Current Trends in
Ecology
Vol. 3, 2012

Review

Plant functional traits: Perspectives from a quantitative literature survey

Adriana Sanchez* and William K. Smith

Department of Biology, Wake Forest University, 1834 Wake Forest Road, Winston-Salem,
NC 27109-7325, USA

ABSTRACT

Studies dealing with the identification of plant functional traits as indicators of an individual or species ecophysiology have become abundant in the literature. Overall, this approach is important for generating proxy data for fundamental physiological traits that are, in general, much more challenging to measure. This popularity in the functional trait approach has now resulted in a host of traits referred to as functional in the literature, but often without specific associations with ecophysiological performance among individuals, species, or habitat types. Most often, correlations are made with the general habitat of occurrence, while fewer studies exist that document direct cause and effect relationships. Moreover, the large number of traits now identified as functional has complicated the choice by investigators of traits for study that might best reflect ecophysiological performance. We report here quantitative results of a literature survey of studies identifying and utilizing functional plant traits, a total of over two hundred publications. We also ranked all traits numerically according to their frequency of occurrence, plus the total number of authors reporting particular traits as functional. A total of 107 traits were identified as being functional, although only a few dominated the studies. We first point out conceptual problems when interpreting the ecophysiological significance of the most commonly studied trait in the literature, specific leaf mass (LMA) and its inverse, specific leaf area (SLA). We also discuss briefly the importance of *a priori* identification of more mechanistic, co-evolved suites of functional traits for evaluating plant adaptations leading to observed distribution patterns.

KEYWORDS: adaptation, ecophysiology, functional traits, habitat characteristics, specific leaf mass, specific leaf area

INTRODUCTION

The general lack of behavioral mobility in terrestrial plants compared to animals is compensated by the complexity and diversity in structure, life history, phenology, spatial patterning, etc. This broad spectrum of potential functionality provides capabilities for tolerating, or even avoiding completely, the negative abiotic or biotic conditions of the environment. In that regard, there has been a host of studies over the past several decades and beyond, attempting to identify ecophysiological function and adaptation from more easily measured plant traits, either phenotypic or genotypic. Two fundamental goals seem to exist within these studies: (1) to better understand the adaptive advantages of individual or suites of traits according to habitat, and (2) to validate the functionality of particular traits by identifying evolutionary convergence in these traits, i.e., their occurrence among species from

---

*Corresponding author: sancheza@wfu.edu

different taxa, but similar habitats [e.g., 1, 2, 3, 4, 5, 6]. Evolutionary convergence in species traits also confirms their adaptive strength according to the number of independent origins and total plant taxa involved. However, convergence in physiological traits (e.g., C4 photosynthesis) can also be viewed as being constrained by leaf and whole-plant structure, plus chemical composition [e.g., 4, 7]. In this regard, convergence in traits due to functionality can be separated from phylogenetic conservatism and parallelism that stems from a common ancestry [8]. Albeit, direct evidence for the adaptive benefit of an individual trait, or suites of co-evolved traits, is challenging due to the difficulty in attributing specific individual traits to increases in actual ecological fitness, i.e. a greater production of viable offspring relative to other, competing individuals or species [2, 8]. An emphasis on the importance of differences in plant structural traits, versus metabolic pathways, occurs in an edited volume addressing photosynthetic adaptation scaled across the broad organizational hierarchy of plant structure [9].

According to Violle *et al.* [10], a functional trait is any trait that impacts fitness indirectly, including traits related to growth, reproduction, and survival. Also, functionality in traits may be driven by scaling factors as simple as plant size [4; see below]. However, it is worth noting that an underlying goal of the functional traits approach is to be able to utilize easily measured plant characteristics that indicate adaptive function, instead of the relatively expensive, time-demanding, and logistically difficult measurements of the actual physiological processes that define functionality. Thus, by employing the functional trait approach, one might predict accurately, for a much larger array of species, such important features as survival potential and fitness in a global-change environment [11, 12]. Additionally, it would be efficacious to identify the most relevant plant traits and their corresponding attributes that are required for adaptive success in a given habitat [e.g., 5, 10].

Comprehensive reviews of plant traits that are associated with specific ecophysiological functions and environments are relatively rare [see 13 for review], as well as associations with individual or suites of interacting traits according to specific resource limitations [e.g., 14, 15, 16, 17, 18, 19]. Our approach here was to compile a quantitative survey of the large array of the different studies on functional plant traits over the past decade. This information may be useful to investigators for selecting particular traits for study depending on the aims of their study and, if for no other reason, could provide a stronger basis for species and habitat comparisons.

Functional traits in the literature

Several studies have already provided a host of functional traits that are important and relevant for understanding functionality in different habitats or across biomes [e.g., 3, 5, 15, 20, 21, 22, 23, 24, 25, 26, 27]. However, to identify plant functional traits most commonly employed today, we surveyed recent literature (year 2000 and later). The results of the citation survey were quantified according to the number of papers found, authors involved, and the relative frequency ranking compared to the total number of papers scored in our literature search (Tables 1 and 2). We also compiled a list of review papers considered particularly comprehensive and/or significant to this area of research based upon the number of times cited (Table 3). For a comprehensive reference list see Tables S1 and S2 (Supporting Information).

Two primary sources were utilized in our survey, *Google Scholar* and *Web of Science*. Key words searched included plant, function(al), characters, traits, structure, and plasticity, and were entered in all possible combinations using “AND” logic until no new publications were identified. Identified papers were then scrutinized for functional trait content by first reading the abstract or summary, and if pertinent, the entire paper was then read to identify the more detailed information provided about specific traits, their function, and the associated habitats. Where specific traits were related to specific ecophysiological or life history parameters, all such relationships were recorded. Ultimately, the total identified papers and traits utilized were scored and ranked quantitatively according to the criteria described in Tables 1 and 2. Because the title and abstract of a particular paper may not always include any reference to a particular trait as being functional, those papers

Table 1. Total of all plant traits identified in the literature as being functional, except those in the top-ten of most cited (see Table 2). Total percentage (% Tot) refers to the percentage of total publications that included the indicated trait. For information on the citations see Table S1 in Supporting Information.

% Tot		Functional trait	% Tot		Functional trait
≥8-9%	1	Growth form (tussock-forming graminoids, rosettes, cushion plants)	≥0-1%	49	Breeding system (dioecy/monoecy)
	2	Phenology		50	Downy inflorescences
	3	Green biomass amount		51	Flower distribution (solitary; inflorescence)
	4	Life history (annual/perennial)		52	Flower location (terminal; lateral)
≥7-8%	5	Stomatal conductance		53	Inflorescence or flower number
	6	Dispersal mode (unassisted, wind, water, animal, hoarding, ant, launching)		54	Inflorescence size
	7	Leaf density (leaf mass:volume ratio)		55	Leaf chlorophyll:N ratio
	8	Leaf P content		56	Leaf K content
≥5-6%	9	Clonal growth (non-clonal, clonal above ground, clonal below ground)		57	Leaf lipids
	10	Life form (meristem position)		58	Leaf shape (lobed, straight-edged, etc.)
	11	Plant diameter (dbh)		59	Leaf succulence (none, lightly, highly)
	12	Leaf C content		60	Leaf thorniness (none, slightly, very)
	13	Leaf dimension (width, length)		61	Leaf type: sclerophyll vs malacophyll
	14	Leaf N:P ratio		62	Mesophyll CO_2 conductance
	15	Dark respiration rate		63	Nutrient uptake process (e.g., N fixers, endo/ectomycorrhiza, root clusters, orchid roots, hemi/holoparasites, mycoheterotrophs, carnivorous)
	16	Dispersule (seed/fruit) size (length)		64	Pigments; antioxidants
	17	Photosynthetic pathway (C3, C4, CAM)		65	Root depth; distribution
	18	Stomatal density		66	Seed number
	19	Leaf C:N ratio		67	Stem specific density (SSD)
	20	Palatability (palatable/unpalatable)		68	Stem type (a-,uni-, multi-caulous)
≥4-5%	21	Leaf inclination (angle, orientation, curling)		69	Bark thickness
	22	Leaf pubescence (trichome density)		70	Blade and Sheath area
	23	Leaf form, including dissection (simple, once-pinnate, twice-pinnate, etc.)		71	Canopy area

Table 1 continued..

