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RESEARCH ARTICLE

Leaf morphological traits as adaptations to multiple climate gradients

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Abstract

1. Leaf morphological traits vary systematically along climatic gradients. However, recent studies in plant functional ecology have mainly analysed quantitative traits, while numerical models of species distributions and vegetation function have focused on traits associated with resource acquisition; both ignore the wider functional significance of leaf morphology.
2. A dataset comprising 22 leaf morphological traits for 662 woody species from 92 sites, representing all biomes present in China, was subjected to multivariate analysis in order to identify leading dimensions of trait covariation (correspondence analysis), quantify climatic and phylogenetic contributions (canonical correspondence analysis with variation partitioning) and characterise co-occurring trait syndromes (*k*-means clustering) and their climatic preferences.
3. Three axes accounted for >20% of trait variation in both evergreen and deciduous species. Moisture index, precipitation seasonality and growing-season temperature explained 8%–10% of trait variation; family 15%–32%. Microphyll or larger, mid- to dark green leaves with drip tips in wetter climates contrasted with nanophyll or smaller glaucous leaves without drip tips in drier climates. Thick, entire leaves in less seasonal climates contrasted with thin, marginal dissected, aromatic and involute/revolute leaves in more seasonal climates. Thick, involute, hairy leaves in colder climates contrasted with thin leaves with marked surface structures (surface patterning) in warmer climates. Distinctive trait clusters were linked to the driest and most seasonal climates, for example the clustering of picophyll, fleshy and succulent leaves in the driest climates and leptophyll, linear, dissected, revolute or involute and aromatic leaves in regions with highly seasonal rainfall. Several trait clusters co-occurred in wetter climates, including clusters characterised by microphyll, moderately thick, patent and entire leaves or notophyll, waxy, dark green leaves.
4. *Synthesis*. The plastic response of size, shape, colour and other leaf morphological traits to climate is muted, thus their apparent shift along climate gradients reflects plant adaptations to environment at a community level as determined by species replacement. Information on leaf morphological traits, widely available

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in floras, could be used to strengthen predictive models of species distribution and vegetation function.

KEYWORDS
leaf functional traits, multivariate analysis, plasticity, species replacement, trait syndromes, trait–environment relationships

1 | INTRODUCTION

Plant functional traits are observable characteristics that reflect adaptive responses to environmental conditions (Lavorel et al., 2007). Recent research has documented variation in quantitative photosynthetic, biophysical and chemical leaf traits along environmental gradients (e.g. Meng et al., 2015; Poorter et al., 2009; Prentice et al., 2011; Xu, Wang, Prentice, Harrison, Wang, & Sun, 2021). Adaptive changes in leaf traits may be generated by plastic responses within an individual through the seasonal cycle or within a species along environmental gradients, as in the case of photosynthetic capacity (Togashi, Prentice, et al., 2018) and the optimal temperature for photosynthesis (Kumarathunge et al., 2019; Vico et al., 2019). In traits which are less plastic, such as leaf mass per area or hydraulic conductance (Dong et al., 2020; Xu, Wang, Prentice, Harrison, & Wright, 2021), changes in community-mean values along environmental gradients are produced mainly by species replacement (Meng et al., 2015). Observed statistical relationships between leaf mass per area (LMA) and longevity have been explained in terms of the economics of leaf growth under environmental constraints, with contrasting traits reflecting alternative, equally effective strategies in terms of faster or slower returns on plant investments in leaves (Reich et al., 2014; Wang et al., 2021; Wright et al., 2004; Wright et al., 2005). The ability of plants to exploit available resources in complementary ways also allows the coexistence of multiple strategies in resource-rich environments (Togashi, Atkin, et al., 2018).

Leaf morphological traits, such as leaf colour, shape, orientation and degree of marginal dissection, are often treated as diagnostic of species and have a long history of use for species identification (Cope et al., 2012; Foster & Gifford, 1989). However, such traits also vary with climate (Givnish, 1979, 1986; Nicotra et al., 2011; Royer & Wilf, 2006; Schmerler et al., 2012; Shaver, 1978). Features such as succulence, the existence of a terminal drip tip or notch, waxy coatings and surface patterning (e.g. Ellenberg, 1985; Goldsmith et al., 2017; Grace, 2019; Johnson, 1975; Malhado et al., 2012; Neinhuis & Barthlott, 1997; Yeats & Rose, 2013) are diagnostic of species' native climates. Particular morphological traits have been interpreted as strategies to promote water conservation in dry climates (e.g. hypostomatism, leaf curling), to mitigate high leaf temperatures in hot climates (e.g. reflective surfaces), or to promote water shedding in wet climates (e.g. terminal drip tips, surface patterning; e.g. Bell, 2012; Holmes & Keiller, 2002; Malhado et al., 2012; Michaletz et al., 2016; Wright et al., 2017). Table S1 summarises some of the hypothesised adaptive significance of the traits considered in this study. For some traits this is relatively well understood but, in most cases, more than one function has been proposed. The fact that it has not been firmly established which function is more important, or whether these traits represent adaptations to more than one feature of the growth environment, is a primary motivation for our analyses.

