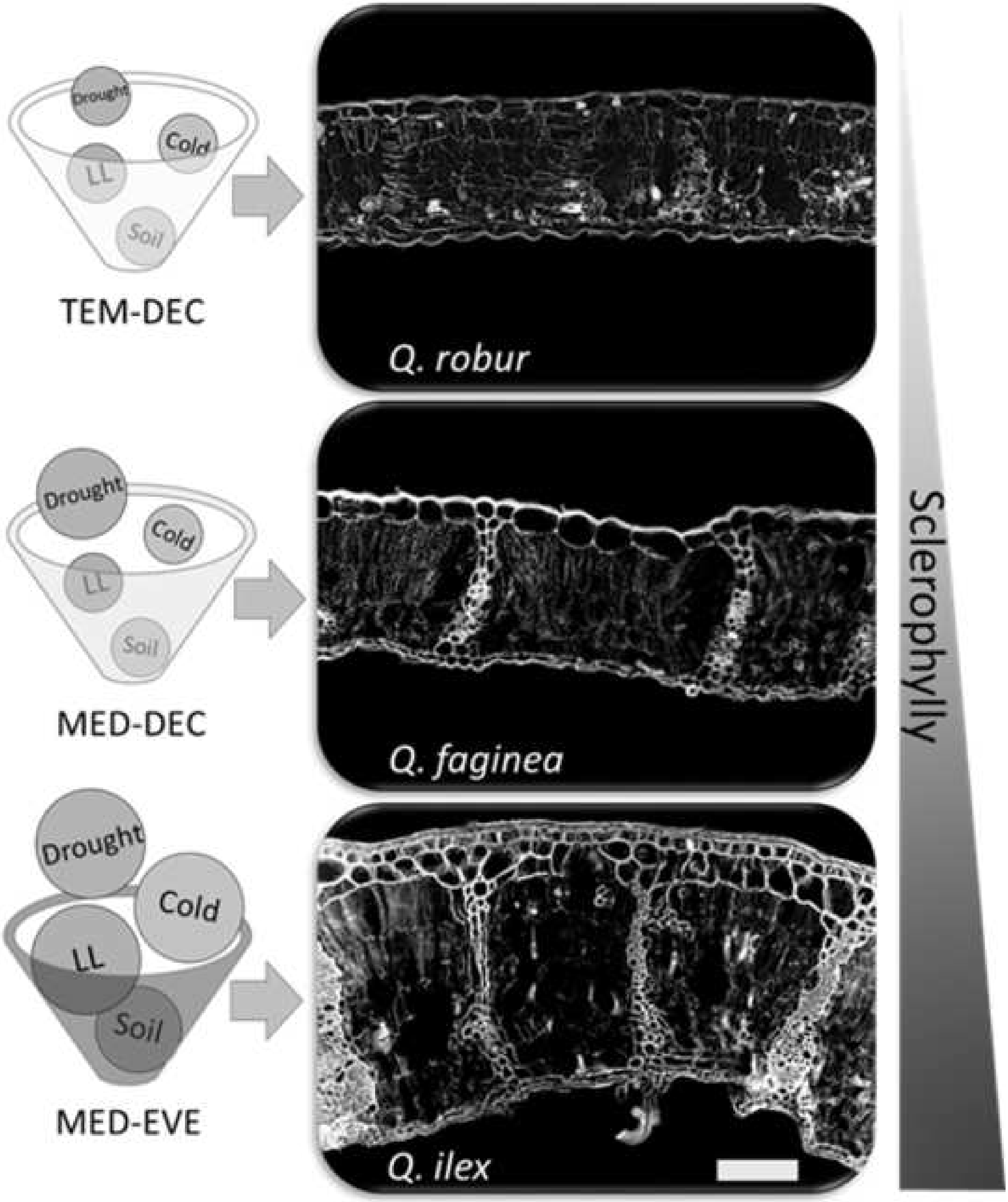

Drought
Cold
LL
Soil
TEM-DEC
Q. robur
Drought
Cold
LL
Soil
MED-DEC
Q. faginea
Drought
Cold
LL
Soil
MED-EVE
Q. ilex
Sclerophylly

Table 1. A list of leaf mechanical properties and their units

	Fracture properties			Elastic properties	
Type of tests	**Structural level**	**Material level**	**Mass level**	**Structural level**	**Material level**
Shearing test	Work to shear (J m^{-1})	Fracture toughness (J m^{-2})	Specific toughness (J m Kg^{-1})	NA	Shear modulus
Punch test	Force to punch (N m^{-1})	Punch strength (N m^{-2})	Specific punch strength (N m Kg^{-1})	NA	NA
Tensile test	Force to tear (N m^{-1})	Tensile strength (N m^{-2})	Specific tensile strength (N m Kg^{-1})	Tensile stiffness (N)	Young's modulus (N m^{-2})
Bending test	NA	NA	NA	Bending stiffness (N m^2)	Young's modulus (N m^{-2})