≥3-4%	24	Leaf venation (venation density)	72	Crown/canopy diameter
	25	Pollination mode	73	Fine root density
	26	Cold tolerance (super-cooling/freezing tolerance)	74	Flammability
	27	Leaf:area ratio	75	Foliage area:stem cross-sectional area ratio
	28	Leaf chlorophyll content and a/b ratio	76	Foliar water mass
	29	Root:shoot ratio	77	Growth form (herbs, lianas, trees)
	30	Water use efficiency	78	Habit (e.g., postrate, erect)
	31	Xylem hydraulics	79	Leaf C/P ratio
≥2-3%	32	Leaf toughness (physical strength)	80	Leaf hydraulic conductivity
	33	Relative growth rate (RGR)	81	Leaf perimeter complexity
	34	Leaf area index (LAI)	82	Leafy shoot density in crown/canopy
	35	Leaf arrangement and distribution (e.g., erosulate, rossettes)	83	Leaf surface structures (pubescence, wax, cuticle, outer cell wall, spiny)
	36	Leaf number per unit shoot size (leafing intensity)	84	Leaf tissue: component densities
<2%	37	Lateral spread of branches	85	Leaf type: sun/shade
	38	Non-structural carbohydrates	86	Leaf water potential
	39	Root type (taproot, fibrous, bulb, rhizomatous)	87	Leaf:weight ratio
	40	Specific root length (SRL)	88	Leaf wettability (droplet repulsion, retention and leaf inclination)
	41	Stem dry matter content (SDMC)	89	Leaf underside color: reddish, blue, etc.
	42	Cuticle C content (isotope composition)	90	Mean fine root diameter
	43	Leaf anatomy	91	Monocarpy or polycarpy
	44	Leaf area:root mass ratio	92	Petiole diameter
	45	Leaf type (needle-like, terete, broad leaves)	93	Starch concentration
	46	Leaf water content	94	Stomata distribution (amphi-, hypo-, hyper, stomatous)
	47	Re-sprouting	95	Stomata – Guard/subsidiary cell dimension
	48	Transpiration flux density	96	Stomata position (sunken, even, raised)
			97	Total soluble sugars

Table 2. Summary of top-ten most cited studies involving plant functional traits (out of a total of 225 publications). Our literature search focused on papers published after 2000, although we included prior literature if cited in review papers. Units of measurement are SI regardless of the units reported in the original paper. Abbreviated headings: total number of papers a given trait was cited (# cited); % of times cited out of total papers surveyed (% of total); total number of journals in which each trait was published (# journ); total number of authors on all papers citing each trait (total # auth); mean number of authors per paper (mean # auth/cit); total papers citing trait from 2009 through 2012 (total # cit 09-12); % of total citations occurring in year 2009 through 2012 per total # of citations found (% cit during 09-12/total # of citations). For information on the citations see Table S2 in Supporting Information.

Trait	**Units**	**# cited**	**% of total**	**# journ**	**Total # auth**	**Mean # auth/cit**	**Total # cit 09-12**	**% cit 09-12 over # of cit**
LMA/SLA	$g\ m^{-2}$, $m^2\ mg^{-1}$, $m^2\ g^{-1}$	96	42	39	488	5.1	44	46
Plant height	m, cm	59	26	28	353	5.6	25	42
Leaf N content	$g\ g^{-1}$, % DM, $mmol\ m^{-2}$	57	25	29	324	5.4	24	42
Leaf area	m^2	45	20	22	211	4.7	17	38
Leaf life span/phenol	months	36	16	20	222	5.4	12	33
Leaf thickness	µm	31	14	20	182	5.9	7	23
LDMC	$mg\ g^{-1}$	30	14	17	190	6.3	15	50
Photosyn. capacity	$\mu mol\ m^{-2}\ s^{-1}$, $\mu mol\ g^{-1}\ s^{-1}$	30	14	19	142	4.7	14	47
Seed mass	g	29	13	20	192	5.8	7	24
Wood density	$g\ m^{-3}$	24	11	15	78	3.3	5	21

may have been missed in our survey. We realize that the number of papers and studies where a specific trait was employed may only reflect the difficulty in assigning functionality, while traits with stronger conclusive evidence of functionality may not receive as much attention in the literature from then on.

Functional trait frequency rankings

A total of 225 publications were identified that reported 107 different traits identified by authors as specifically being ‘functional’ (Table 1 and 2). Of these total traits, ones that were outside the most frequently studied, top-ten list (see Table 2 below), occurred in less than 9% [e.g., (19/225)*100] of the papers found in the survey (see Table S1 for a detailed list of references). A total of 68 publications, or 30% (68/225) of all papers identified in our search, also contained other traits reported in <2% of the total papers recorded. Thus, the top-ten most frequently studied functional traits (Table 2) were found in approximately 90% of the total papers identified in the survey.

Table 2 ranks the top-ten plant traits that were cited most often as functional (for a detailed list of references see Table S2). The total number of different journals reporting each of the top-ten traits was greatest for the LMA (= 1/SLA) trait, but that number declined substantially down the list, as did the total number of authors working on each trait. By far, specific leaf mass (LMA, leaf mass per leaf area) or the inverse equivalent, specific leaf area (SLA, leaf area per leaf mass), were the most common functional traits reported (43% of all publications identified) and involved

Table 3. Listing of significant papers based upon the number of functional traits discussed and the amount of evidence associating particular traits with a specific function. Complete references are provided in the Reference section.

Year	Author(s)	Title
1999	Niinemets [30]	Components of Leaf Dry Mass Per Area-Thickness and Density-Alter Leaf Photosynthetic Capacity in Reverse Directions in Woody Plants
1999	Weiher *et al.* [22]	Challenging Theophrastus: A Common Core List of Plant Traits for Functional Ecology
2002	Westoby *et al.* [29]	Plant ecological strategies: Some leading dimensions of variation between species
2003	Reich *et al.* [2]	The evolution of plant functional variation: traits, spectra, and strategies
2004	Wright *et al.* [26]	The worldwide leaf economics spectrum
2006	Westoby & Wright [53]	Land-plant ecology on the basis of functional traits
2007	Brodribb *et al.* [54]	Leaf maximum photosynthetic rate and venation are linked by hydraulics
2007	Niklas *et al.* [55]	"Diminishing returns" in the scaling of functional leaf traits across and within species groups
2009	Niinemets *et al.* [56]	Role of mesophyll diffusion conductance in constraining potential photosynthetic productivity in the field
2009	Poorter *et al.* [18]	Causes and consequences of variation in leaf mass per area (LMA): A meta-analysis

over 480 contributing authors (including co-authorships). Although we grouped LMA and SLA data as the same functional trait, it is worth noting here that SLA was the value reported most frequently in earlier literature (especially agricultural), but most recently LMA has been favored in an ecophysiological, as well as ecosystem context. There may also be logical reasons for favoring the use of LMA over SLA, especially when evaluating leaf-level effects on photosynthetic capabilities [e.g., 28], but not when evaluating whole-plant economics (non-photosynthetic stem tissue) and leaf life span considerations [e.g., 26, 29]. From here on, LMA is used to represent SLA as well.