Information on the modern relationships between climate and leaf size and dissection has been used in one specific field of application, to reconstruct climates of the deep geological past based on the leaf morphology of plants (e.g. Greenwood, 2005; Greenwood et al., 2004; Miller et al., 2006; Peppe et al., 2011; Royer, 2012; Uhl et al., 2003; Utescher et al., 2000), including a number of studies from different regions of China (e.g. Chen et al., 2014; Chen et al., 2019; Li et al., 2016; Su et al., 2010). However, the existence of systematic trait–climate relationships suggests a wider potential field of application in models used to project impacts of contemporary climate change on plants and ecosystems. Species distribution models (SDMs), for example, are mainly derived by relating species occurrence or abundance data to climate by statistical methods (Elith & Leathwick, 2009). Although some SDMs explicitly include traits to represent the leaf economic spectrum and plant resource acquisition strategy in order to simulate community assembly (e.g. Jamil et al., 2013; Laughlin et al., 2012; Pollock et al., 2012; Rolhauser et al., 2021; Vesk et al., 2021), but do not consider the leaf morphological traits that govern leaf energy balance. Current models for vegetation dynamics, land-surface exchanges and carbon cycling recognise distinctions of quantitative ecophysiological or leaf economics traits, such as photosynthetic capacities and LMA, but disregard morphological traits that govern leaf energy balance. Even leaf size is absent from these models, despite historic recognition of its climatic significance (Raunkiær, 1916), its well-established connection to leaf energy balance (Gates, 1980), and the apparent independence of energy-balance traits from other commonly recorded traits (Blonder et al., 2020). The use of quantitative ecophysiological and leaf economics traits in models is facilitated by the wealth of available data. Empirical studies in plant functional ecology over the past three decades have provided large datasets on quantitative traits, such as leaf size, LMA, leaf dry matter content and leaf chemistry, and described their relationships to climatic and other environmental variables. Recently, theoretical analyses based on eco-evolutionary optimality principles (Harrison et al., 2021) have begun to establish a predictive understanding of these

trait–environment relationships. By contrast, leaf morphological traits which are described only in terms of presence/absence or by categorical measurements have been largely neglected in field surveys, theoretical analyses and models.

This paper represents an exploration of the controls of leaf morphological traits, exploiting the power of multivariate analysis to identify quantitative patterns (trait–trait and trait–environment relationships) in large, qualitative or semi-quantitative datasets. An extensive dataset of leaf traits collected from sites across China, covering all biomes, was used to characterise trait covariation and to investigate how and to what extent trait variation is related to climate, site and phylogeny. We used cluster analysis to identify trait syndromes within the trait-species pool, and related the occurrence of these syndromes to geographic variation in climate.

2 | MATERIALS AND METHODS

2.1 | Trait data

The trait data were derived from the China Plant Trait Database (CPTD: Wang et al. (2018)). This contains leaf morphological, biophysical, chemical and photosynthetic trait data for more than 1215 species from 122 sites. The field sampling strategy was designed to ensure adequate representation of all strata at each site: details of sampling and trait measurement methods are given in Wang et al. (2018). The sites sample the range of biomes and climates present in China, with sites in the northeast spanning an aridity gradient from steppe through grassland to temperate deciduous forest and boreal forests, those in central China sampling temperate deciduous forest, and those in the southwest sampling the gradient from tropical and subtropical evergreen broadleaf forests to tropical dry woodlands. The CPTD also provides information on life-form and family for each species, and location, elevation and climate data for each site. Data from the CPTD have been used previously to investigate various aspects of trait–climate variability (Meng et al., 2015; Prentice et al., 2011; Yang et al., 2019).

We extracted data for 25 leaf morphological traits for all woody species (trees, shrubs and lianas) from the CPTD. The leaf morphological traits were originally recorded either in terms of simple presence/absence (e.g. spines: present or absent) or assigned to multiple predefined categories (e.g. leaf size, leaf texture, leaf margin) in the CPTD because this allowed rapid assessment in the field. However, the variables were measured and recorded in the field by the same individuals over 15 years, following a standard protocol and using standardised reference sheets (Figure S1) to minimise systematic error. Species that occurred in multiple sites were assessed and recorded at each site separately to assess the degree of intraspecific variation in the morphological traits. Although both adaxial and abaxial leaf colour are recorded in the CPTD, we included only adaxial colour in the analyses as being more likely diagnostic of environmental conditions. Some traits or types were present in only a few samples. We first amalgamated some of the categories separated in the field (e.g. combining erect, semi-erect, pendulous and reclinate leaves into a single category in contrast to patent leaves) and then excluded traits that occur in >2% of the samples from further analysis. This filtering process resulted in the selection of 22 traits (Figure S2) for analysis, and yielded 1094 samples of 662 species across 92 sites. These sites cover the range of vegetation types and major climate types across the region (Figure 1; Figure S3). In

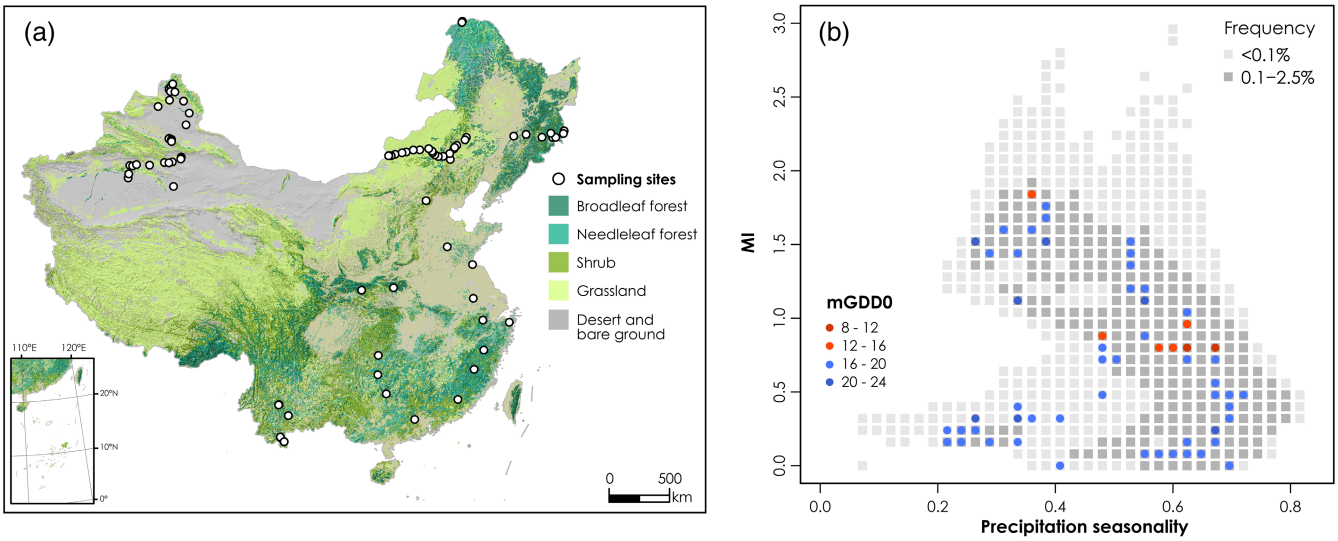


FIGURE 1 Geographic distribution and climatic coverage of the sample sites. Plot (a) shows the sites as dots superimposed on the simplified vegetation Atlas of China [1: 1,000,000, Hou, 2001] map; (b) the distribution of sites in climate space. The grey cells show the frequency distribution of 10 km grid cells across the whole of China in the climate space characterised by moisture index (MI) and precipitation seasonality. The coloured dots show the location of the sampling sites in this climate space, where the colour indicates the daily mean temperature during the thermal growing season (mGDD0). MI is defined as the ratio of mean annual precipitation to annual equilibrium evapotranspiration. The geographic distributions of the three bioclimatic variables are shown in Figure S3

addition to analysing all the woody species together, we made separate analyses of evergreen and deciduous woody plants. Traits or categories were included in the analysis for evergreen species only if they occurred in >2% of the sites with evergreens present, and similarly for deciduous species. For this reason, there are some differences in the sets of traits analysed for evergreen and deciduous species (Figure S2).

2.2 | Multivariate analysis

Correspondence analysis (CA: Legendre and Legendre (2012)) was performed to determine the leading dimensions of covariation among individual traits, and canonical correspondence analysis (CCA: Ter Braak (1987)) to identify dimensions of trait variability that maximally correlate with environmental variables. In both analyses, presence/absence (1 or 0 respectively) scores were assigned to each trait category including for traits which were originally represented by multiple categories (e.g. leaf size and shape). As a result, the analyses were performed on 48 trait categories.

To select climate variables to include in the CCA, we first calculated pairwise correlations of 21 variables (Figure S4). Thirteen of these were bioclimatic variables derived directly from the CPTD; the remaining eight variables include annual or seasonal indices (e.g. precipitation during the driest 3 months) that have been used in species distribution modelling and other trait-based analyses (e.g. Chen et al., 2019) and were calculated from the monthly values of temperature, precipitation and radiation for each site provided in the CPTD. We then selected the three variables showing least correlation with one another (pairwise correlation coefficients <0.35) to avoid unnecessary redundancy in the explanatory variables: mean daily temperature during the thermal growing season (the period with daily temperatures >0°C; $mGDD_0$, °C), precipitation seasonality (Pseas) and a moisture index (MI) calculated as the ratio of annual precipitation to estimated annual equilibrium evapotranspiration. Those variables also represent key aspects of the growth conditions that plants adapt to and have been widely used in process-based trait analyses and vegetation modelling (Harrison et al., 2010).

2.3 | Variation partitioning

Variation partitioning quantifies the amount of variation in a predicted quantity or set of quantities that is explained by different predictors (Legendre & Legendre, 2012). We used the Legendre method (Legendre & Anderson, 1999; Peres-Neto et al., 2006), which accounts for the non-independence of different groups of predictors by distinguishing both unique and overlapping contributions. The method was used here with results from the CCA to assign trait variation to components linked to climate, sites and families, and the intersections of these controls. Results of variance partitioning were displayed as Venn diagrams.

2.4 | Cluster analysis

We used *k*-means cluster analysis (Hartigan & Wong, 1979) to investigate whether certain traits consistently occur together. Consistent occurrence could indicate that there are trait syndromes adapted to particular environments, or multiple strategies that confer adaptation to given environmental conditions. However, *k*-means clustering operates in a Euclidean space. The Euclidean distance between categorical traits is inversely related to the simple matching coefficient, which has the undesirable property that rare traits are treated as similar to one another simply because they share many zeroes. Therefore, we created a modified Euclidean space by first calculating the matrix of Jaccard coefficients (Hancock, 2014) between traits, then performing a principal coordinate analysis (Zuur et al., 2007) on these values, before running the clustering in the space generated by the first three principal coordinate axes. The optimal number of clusters was estimated from the gap statistic for each *k* value based on 1000 iterations, resulting in the choice of 11 clusters. We ran the clustering algorithm 20 times to assess the stability of the membership in each cluster. On the basis of this assessment, traits were allocated to a consensus cluster which represents the cluster to which they were most frequently assigned. These clusters were superimposed on the CCA plots in order to examine their position in climate space.

3 | RESULTS

3.1 | Dimensions of trait variation

The first three components of the CA accounted for slightly more than 20% of trait variation in separate analyses of evergreen (22%) and deciduous (24%) species (Figure 2; Table S2). The ordering of leaf size (from small to large) and leaf width (from linear to wide) is similar in deciduous and evergreen species. There are more distinctions in leaf colour in deciduous than evergreen species and hence they occupy a larger part of the CA space and show a clearer shift from light to darker colours. The range in leaf thickness differs between the two categories since thick leaves only occur in evergreen species, but there are clear trends from thick to medium to thin leaves along the second CA axis. The trends in leaf margin and texture were less clear than those for other traits, but nevertheless show some separation along the CA axes. CA1 (*c.* 10%) opposed larger, darker green leaves with drip tips to smaller, more glaucous, vertically oriented leaves without drip tips. CA2 (*c.* 7–8%) opposed thinner, more dissected, aromatic and involute or revolute leaves to thicker, less dissected leaves lacking the other traits. CA3 (*c.* 6%) opposed thicker, hairy, involute leaves with conspicuous surface patterning to thinner leaves lacking the other traits.