Studies on LMA accounted for 43% of the total studies identified, while plant height (26%), leaf nitrogen content (25%) and leaf area (20%), were studied less (Table 2). Another decrease in frequency among total studies of specific functional traits occurred for the bottom six of the top-ten list where ≤16% of the studies identified the following traits: leaf life span, leaf thickness, leaf dry matter content (LDMC), photosynthetic capacity, seed mass, and wood density. The total number of authors involved in studies on LMA/SLA was over two-fold greater than the number of total authors reporting the fourth most studied trait, leaf area. Also, the mean number of authors collaborating on studies of specific traits was relatively consistent at between 4.7-6.3 authors per paper, except for the wood density trait (3.3 authors per paper). Thus, a high level of collaborative agreement was apparent for individual studies on the most popular traits, as well as the total number of different authors supporting their classification as functional.

Temporally, the number of the most recent (2009-12) studies was also greatest for LMA (46%) and then declined steadily for traits occurring further down the frequency list (Table 2). The percentage of most recent (2009-12), top-ten papers citing each trait remained very near or within the 35% range for the top five traits, and then declined into the 20% range except for the traits, leaf dry matter content (LDMC = 50%) and photosynthetic capacity (47%). Overall, the total number of papers published prior to 2009 was less than half the number of the most recent (2009-2012) papers. Thus, the data in Table 2 show a distinct quantitative emphasis on LMA for indicating a functional capability such as leaf-level photosynthesis among terrestrial plants. Over 50% of LMA studies were directly related to predicting photosynthetic or growth potential. However, one must remember that scaling from the leaf to the whole-plant level may reveal a quite different picture of a species carbon gain capabilities, with a completely different determination of SLA (1/LMA) based on whole-plant architecture and stem biomass [e.g., 4, 9]. To help clarify the application of more easily measured functional traits for understanding the ecology and physiology of a species, we also compiled a list of review papers since 2000 that we considered particularly comprehensive and/or significant to this area of research (Table 3).

Functional relationship between LMA and photosynthesis

As mentioned above, the most common functional trait cited, by far, was LMA (Table 2) and approximately 50% of this dominant number of citations involved the use of LMA for predicting photosynthesis or growth potential in a species. Yet, it is notable that our evaluation of the functional interpretation of LMA revealed a conceptual problem in connecting this trait to photosynthetic capacity at the leaf level, thus growth potential. Key to understanding LMA as an indicator of the potential for photosynthetic carbon gain of leaves [expressed per unit leaf area (A_{area}) or unit leaf mass (A_{mass})] is the amount of mesophyll cell material and its photosynthetic potency per unit leaf area or mass (Figure 1). For example, additional or larger cells inside a thicker leaf could be identical photosynthetically to the cells of a thinner leaf. Or, these cells could be more photosynthetically potent (e.g. chloroplast content or arrangement), or substantially less potent (i.e. more cuticle and cell wall material typical of sclerophylly). If leaf thickness does not increase in a species or phenotype, then leaf density (LMV, leaf mass per volume), or leaf dry matter content (LDMC), must increase to produce increases in LMA, followed by corresponding increases in A_{area}, and A_{mass}, unless increases in leaf density (LMV) are due to the addition of the non-photosynthetic mass mentioned above (Figure 1). If leaf thickness does increase, several possibilities for changes in A_{area} and A_{mass} are possible depending, once again, on the photosynthetic potential of the added or modified cells. Thus, we believe that the measurement of LMA should be accompanied by the additional measurements described above (and shown schematically in Figure 1) so that a better prediction of photosynthetic and growth potential at the leaf level is possible. The importance of LMV (leaf density) photosynthetically has been considered previously [e.g., 30], as has the constancy of SLA within a species, except for sun/shade leaf differences [e.g., 31, 32].

An often missing component in the literature appears to be measured comparisons between LMA, LMV, and leaf thickness within the framework shown in Figure 1, especially the photosynthetic potential of the LMV term. This is despite the past focus on leaf thickness in the literature for explaining the higher photosynthesis (A_{area}) of sun-versus shade-type leaves in a large number of vascular plant species [see 33 for review]. Leaf thickness has been estimated from SLA (= 1/LMA) and leaf dry matter content (LDMC, dry leaf density) for a variety of species with laminar leaves and growing within contrasting habitat types [32, 34]. Thus, both leaf density and leaf thickness are computable from measurements of leaf dry matter content and LMA. In addition, LDMC may reflect LMV directly, but will still not provide information about photosynthetic potency (see below and Figure 1). As summarized in Shipley [35], the cellular composition of the leaf interior (cell/chloroplast size, number, and shape) is much more variable among plant species compared to the relatively constant components of the subcellular physiological processes such as photosynthesis and respiration [see also 9]. Even the addition of presumably, non-photosynthetic