3.2 | Climate controls on trait variation

The three bioclimatic variables together accounted for 8% of trait variation among all species together, and 7%–8% among

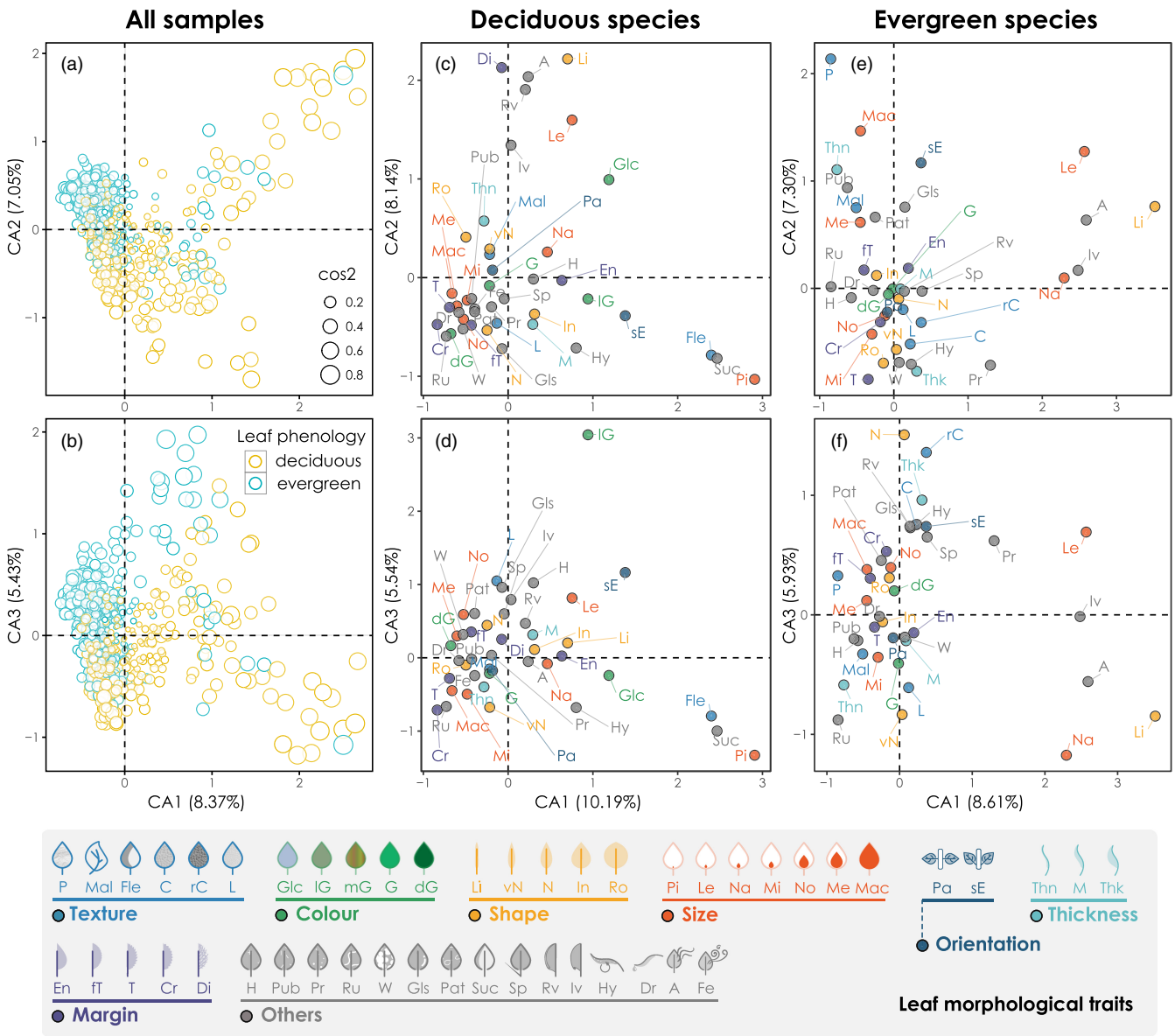


FIGURE 2 Trait dimensions from correspondence analysis (CA) of (a, b) all samples, (c, d) deciduous and (e, f) evergreen species. The *y*-axis represents CA2 in the upper and row and CA3 in the lower row. The colours in (a) and (b) distinguish evergreen and deciduous species. cos2 indicates the importance of the plotted components in determining the location of each sample. Trait abbreviations are given in Figure S2

evergreen and deciduous species separately (Figure 3; Figure S5; Table S3). There is a clear separation of traits along climate gradients and a straightforward first-order mapping from the CAs of evergreen and deciduous species to the CCA axes. Overall, the first CCA axis was closely related to the gradient from low to high moisture index, and was overwhelmingly dominant, accounting for >60% of climate-constrained trait variation. With increasing moisture, traits were arranged from glaucous and light green to mid-green and dark green leaves; from smaller (pico-, lepto- and nanophyll) to larger (micro-, noto- and mesophyll) leaves; and from semi-erect to patent orientations. Fleshy or succulent leaves occur in the driest climates. Hairy leaves are typical in drier climates and pubescent leaves in wetter climates. Leaf margins are most dissected in dry climates and commonly entire, crenate or crenulate in wet climates. Leaf shape, however, shows no such clear pattern, suggesting a lack of functional significance. The second axis was closely related to the gradient from low to high precipitation seasonality. With increasing seasonality, traits were arranged from thick and medium to thin leaves, and from entire to marginal dissected leaves. Aromatic, and revolute or involute, leaves were also characteristic of more seasonal climates. The third axis was closely related to the gradient from colder to warmer climates. With increasing warmth, traits were arranged from thick and medium to thin leaves, and from hairy to pubescent leaves. Both spines and surface patterning are found in wet climates with highly seasonal precipitation. Along the axis closely