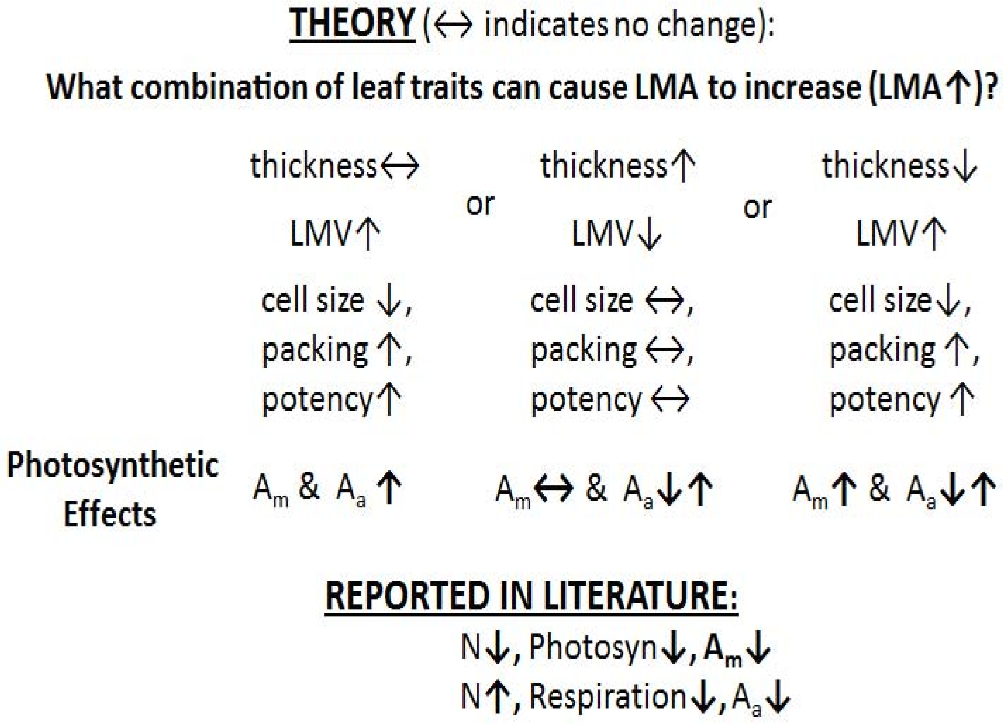

Figure 1. Schematic diagram showing the combinations of leaf functional traits possible that could lead to changes in the most commonly reported functional trait, LMA (= 1/SLA), specifically increases in LMA and, thus, the assumed photosynthetic potential of a leaf. **THEORY**: indicates the conceptual relationships between leaf functional traits and the effects on photosynthesis expressed on a leaf area (A_a) or mass (A_m) basis. Vertical arrows indicate an increase, downward arrows indicate a decrease, and horizontal arrows indicate no change. LMV = Leaf mass per volume (or leaf density). Leaf dry matter content (LDMC) is another expression of leaf density, although the photosynthetic potency of LDMC would still be unknown. **REPORTED IN LITERATURE**: indicates specific relationships reported in the literature, including leaf nitrogen contents (N = nitrogen content) that have been shown to alter photosynthesis. See text for more detailed explanation. A review of the application of most of these parameters for interpreting ecophysiological relationships for species with certain LMA values can be found in Poorter *et al.* [18].

tissue such as thicker mesophyll cell walls (e.g., sclerophylly) may have strong effects on cellular CO_2 diffusion to chloroplasts, possibly similar in magnitude to stomatal limitations [36]. Differences in mesophyll anatomy (e.g., palisade versus spongy mesophyll cells) are also known to vary consistently with such environmental factors as leaf orientation and sunlight exposure [e.g., 37]. An in-depth review of the literature dealing with LMA as a functional trait is found in Poorter *et al.* [18], while a recent study links LMA to the photosynthetic light response curves measured for different species, an example of a relatively rare coupling between a functional trait and a specific ecophysiological parameter [19].

Associating specific functional traits with specific physiological function

According to the schematic in Figure 1, measuring leaf thickness and density would provide greater accuracy for predicting photosynthetic capabilities from LMA [also see 30], but there are additional leaf traits that would also enable a better prediction of potential photosynthetic CO_2 uptake when expressed on both a leaf area or mass basis. These traits include the occurrence of palisade mesophyll, stomatal distribution pattern, and leaf orientation, all of which can be measured relatively quickly and inexpensively in the field [e.g., 37]. The recent report by Brodribb & Feild [38] identifies an easily measureable trait (vein density) that has also been used recently identify photosynthetic potential in plants. They point out that a more rapid water supply to leaf tissue and, thus, stomata, paralleled the evolutionary explosion in angiosperms, probably fuelled by their high photosynthetic capacity expressed today. Several other traits related to plant hydraulics might fit the criteria for a usable functional trait although many of these traits are physiological, requiring considerably greater measurement effort and expense. For one example, there is a strong correlation between water supply efficiency versus mechanical support, especially for taller tree species, the second most cited trait in Table 2.

Identifying critical functional traits: A case history

Can plant functional traits be used to predict future shifts in community spatial patterns, such as in response to climate change? Do functional traits exist, such as the most-reported LMA, which can play dominant roles in establishing community spatial patterns [see 39 for a more detailed discussion]? Consider, as only one example, a strongly contrasting pair of contiguous plant communities-- the subalpine forest and alpine tundra that are commonly separated by the treeline ecotone [e.g., 40, 41, 42, 43, 44, 45]. What functional traits might be most revealing about the mechanisms behind such an abrupt change in community structure? The second most frequently cited trait in Table 2, plant height, has now been identified as a critical functional trait that prevents forest tree survival in the alpine treeline ecotone. The capability for forming a distorted, more bush-like habit closer to the warmer and protective ground surface is important, especially during winter when snow burial can be critical for survival [e.g., 42, 44, 45]. The low stature of alpine vegetation ensures snow burial in winter and protection from the high speed winds, low air temperatures, and desiccation death characteristic of even conifer needles of temperate treelines, and elsewhere [44, 45, 46]. Yet, besides the capability for surviving with a stunted growth form, accompanying differences in leaf, stem, and whole-plant architecture are also critical to survival in the high elevation environment, e.g. evergreen trees with such tall stature [28, 47]. Thus, a suite of developmental, probably co-evolved structural traits, combined with the capability for altering plant height, insure survival of these evergreen tree species [28, 42, 45]. For example, the protective needle-like leaf form of conifer trees replaces the fragile laminar leaf form of the alpine vegetation, yet still enables classical sun/shade phenotypic plasticity via needle packing along sun-exposed stems that enables the thermal capability of a broadleaf to uncouple from air temperature [e.g., 9, 48], as well as the capability for flattening needles and a more planar arrangement on stems, maximizing sunlight absorption in shade shoots. Also, the disappearance of the mesophyll palisade layer typical of a laminar leaf, and the loss of optical propagation of absorbed sunlight found so often in broadleaf species, is replaced functionally by a thicker and more cylindrical needle shape that generates radial diffusion where by both absorbed CO_2 molecules and sunlight photons concentrate toward the center of the leaf [37]. Also critical for taller tree species is the capability for reducing vertical height via prolific lateral bud development, in response to bud death on apical stems that are exposed above the protective snow cover [e.g., 42, 49, 50]. Thus, one might argue that the suite of functional, co-evolved structural traits mentioned above is critical for tree survival above treeline. Several species (e.g., *Pinus* spp) of high elevation trees occur only occasionally at treeline and do not possess the capability for such extreme reduction in height, along with the host of accompanying adaptive traits mentioned above, are found always in highly sheltered microsites, and perish as soon as they grow beyond the boundaries of their protective microsites.

CONCLUSIONS

Informative outcomes of this survey of plant trait studies, identified as involving functional traits, include the recognition of an increasingly large number and variability of functional traits (Table 1 and 2), but also a dominance of papers focusing on a relatively small number of these traits (Table 3). Thus, the choice of which ‘functional’ traits to study is becoming more and more difficult for researchers attempting to link easily measured traits to observed ecophysiological patterns.

Moreover, even the most dominant, cited trait (LMA=1/SLA), appears to need a more definitive, functional determination when interpreting a specific ecophysiological trait such as photosynthetic potential. Although correlative studies comparing possible functional traits with habitat types will continue to provide clues about functionality, more mechanistic studies that better validate the mechanistic functionality of a given trait, or suites of traits, are needed. Thus, identifying traits that serve as the best proxies for ecophysiological adaptation is a distinct challenge for the future, as also recognized previously by others [e.g., 5, 51, 52].

Table S1. References used for values on Table 1.

Trait #	# cit	References
1	20	Albert *et al.* 2010a; Baptist *et al.* 2010; Campbell *et al.* 2010; Cornelissen *et al.* 2003; Díaz *et al.* 2007; Doležal *et al.* 2011; Duckworth *et al.* 2000; Givnish 1987; Harrison *et al.* 2010; Iversen *et al.* 2009; Lavorel and Garnier 2002; Leishman and Westoby 1992; Ma *et al.* 2010; Niu *et al.* 2010; Pellissier *et al.* 2010; Pillar and Sosinski 2003; Ramsay and Oxley 1997; Sieben *et al.* 2009; Sklenář *et al.* 2010; Vile *et al.* 2005
2	19	Acosta *et al.* 2008; Baptist and Choler 2008; Baptist *et al.* 2009; Chu *et al.* 2009; Evju *et al.* 2009; Hallik *et al.* 2009; Kamiyama *et al.* 2010; Li *et al.* 2004; Ma *et al.* 2010; Milla *et al.* 2009; Montalvo *et al.* 1991; Niinemets *et al.* 2006; Niinemets *et al.* 2007b; Niu *et al.* 2010; Oyarzabal *et al.* 2008; Pérez-Camacho *et al.* 2012; Petchey *et al.* 2004; Reich *et al.* 2003; Weiher *et al.* 1999
3	18	Acosta *et al.* 2008; Ansquer *et al.* 2009; Bernhardt-Romermann *et al.* 2008; Doležal *et al.* 2011; Duckworth *et al.* 2000; Evju *et al.* 2009; Funk *et al.* 2008; Harrison *et al.* 2010; Hülber *et al.* 2010; Iversen *et al.* 2009; Montalvo *et al.* 1991; Pakeman and Quested 2009; Pakeman *et al.* 2009; Pérez-Camacho *et al.* 2012; Pywell *et al.* 2003; Thuiller *et al.* 2004; Trtikova *et al.* 2010; Weiher *et al.* 1999
4	17	Acosta *et al.* 2008; Alexander *et al.* 2009; Bernhardt-Romermann *et al.* 2008; Campbell *et al.* 2010; Craine *et al.* 2001; Díaz *et al.* 2001; Díaz *et al.* 2007; Givnish 1987; Hodgson *et al.* 2005; Lavorel and Garnier 2002; Montalvo *et al.* 1991; Pakeman and Quested 2009; Pillar and Sosinski 2003; Pywell *et al.* 2003; Reich *et al.* 2003; Rossetto *et al.* 2009; Weiher *et al.* 1999
5	17	Azócar *et al.* 2007; Feild *et al.* 2009; Givnish 1987; Grulke 2010; Jin *et al.* 2011; Kramer *et al.* 2010; Meinzer 2003; Niinemets *et al.* 2007b; Niinemets *et al.* 2009a; Poorter and Bongers 2006; Reich *et al.* 2003; Santiago *et al.* 2004; Santiago and Wright 2007; Smith *et al.* 2009; Smith *et al.* 2011; Wright *et al.* 2004; Zhang *et al.* 2011
6	16	Acosta *et al.* 2008; Bernhardt-Romermann *et al.* 2008; Cornelissen *et al.* 2003; Díaz *et al.* 1998; Dirnböck and Dullinger 2011; Doležal*et al.* 2011; Duckworth *et al.* 2000; McIntyre *et al.* 1995; Montalvo *et al.* 1991 Pakeman and Quested 2009; Pakeman *et al.* 2009; Pellissier *et al.* 2010; Pywell *et al.* 2003; Řěhounková and Prach 2010; Thuiller *et al.* 2004; Weiher *et al.* 1999
7	16	Bussotti 2008; Craine and Towne 2010; Harrison *et al.* 2010; Hodgson *et al.* 2005; Hoch and Körner 2005; Kitajima and Poorter 2010; Milla *et al.* 2009; Milla and Reich 2011; Niinemets 1999; Niinemets 2001; Niinemets *et al.* 2007a; Niinemets *et al.* 2009a; Niklas *et al.* 2007; Prior *et al.* 2003; Shipley and Vu 2002; Vernescu and Ryser 2009
8	15	Cornelissen *et al.* 2003; Doležal *et al.* 2011; Evju *et al.* 2009; Lavorel *et al.* 2010; Leishman *et al.* 2007; Macek *et al.* 2009; Niinemets 1999; Niklas *et al.* 2007; Prior *et al.* 2003; Quétier *et al.* 2007; Reich *et al.* 2003; Santiago and Wright 2007; Smith *et al.* 2011; Ustin and Gamon 2010; Wright *et al.* 2004
9	13	Bernhardt-Romermann *et al.* 2008; Cornelissen *et al.* 2003; Díaz and Cabido 1997; Doležal *et al.* 2011; Duckworth *et al.* 2000; Evju *et al.* 2009; McIntyre *et al.* 1995; Pakeman and Quested 2009; Pakeman *et al.* 2009; Pellissier *et al.* 2010; Pywell *et al.* 2003; Rehounkova and Prach 2010; Weiher *et al.* 1999

Table S1 continued..

10	13	Cornelissen *et al.* 2003; Doležal *et al.* 2011; Duckworth *et al.* 2000; Garnier *et al.* 2001; Harrison *et al.* 2010; Kamiyama *et al.* 2010; Leishman and Westoby 1992; McIntyre *et al.* 1995; Pakeman *et al.* 2009; Pellissier *et al.* 2010; Pillar and Sosinski 2003; Pywell *et al.* 2003; Rehounkova and Prach 2010
11	13	Brzeziecki and Kienast 1994; Ceriani *et al.* 2009; Cierjacks *et al.* 2008; Duckworth *et al.* 2000; Fajardo and Piper 2011; Gonzalo-Turpin and Hazard 2009; Kabeya 2010; Kraft *et al.* 2008; Li *et al.* 2004; Milla 2009; Milla *et al.* 2009; Scheepens *et al.* 2010; Trtikova *et al.* 2010
12	12	Albert *et al.* 2010b; Ansquer *et al.* 2009; Baptist *et al.* 2010; Ceriani *et al.* 2009; Grulke *et al.* 2010; Li *et al.* 2004; Macek *et al.* 2009; Niinemets *et al.* 2006; Niinemets *et al.* 2007b; Oyarzabal *et al.* 2008; Pakeman *et al.* 2009; Quétier *et al.* 2007
13	12	Aerts and Chapin 2000; Cornelissen *et al.* 2003; Hedin 2004; Kerkhoff *et al.* 2005; Koerselman and Meuleman 1996; Leishman *et al.* 2007; Macek *et al.* 2009; McGroddy *et al.* 2004; Niklas *et al.* 2005; Reich and Oleksyn 2004; Westoby and Wright 2006; Wright *et al.* 2004
14	11	Azócar *et al.* 2007; Hattenschwiler 2001; Leishman *et al.* 2007; Lusk *et al.* 2008; Poorter and Bongers 2006; Reich *et al.* 1997; Reich *et al.* 1998; Reich *et al.* 2003; Trouwborst *et al.* 2011; Ustin and Gamon 2010; Wright *et al.* 2005
15	11	Ackerly 2009; Alexander *et al.* 2009; Cornelissen *et al.* 2003; Díaz *et al.* 1998; Dirnböck and Dullinger 2009; Duckworth *et al.* 2000; Niu *et al.* 2010; Pellissier *et al.* 2010; Pywell *et al.* 2003; Rossetto *et al.* 2009; Trtikova *et al.* 2010
16	11	Givnish 1987; Kessler *et al.* 2007; Martorell and Ezcurra 2007; Niklas *et al.* 2007; Oyarzabal *et al.* 2008; Price and Enquist 2007; Reich *et al.* 2003; Vernescu and Ryser 2009; Wilson *et al.* 1999; Zhu *et al.* 2009; Zhu *et al.* 2010
17	11	Brodribb *et al.* 2007; Brodribb and Feild 2010; Feild *et al.* 2009; Feild *et al.* 2011; Kessler *et al.* 2007; Kitajima and Poorter 2010; Niinemets *et al.* 2007b; Roth-Nebelsick *et al.* 2001; Uhl 1999; Uhl and Moosebrugger 1999; Walls 2011
18	11	Acosta *et al.* 2008; Cornelissen *et al.* 2003; Díaz and Cabido 1997; Duckworth *et al.* 2000; Edwards and Still 2008; Givnish 1987; Kindscher and Wells 1995; Lavorel and Garnier 2002; Oyarzabal *et al.* 2008; Reich *et al.* 2003; Sieben *et al.* 2010
19	11	Chen *et al.* 2001; Feild *et al.* 2011; Kessler *et al.* 2007; Jin *et al.* 2011; Köerner *et al.* 1989; McElwain 1998; McElwain *et al.* 1999; Premoli and Brewer 2007; Schoettle and Rochelle 2000; Woodward 1987; Zhang *et al.* 2011
20	10	Ansquer *et al.* 2009; Baptist *et al.* 2009; Ceriani *et al.* 2009; De Deyn *et al.* 2008; Doležal *et al.* 2011; Evju *et al.* 2009; Louault *et al.* 2005; Macek *et al.* 2009; Pakeman *et al.* 2009; Reich *et al.* 2003
21	10	Aryal and Neuner 2010; Baptist and Choler 2008; Craine *et al.* 2011; Díaz *et al.* 1998; Duckworth *et al.* 2000; Givnish 1987; Kamiyama *et al.* 2010; Russell *et al.* 2009; Ustin and Gamon 2010
22	10	Acosta *et al.* 2008; Duckworth *et al.* 2000; Gutschick 1999; Kadioglu *et al.* 2012; Kessler *et al.* 2007; Leishman and Westoby 1992; Manetas 2003; Press 1999; Watkins *et al.* 2006; Zhu *et al.* 2010
23	9	Acosta *et al.* 2008; Díaz and Cabido 1997; Díaz *et al.* 2007; Duckworth *et al.* 2000; Kitajima and Poorter 2010; Leishman and Westoby 1992; Montalvo *et al.* 1991; Smith *et al.* 2011; Weiher 1999
24	8	Chaoner and Creber 1990; Givnish 1987; Kessler *et al.* 2007; Koehl 1996; Niinemets and Kull 1999; Niinemets *et al.* 2006; Press 1999; Yang *et al.* 2009
25	8	Bernhardt-Romermann *et al.* 2008; Díaz and Cabido 1997; Doležal *et al.* 2011; Duckworth *et al.* 2000; Hülber *et al.* 2010; Kindsher and Wells 1995; Pakeman *et al.* 2009; Rehounkova and Prach 2010