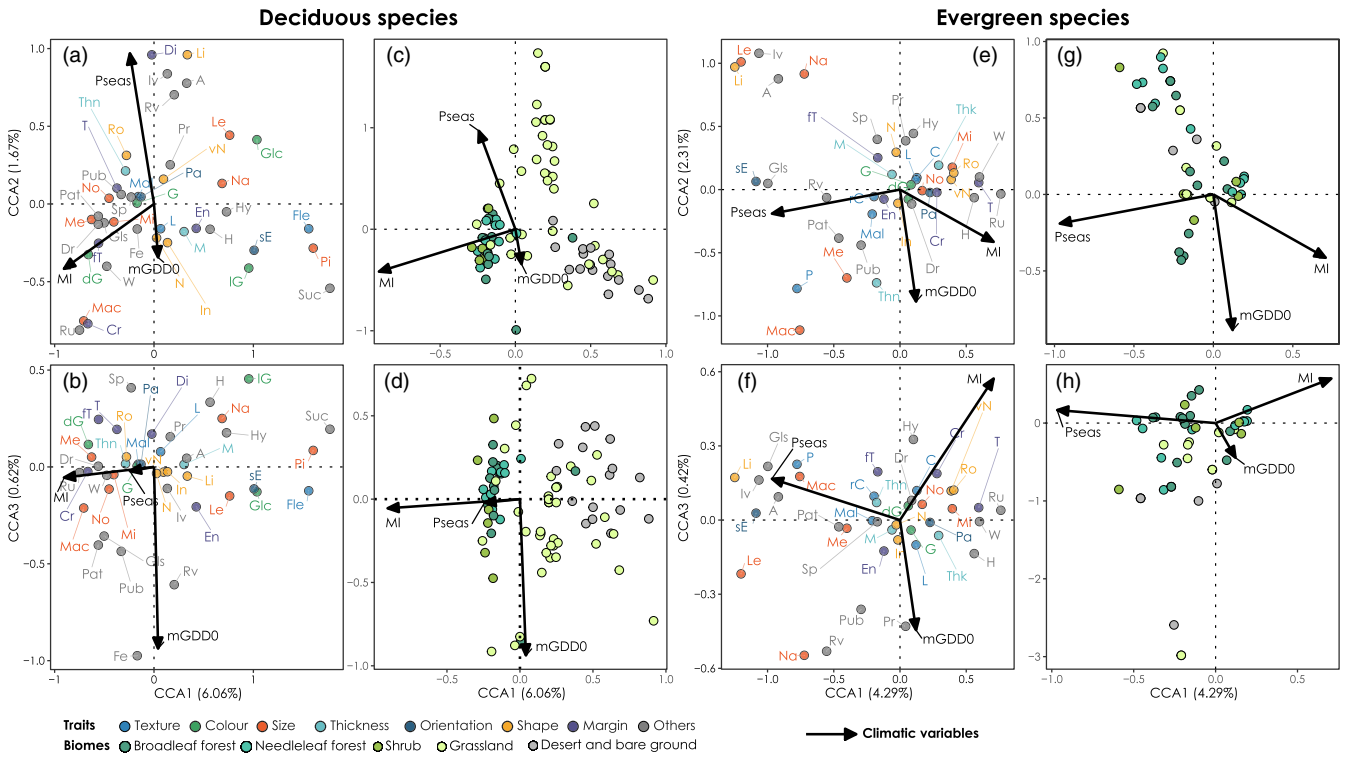


FIGURE 3 Climate-related trait dimensions from canonical correspondence analysis (CCA) of (a, b) deciduous and (e, f) evergreen species. (c, d) and (g, h) show the same results but with biome types of sampling sites imposed. The *y*-axis represents CCA2 in the upper row and CCA3 in the lower row. Climate variables are moisture index (MI), precipitation seasonality (Pseas) and daily mean temperature during the thermal growing season ($mGDD_0$). MI is defined as the ratio of mean annual precipitation to annual equilibrium evapotranspiration. The traits are shown as dots; the colours represent different categorical traits (Figure S2). Trait abbreviations are given in Figure S2. Grey open circles represent the samples

related to the gradient from colder to warmer climates, there is a gradient from thick and medium to thin leaves. Involute leaves were found in colder climates; surface patterning in warmer climates. These patterns were largely replicated in separate analyses of evergreen and deciduous species (although seasonality was relegated to the third axis among evergreens). Additional patterns noted in these analyses included the prevalence of fleshy and succulent leaves among deciduous species in dry climates; linear, very narrow and round leaves in dry climates; waxy and glossy leaves in wet climates; and pruinose or rugose leaves in cold climates; surface patterning in wetter climate (deciduous species) or higher rainfall seasonal climates (evergreen species); hairy leaves in drier climates (deciduous species) or less rainfall seasonal climates (evergreen species), and pubescent leaves in wetter or warmer climate.

The shifts in trait abundance along these three climate gradients are mirrored by changes in vegetation (Figure 3). The importance of the moisture gradient corresponds to the transition from deserts through grasslands, shrubland and into forests. Broadleaved forests are distinguished from needle-leaved forests on the $mGDD_0$ axis. Rainfall seasonality separates deciduous forests and woodlands (and also open vegetation) from evergreen forests. This supports the idea that climate plays a role in the patterns of change in trait abundance.

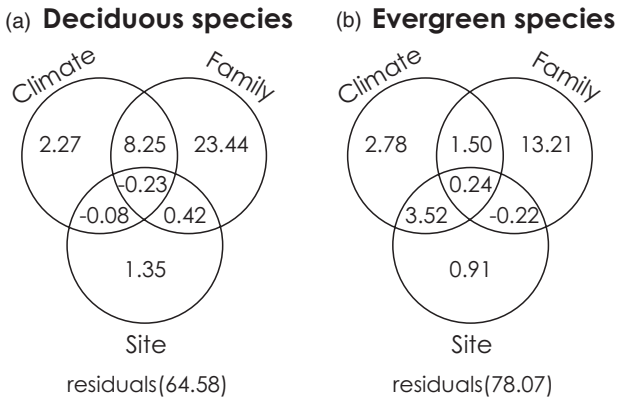


FIGURE 4 Variance partitioning (%) by site, climate and family (a) for deciduous species and (b) for evergreen species

3.3 | Other controls of trait variation

Venn diagrams (Figure 4) summarise the percentage contributions of climate, site and family (unique and overlapping contributions) to total trait variation. Together, these three controls accounted for 35% and 22% of total trait variation in deciduous and evergreen species respectively. Family had the largest unique effect (23% for deciduous species, 13% for evergreen species). Climate was also important, with

3% of the variability due to climate alone and 6% due to the overlap between climate and family. Site accounted for only 1% of the total variation; its interactions with climate and family were also small.

3.4 | Trait syndromes

The gap statistic identified 11 *k*-means clusters of traits (Figure S6; Table S4). The traits included in each cluster varied slightly between the 20 repetitions of the analysis (Figure 5; Figure S7). However, some traits were consistently grouped together, and the location of these trait 'syndromes' in climate space was more or less stable (Figure 6; Figure S7). The following text summarises the resulting consensus clusters and their climatic ranges as indicated in Figure 5. The clusters are numbered according to their location on the dominant climate gradient from low to high moisture index values. Clusters with a similar distribution along this gradient are ordered from lower to higher precipitation, where applicable; otherwise their

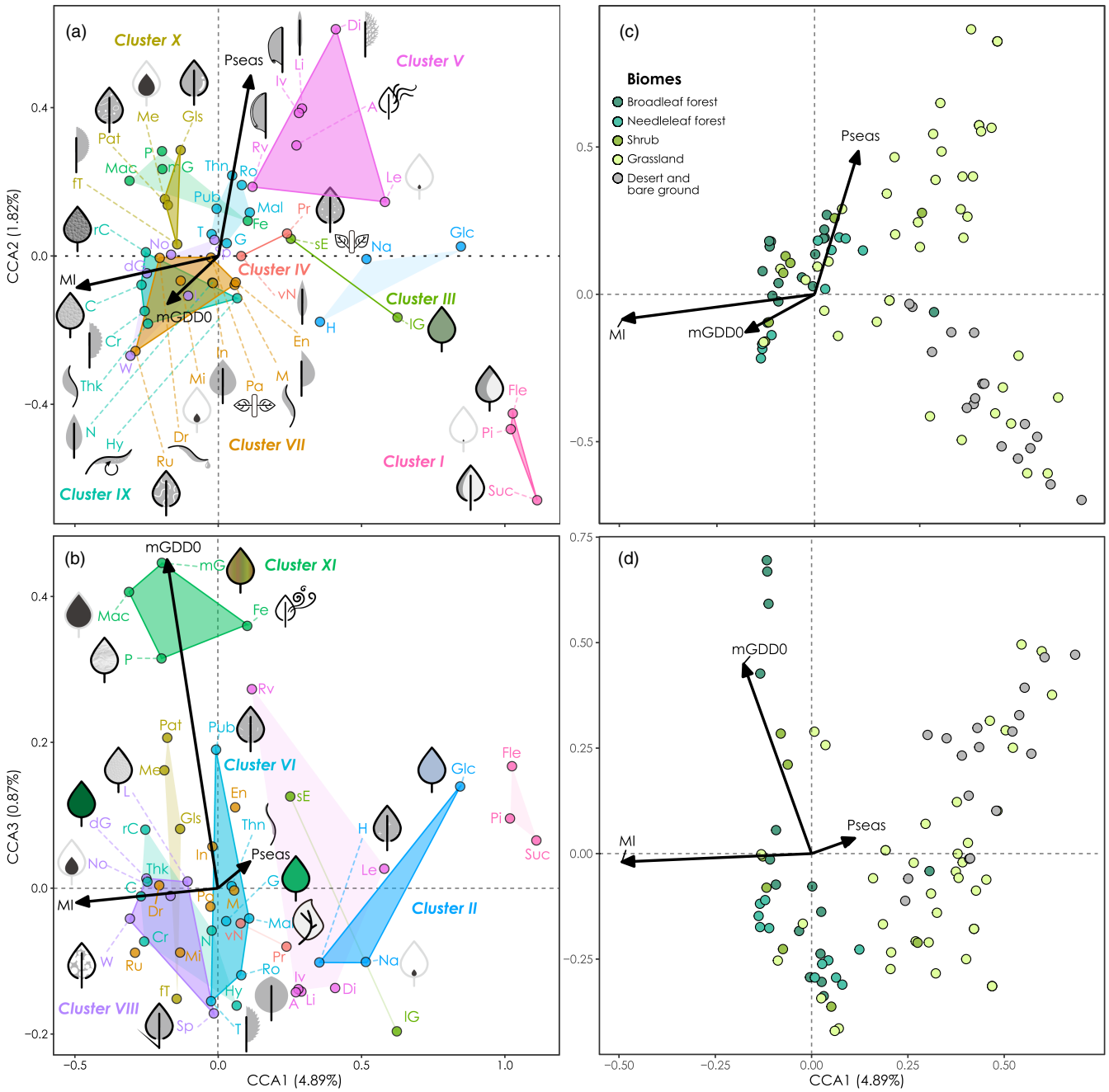


FIGURE 5 Consensus clusters of traits from *k*-means cluster analysis. Traits belonging to the same cluster are represented by dots of the same colour, and shown in the space defined by climate-related trait dimensions from canonical correspondence analysis (CCA): (a) CCA1 versus CCA2 and (b) CCA1 versus CCA3. (c, d) show the same results with the biome types of each sampling sites imposed. Trait abbreviations are given in Figure S2