Table S1 continued..

26	7	Azócar *et al*. 2007; Baptist *et al*. 2009; Cornelissen *et al*. 2003; Harrison *et al*. 2010; Rada *et al*. 2008; Sklenář *et al*. 2010; Viveros-Viveros *et al*. 2009
27	7	Givnish 1987; Hallik *et al*. 2009; Jin *et al*. 2011; Poorter and Bongers 2006; Prior *et al*. 2003; Trouwborst *et al*. 2011; Velázquez-Rosas *et al*. 2010
28	7	Duckworth *et al*. 2000; Evju *et al*. 2009; van Kleunen *et al*. 2010; Ma *et al*. 2010; Reader 1993; Reich *et al*. 2003; Ustin and Gamon 2010
29	7	Grulke *et al*. 2010; Meinzer 2003; Oyarzabal *et al*. 2008; Poorter and Bongers 2006; Premoli and Brewer 2007; Smith *et al*. 2009; Smith *et al*. 2011
30	7	Chave *et al*. 2009; Maherali *et al*. 2004; Reich *et al*. 2003; Santiago *et al*. 2004; Smith *et al*. 2011; Sperry 2005; Westoby and Wright 2006
31	6	Hattenschwiler 2001; Kamiyama *et al*. 2010; van Kleunen *et al*. 2010; Ma *et al*. 2010; Poorter and Navas 2003; Reich *et al*. 2003
32	5	Baptist and Choler 2008; Baptist *et al*. 2009; Cohen *et al*. 1995; van Kleunen *et al*. 2010; Kamiyama *et al*. 2010
33	5	Acosta *et al*. 2008; Bernhardt-Romermann *et al*. 2008; Doležal *et al*. 2011; Givnish 1987; Montalvo *et al*. 1991
34	5	Duckworth *et al*. 2000; Hills *et al*. 1994; Milla 2009; Milla and Reich 2011; Yang *et al*. 2010
35	5	Díaz *et al*. 2001; Díaz *et al*. 2004; Kitajima and Poorter 2010; Pillar and Sosinski 2003; Quétier *et al*. 2007
36	5	Hodgson *et al*. 2005; Poorter and Navas 2003; Poorter and Bongers 2006; Reich *et al*. 2003; Shipley 2006
37	4	Bansal and Germino 2010; Hoch and Körner 2005; Kabeya 2010; Li *et al*. 2004
38	4	Acosta *et al*. 2008; Duckworth *et al*. 2000; Leishman and Westoby 1992; Montalvo *et al*. 1991
39	4	Craine *et al*. 2001; Cornelissen *et al*. 2003; Hattenschwiler 2001; Lavorel and Garnier 2002
40	4	Cornelissen *et al*. 2003; Doležal *et al*. 2011; Pakeman and Quested 2007; Trtikova *et al*. 2010
41	3	Díaz and Cabido 1997; Duckworth *et al*. 2000; Macek *et al*. 2009
42	3	Bernhardt-Romermann *et al*. 2008; Brodribb *et al*. 2007; Pellissier *et al*. 2010
43	3	Hattenschwiler 2001; Li *et al*. 2004; Ma *et al*. 2010
44	3	Bernhardt-Romermann *et al*. 2008; Dirnböck and Dullinger 2004; Petchey *et al*. 2004
45	3	Niinemets 1999; Pellissier *et al*. 2010; Reich *et al*. 1998
46	3	Hulshof and Swenson 2010; Vendramini *et al*. 2002; Weiher *et al*. 1999
47	3	Cornelissen *et al*. 2003; Rossetto *et al*. 2009; Weiher *et al*. 1999
48	3	Azócar *et al*. 2007; Jin *et al*. 2011; Macek *et al*. 2009
49	2	Aryal and Neuner 2010; Tsukaya and Tsuge 2001
50	2	Acosta *et al*. 2008; Montalvo *et al*. 1991
51	2	Acosta *et al*. 2008; Montalvo *et al*. 1991
52	2	Cierjacks *et al*. 2008; Trtikova *et al*. 2010
53	2	Zhu *et al*. 2009; Zhu *et al*. 2010
54	2	Givnish 1987; Hallik *et al*. 2009
55	2	Hoch and Körner 2005; Villar and Merino 2001
56	2	Givnish 1987; Niinemets *et al*. 2007b

Table S1 continued..