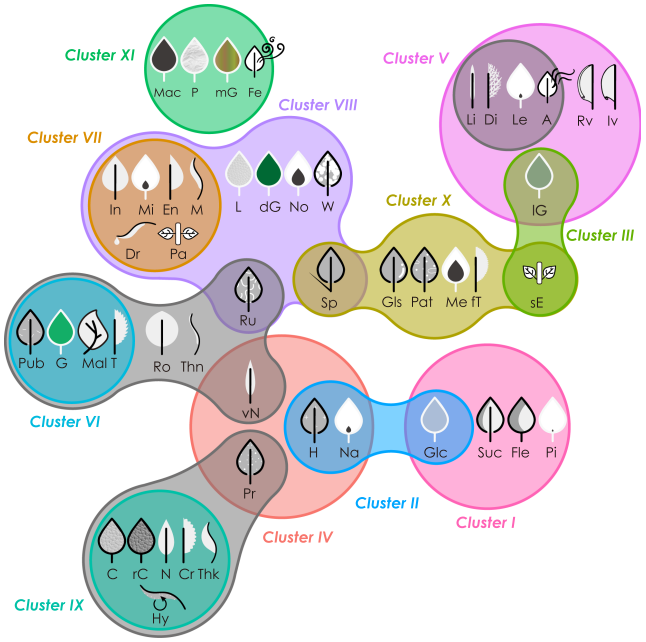


FIGURE 6 Summary of trait combinations from 20 repetitions of the *k*-means clustering. The clusters represent the consensus of the most frequently allocated cluster membership in these repetitions. Traits appearing in the same colour-coded shape are those occurring in that cluster; traits occurring in multiple shapes are assigned to different clusters in different repetitions.
The abbreviations of each trait are given here as follow: Pi (pico), Fle (fleshy), Suc (succulent), Glc (glaucous), H (hairy), Na (nano), Pr (pruinose), vN (very narrow), C (coriaceous), N (narrow), Thk (thick), rC (rigidly coriaceous), Hy (hypostomatic), Cr (crenate), Mac (macro), mG (mottled green), P (papery), Fe (fetid), Pub (pubescence), T (toothed), Mal (malacophyll), G (green), Thn (thin), Ro (round), Ru (rugose), Dr (drip tips), In (intermediate), Pa (patent), Mi (micro), M (medium), En (entire), W (waxy), L (leathery), No (noto), dG (dark green), A (aromatic), Di (dissected), Le (lepto), Li (linear), Rv (revolute), Iv (involute), sE (semi-erect/pendulous), Gls (glossy), Pat (surface patterning), Me (meso), fT (finely toothed/crenulate), Sp (spines/thorn) and IG (grey-green/pale green/bright green)

ordering is arbitrary. Biome distributions in this climate space are shown for comparison (Figure 5c,d).

I Picophyll, fleshy and succulent leaves occurred in the driest climates with the least seasonal precipitation.
II Nanophyll, glaucous and hairy leaves occurred in dry climates with intermediate precipitation seasonality.
III Light green and semi-erect leaves formed a separate cluster in similar climates to cluster II.
IV Pruinose and very narrow leaves occurred in slightly wetter climates than clusters II and III.
V Leptophyll, linear, dissected, revolute or involute and aromatic leaves occurred in moderately dry climates with highly seasonal precipitation.
VI Malacophyll, thin, green, rugose or pubescent, toothed and round leaves occurred in moist climates (wetter than the previous five clusters) with intermediate precipitation seasonality.
VII Microphyll, medium-thickness, patent, entire, intermediate-shaped, leaves with drip tips formed one cluster in wet climates with intermediate precipitation seasonality.
VIII Notophyll, waxy or leathery, dark green leaves formed a second cluster in similar climates to cluster VII.
IX Coriaceous or rigidly coriaceous, thick, narrow, crenate and hypostomatic leaves formed a third cluster in similar climates to clusters VII and VIII.
X Mesophyll, glossy, finely toothed or crenulate leaves with spines and surface patterning occurred in wet climates with highly seasonal precipitation.
XI Macrophyll, papery, mottled green and fetid leaves occurred in the warmest and wettest climates.

4 | DISCUSSION

Variations in leaf morphological traits have a strong phylogenetic component, as represented by family. Climate alone accounted for only 3% of the variation in morphological traits but variation linked to both climate and phylogeny was more important, especially in deciduous species where it accounted for 8% of trait variation. This overlap is to be expected if shifts in the abundance of morphological traits are determined mainly by the progressive replacement of taxa along the climate gradients. The limited plasticity of morphological traits contrasts with ecophysiological traits such as maximum carboxylation capacity or the internal-to-ambient CO_2 ratio, which are highly plastic; and leaf nitrogen content or specific leaf area, which are intermediate (Dong et al., 2020; Meng et al., 2015; Xu, Wang, Prentice, Harrison, & Wright, 2021).

The combined contribution of family, climate and site factors explains only a relatively small part of the observed variation in leaf morphological traits. The unexplained variation was 65% in deciduous species and 78% in evergreen species. This is not a function of the use of bioclimate variables since more conventional meteorological variables, such as mean annual precipitation or mean annual temperature, have a somewhat lower explanatory power when applied to our dataset (Figure S8). Such a large unexplained variation probably reflects the categorical nature of the trait data since this is not typical of analyses of quantitative traits. Yang et al. (2019), for example, showed that 70% of the combined variation in leaf area, specific leaf area, leaf dry matter content, nitrogen content, internal-to-ambient CO_2 ratio and photosynthetic capacities could be explained by family, life-form, climate and site. Furthermore, when leaf size is treated as a continuous trait (e.g. Wright et al., 2017; Yang et al., 2019), the explanatory power of climate and other factors is larger than when it was grouped into categories. Given the advantages of using categorical traits for rapid field assessment, and that the climate effect on their variation is clear from the fact that these categories occupy distinctive parts of the CCA space, we argue that the analysis of categorical traits has merit and can be diagnostic of climate adaptations. Nevertheless, quantitative measures could

usefully be devised for many of the traits that are conventionally treated as categorical to improve the diagnosis of trait–climate relationships.