57	2	Díaz and Cabido 1997; Duckworth *et al*. 2000
58	2	Díaz and Cabido 1997; Duckworth *et al*. 2000
59	2	Harrison *et al*. 2010; Pellissier *et al*. 2010
60	2	Niinemets *et al*. 2009a,b
61	2	Trtikova *et al*. 2010; Velázquez-Rosas *et al*. 2010
62	2	Ceriani *et al*. 2009; Evju *et al*. 2010
63	2	Cornelissen *et al*. 2003; Weiher *et al*. 1999
64	2	Acosta *et al*. 2008; Montalvo *et al*. 1991
65	1	Cornelissen *et al*. 2003
66	1	Oyarzabal *et al*. 2008
67	1	Vamosi and Queenborough 2010
68	1	Milla *et al*. 2009
69	1	Cierjacks *et al*. 2008
70	1	Craine *et al*. 2001
71	1	Cornelissen *et al*. 2003
72	1	Li *et al*. 2004
73	1	Niklas *et al*. 2007
74	1	Santiago and Wright 2007
75	1	Díaz *et al*. 2007
76	1	Evju *et al*. 2010
77	1	Santiago *et al*. 2004
78	1	Santiago and Wright 2007
79	1	Milla and Reich 2011
80	1	Cohen *et al*. 1995
81	1	Pillar and Sosinski 2003
82	1	Niinemets 1999
83	1	Velázquez-Rosas *et al*. 2010
84	1	Azócar *et al*. 2007
85	1	Funk *et al*. 2008
86	1	Aryal and Neuner 2010
87	1	Givnish 1987
88	1	Craine *et al*. 2001
89	1	Pywell *et al*. 2003
90	1	Cornelissen *et al*. 2003
91	1	Price and Enquist 2007
92	1	Cornelissen *et al*. 2003
93	1	Li *et al*. 2004
94	1	Givnish 1987

Table S1 continued..

95	1	Zhang *et al*. 2011
96	1	Zhang *et al*. 2011
97	1	Li *et al*. 2004

Full references for Table S1

Ackerly, D. 2009, Proc. Natl. Acad. Sci. USA, 106(Suppl.), 19699.

Acosta, B., Sánchez-Jardón, L., del Pozo, A., García-Ibáñez, E., Casado, M. A., Montalvo, J. and Pineda, F. D. 2008, Acta Oecol., 34, 26.

Aerts, R. and Chapin, F. I. 2000, Adv. Ecol. Res., 30, 1.

Albert, C. H., Thuiller, W., Yoccoz, N. G., Soudant, A., Boucher, F., Saccone, P. and Lavorel, S. 2010a, J. Ecol., 98, 604.

Albert, C. H., Thuiller, W., Yoccoz, N. G., Douzet, R., Aubert, S. and Lavorel, S. 2010b, Funct. Ecol., 24, 1192.

Alexander, J. M., Edwards, P. J., Poll, M., Parks, C. G. and Dietz, H. 2009, Ecology, 90, 612.

Ansquer, P., Duru, M., Theau, J. P. and Cruz, P. 2009, Ecol. Indic., 9, 1020.

Aryal, B. and Neuner, G. 2010, Oecologia, 162, 1.

Azócar, A., Rada, F. and García-Núñez, C. 2007, Interciencia, 32, 663.

Bansal, S. and Germino, M. J. 2010, J. Veg. Sci., 21, 133.

Baptist, F. and Choler, P. 2008, Ann. Bot., 101, 549.

Baptist, F., Yoccoz, N. G. and Choler, P. 2009, Plant Soil, 328, 397.

Baptist, F., Flahaut, C., Streb, P. and Choler, P. 2010, Plant Biol., 12, 755.

Bernhardt-Romermann, M., Romermann, C., Nuske, R., Parth, A., Klotz, S., Schmidt W. and Stadler, J. 2008, Oikos, 117, 1533.

Brodribb, T. J., Feild, T. S. and Jordan, G. J. 2007, Plant Physiol., 144, 1890.

Brodribb, T. J. and Feild, T. S. 2010, Ecol. Lett., 13, 175.

Brzeziecki, B. and Kienast, F. 1994, Forest Ecol. Manag., 69, 167.

Bussotti, F. 2008, Glob. Change Biol., 14, 2727.

Campbell, W. B., Freeman, D. C., Emlen, J. M. and Ortiz, S. L. 2010, Ecol. Indic., 10, 676.

Ceriani, R. M., Pierce, S. and Cerabolini, B. 2009, Plant Ecol., 204, 1.

Chaloner, W. G. and Creber, G. T. 1990, J. Geol. Soc., 147, 343.

Chave, J., Coomes, D., Jansen, S., Lewis, S. L., Swenson, N. G. and Zanne, A. E. 2009, Ecol. Lett., 12, 351.

Chen, L.-Q., Li, C.-S., Chaloner, W. G., Beerling, D. J., Sun, Q-J., Collinson, M. E. and Mitchell, P. L. 2001, Am. J. Bot., 88, 1309.

Chu, C., Wang, Y., Li, Q., Zhao, L., Ren, Z., Xiao, S., Yuan, J. and Wang, G. 2009, J. Plant Ecol., 2, 135.

Cierjacks, A., Salgado, S., Wesche, K. and Hensen, I. 2008, Biotropica, 40, 176.

Cohen, S., Mosoni, P. and Meron, M. 1995, Agr. Forest Meterol., 76, 185.

Cornelissen, J. H. C. A., Lavorel, S. B., Garnier, E. B., Díaz, S., Buchmann, N., Gurvich, D. E., Reich, P. B., ter Steege, H., Morgan, H. D., van der Heijden, M. G. A., Pausas, J. G. and Poorter, H. 2003, Aus. J. Bot., 51, 335.

Craine, J. M., Froehle, J., Tilman, D. G., Wedin, D. A. and Chapin III, F. S. 2001, Oikos, 93, 274.

Craine, J. M. and Towne, E. G. 2010, Plant Soil, 337, 193.

De Deyn, G. B., Cornelissen, J. H. C. and Bardgett, R. D. 2008, Ecol. Lett., 11, 516.

Díaz, S. and Cabido, M. 1997, J. Veg. Sci., 8, 463.

Díaz, S., Cabido, M. and Casanoves, F. 1998, J. Veg. Sci., 9, 113.

Díaz, S., Noy-Meir, I. and Cabido, M. 2001, J. App. Ecol., 38, 497.

Díaz, S., Hodgson, J. G., Thompson, K., Cabido, M., Cornelissen, J. H. C., Jalili, A., Montserrat-Martí, G., Grime, J. P., Zarrinkamar, F., Asri, Y., Band, S. R., Basconcelo, S., Castro-Díez, P., Funes, G., Hamzehee, B., Khoshnevi, M., Pérez-Harguindeguy, N., Pérez-Rontomé, M. C., Shirvany, F. A., Vendramini, F., Yazdani, S., Abbas-Azimi, R., Bogaard, A., Boustani, S., Charles, M., Dehghan, M., de Torres-Espuny, L., Falczuk, V., Guerrero-Campo, J., Hynd, A., Jones, G., Kowsary, E., Kazemi-Saeed, F., Maestro-Martínez, M., Romo-Díez, A., Shar, S., Siavash, B., Villar-Salvador, P. and Zak, M. R. 2004, J. Veg. Sci., 15, 295.

Díaz, S., Lavorel, S., McIntyre, S., Falczuk, V., Casanoves, F., Milchunas, D. G., Skarpe, C., Rusch, G., Sternberg, M., Noy-Meir, I., Landsberg, J., Zhang, W., Clark, H. and Campbell, B. D. 2007, Glob. Change Biol., 13, 313.

Dirnkböck, T. and Dullinger, S. 2011, J. Veg. Sci., 15, 77.

Doležal, J., Mašková, Z., Lepš, J., Steinbachová, D., de Bello, F., Klimešová, J., Tackenberg, O., Zemek, F. and Kvet, J. 2011, Agr. Ecosyst. Env., 145, 10.

Duckworth, J. C., Kent, M. and Ramsay, P. M. 2000, Prog. Phys. Geog., 4, 515.

Edwards, E. J. and Still, C. J. 2008, Ecol. Lett., 11, 266.