It has been shown that leaf size, shape, texture, thickness and degree of marginal dissection are all associated with gradients in temperature (Chen et al., 2019; McKee et al., 2019; Yang et al., 2015). One explanation is because they affect boundary-layer conductance and therefore the leaf energy balance (Givnish & Vermeij, 1976; Grace et al., 1980; Jensen & Zwieniecki, 2013; Parkhurst & Loucks, 1972). However, the leaf energy balance can also be influenced by factors other than temperature. In our analyses, leaf size and marginal dissection show strong relationships with the first CCA axis, which indicates (and the cluster analysis confirms) that these traits are ordered principally along the moisture gradient. Chen et al. (2019) found a strong relationship between the presence/absence of toothed margins and mean annual temperature, but their analysis was confined to woody species in regions of China that had mean annual precipitation above 400 mm. In an earlier study, considering a wider range of moisture conditions, Li et al. (2016) showed that the relationship between leaf marginal dissection and temperature was affected by precipitation levels. Indeed, the strength of the relationship between leaf marginal dissection and temperature has been shown to vary considerably between different regions of the world (Chen et al., 2014; Gregory-Wodzicki, 2000; Su et al., 2010) as a function of differences in moisture availability (Chen et al., 2014; Davis & Taylor, 1980). Thus, it is perhaps unsurprising that our multivariate analysis indicates a strong influence of moisture on leaf dissection. This finding is nonetheless consistent with control by daytime leaf temperature, which becomes progressively higher relative to air temperature as transpiration is reduced (Wright et al., 2017). Recent work has also recognised a constraint on leaf size related to night-time temperature (Wright et al., 2017), as leaves are generally cooler than the surrounding air at night and larger leaves are then potentially more susceptible to frost damage (Lusk et al., 2018). Recent studies have revealed complexities in the relationship between leaf traits and leaf energy balance (Blonder et al., 2020; Leigh et al., 2012; Leigh et al., 2017; McKee et al., 2019; Still et al., 2021). Blonder et al. (2020) showed that leaf area and leaf angle are poor predictors of leaf temperature, and Leigh et al. (2017) showed that leaf dissection was not measurably related to leaf temperature under field conditions. On the other hand, water availability is recognised as centrally important for leaf temperature regulation (Dong et al., 2017; Leigh et al., 2017; Peguero-Pina et al., 2020). This may help to explain the importance of moisture availability in influencing variation in leaf size and dissection in our dataset. Nevertheless, the way individual morphological traits influence leaf energy balance is complex and, as suggested by the multiplicity of alternative hypotheses (Table S1), many morphological features may serve multiple functions.

The increase in leaf thickness with aridity has been interpreted as a way to reduce the likelihood of transient excursions to damaging high temperatures when other means of reducing leaf temperature (most importantly by transpiration) are lacking. Additional adaptive functions of thick leaves include enhanced leaf strength, and the ability to attain high photosynthetic capacity in high-light environments (Table S1). Our analysis also points to a moisture-dependent leaf texture gradient (Table S1), with coriaceous and leathery leaves common in wet regions, and malacophyll or papery leaves in regions with high rainfall seasonality (Figure 5). Leaf orientation and colour relate to leaf energy balance: more vertically oriented leaves receive less radiation load during the midday period, while glaucous or grey leaves reflect more radiation—both adaptive under conditions of high radiation and restricted transpiration (Table S1). The ratio of chlorophyll a to b declines with increasing shade, consistent with the fact that chlorophyll b absorbs more strongly in the spectral range that is transmitted through leaves (Table S1).

Several clusters (trait syndromes) were found to occupy similar climatic ranges in wetter climates. Our analytical method identifies traits that cluster together in climate space, not necessarily traits that co-occur in a single plant. That traits can belong to more than one cluster in independent repetitions of the cluster analysis suggests that different trait syndromes intergrade. The co-occurrence of different clusters in the same mid-range of climate space mainly reflects different degrees of habitat specialisation. For example, cluster IX (coriaceous or rigidly coriaceous, thick, narrow, crenate and hypostomatic leaves) is restricted to subtropical forests, while cluster VIII (notophyll, waxy or leathery, dark green leaves) extends to both tropical rainforests and temperate forests, and cluster VII (microphyll, medium-thickness, patent, entire, intermediate-shaped, leaves with drip tips) is even more widely distributed (Figure S9).

Leaf morphological trait variations could be exploited in models used to assess the consequences of climate change for species and ecosystems. Trait variations that correlate with climatic gradients can reasonably be assumed to have adaptive significance, since otherwise they would be eliminated through natural selection, and indeed this adaptive significance is the basic assumption of plant biogeogeography and vegetation modelling. Analyses that span multiple gradients allow responses to different climate variables to be distinguished. Several leaf morphological traits commonly recorded in regional floras convey additional, neglected information about the potential distribution of species in climate space that could complement information on the actual observed distribution. Moreover, species turnover in response to spatial gradients—the key mechanism by which adaptive, non-plastic trait distributions are generated—means that the standard representations of plant diversity in global vegetation models, whereby plants are either assigned to small number of homogeneous plant functional types characterised by a small number of traits, cannot adequately represent the role of functional diversity in allowing plant communities to adjust to climate change. Our results also indicate that some traits may serve multiple functions. This suggests it would be beneficial to conduct experimental studies (e.g. on closely related species differing in specific traits) to clarify, and quantify, the functional significance of leaf morphological traits.

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CONFLICT OF INTEREST

The authors declare that there is no conflict of interest.

AUTHORS' CONTRIBUTIONS

H.W. and S.P.H. designed the study and wrote the first draft of the paper; S.P.H. and I.C.P. collected the field data. R.W. carried out the statistical analyses. All authors contributed to the final draft.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

The data are stored as the China Plant Trait Database (Wang et al., 2018) in PANGAEA https://doi.pangaea.de/10.1594/PANGAEA.871819 (Wang et al., 2017).

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