Evju, M., Austrheim, G., Halvorsen, R. and Mysterud, A. 2009, Oecologia, 161, 77.

Fajardo, A. and Piper, F. I. 2011, New Phytol., 189, 259.

Feild, T. S., Chatelet, D. S. and Brodribb, T. J. 2009, Geobiology, 7, 237.

Feild, T. S., Upchurch, G. R., Chatelet, D. S., Brodribb, T. J., Grubbs, K. C., Samain, M-S. and Wanke, S. 2011, Paleobiology, 37, 195.

Funk, J. L., Cleland, E. E., Suding, K. N. and Zavaleta, E. S. 2008, Trends Ecol. Evol., 23, 695.

Garnier, E., Laurent, G. and Bellmann, A. 2001, New Phytol., 152, 69.

Givnish, T. J. 1987, New Phytol., 106, 131.

Gonzalo-Turpin, H. and Hazard, L. 2009, J. Ecol., 97, 742.

Grulke, N. E. 2010, Environ. Pollut., 158, 2032.

Gutschick, V. P. 1999, New Phytol., 143, 3.

Hallik, L., Kull, O., Niinemets, Ü. and Aan, A. 2009, Basic Appl. Ecol., 10, 309.

Harrison, S. P., Prentice, I. C., Barboni, D., Kohfeld, K. E., Ni, J. and Sutra, J-P. 2010, J. Veg. Sci., 21, 300.

Hättenschwiler, S. 2001, Oecologia, 129, 31.

Hedin, L. O. 2004, Proc. Natl. Acad. Sci. USA, 101, 10849.

Hills, J. M., Murphy, K. J., Pulford, I. D. and Flowers, T. H. 1994, Funct. Ecol., 8, 242.

Hoch, G. and Körner, C. 2005, Funct. Ecol., 19, 941.

Hodgson, J. G., Montserrat-Martí, G., Cerabolini, B., Ceriani, R. M., Maestro-Martínez, M., Peco, B., Wilson, P. J., Thompson, K., Grime, J. P., Band, S. R., Bogard, A., Castro-Díez, P., Charles, M., Jones, G., Pérez-Rontomé, M. C., Caccianiga, M., Alard, D., Bakker, J. P., Cornelissen, J. H. C., Dutoit, T., Grootjans, A. P., Guerrero-Campo, J., Gupta, P. L., Hynd, A., Kahmen, S., Poschold, P., Romo-Díez, A., Rorison, I. H., Rosén, E., Schreiber, K-F., Tallowin, J., de Torres Espuny, L. and Villar-Salvador, P. 2005, Basic Appl. Ecol., 6, 119.

Hülber, K., Winkler, M. and Grabherr, G. 2010, Funct. Ecol., 24, 245.

Hulshof, C. M. and Swenson, N. G. 2010, Funct. Ecol., 24, 217.

Iversen, M., Bråthen, K. A., Yoccoz, N. G. and Ims, R. A. 2009, J. Veg. Sci., 20, 903.

Jin, B., Wang, L., Wang, J., Jiang, K-Z., Wang, Y., Jiang, X-X., Ni, C-Y., Wang, Y-L. and Teng, N-J. 2011, BMC Plant Biol., 11, 35.

Kabeya, D. 2010, Arct. Antarct. Alp. Res., 42, 430.

Kadioglu, A., Terzi, R., Saruhan, N. and Saglam, A. 2012, Plant Science, 182, 42.

Kamiyama, C., Oikawa, S., Kubo, T. and Hikosaka, K. 2010, Oecologia, 164, 591.

Kerkhoff, A. J., Enquist, B. J., Elser, J. J. and Fagan, W. F. 2005, Global Ecol. Biogeogr., 14, 585.

Kessler, M., Siorak, Y., Wunderlich, M. and Wegner, C. 2007, Funct. Plant Biol., 34, 963.

Kindscher, K. and Wells, P. V. 1995, Vegetatio, 117, 29.

Kitajima, K. and Poorter, L. 2010, New Phytol., 186, 708.

van Kleunen, M., Weber, E. and Fischer, M. 2010, Ecol. Lett., 13, 235.

Koehl, M. A. R. 1996, Annu. Rev. Ecol. Evol. S., 27, 501.

Köerner, C., Neumayer, M., Menendez-Reidl, S. P. and Smeets-Scheel, A. 1989, Flora, 182, 353.

Koerselman, W. and Meuleman, A. F. M. 1996. J. App. Ecol., 33, 1441.

Kraft, N. J. B., Valencia, R. and Ackerly, D. D. 2008, Science, 322, 580.

Kramer, K., Degen, B., Buschbom, J., Hickler, T., Thuiller, W., Sykes, M. T. and de Winter, W. 2010, Forest Ecol. Manag., 259, 2213.

Lavorel, S. and Garnier, E. 2002, Funct. Ecol., 16, 545.

Lavorel, S., Grigulis, K. and Lamarque, P. 2010, J. Ecol., 99, 135.

Leishman, M. R. and Westoby, M. 1992, J. Ecol., 80, 417.

Leishman, M. R., Haslehurst, T., Ares, A. and Baruch, Z. 2007, New Phytol., 176, 635.

Li, C., Liu, S. and Berninger, F. 2004, Trees - Struct. Funct., 18, 277.

Louault, F., Pillar, V. D., Garnier, E. and Soussana, J. F. 2005, J. Veg. Sci., 16, 151.

Lusk, C. H., Reich, P. B., Montgomery, R. A., Ackerly, D. D. and Cavender-Bares, J. 2008, Trends Ecol. Evol., 23, 299.

Ma, W., Shi, P., Li, W., He, Y., Zhang, X., Shen, X. and Chai, S. 2010, Science China, 53, 1142.

Macek, P., Macková, J. and de Bello, F. 2009, Acta Oecol., 35, 778.

Maherali, H., Pockman, W. T. and Jackson, R. B. 2004, Ecology, 85, 2184.

Manetas, Y. 2003, New Physiol., 158, 503.

Martorell, C. and Ezcurra, E. 2007, Oecologia, 151, 561.

McElwain, J. C. 1998. Philos.T. Roy. Soc. B, 353, 83.

McElwain, J. C., Beerling, D. J. and Woodward, F. I. 1999, Science, 285, 1386.

McGroddy, M. E., Daufresne, T. and Hedin, L. O. 2004, Ecology, 85, 2390.

McIntyre, S., Lavorel, S. and Tremont, R. M. 1995, J. Ecol., 83, 31.

Meinzer, F. C. 2003, Oecologia, 134, 1.

Milla, R. 2009, J. Ecol., 97, 972.

Milla, R., Giménez-Benavides, L., Escudero, A. and Reich, P. B. 2009, Funct. Ecol., 23, 111.

Milla, R. and Reich, P. B. 2011, Ann. Bot., 107, 455.

Montalvo, J., Casado, M. A., Levassor, C. and Pineda, F. D. 1991, J. Veg. Sci., 2, 655.

Niinemets, Ü. 1999, New Phytol., 144, 35.

Niinemets, Ü. 2001, Ecology, 82, 453.

Niinemets, Ü. and Kull, O. 1999, Tree Physiol., 18, 467.

Niinemets, Ü., Portsmuth, A. and Tobias, M. 2006, New Phytol., 171, 91.

Niinemets, Ü., Portsmuth, A., Tena, D., Tobias, M., Matesanz, S. and Valladares, F. 2007a, Ann. Bot., 100, 283.

Niinemets, Ü., Portsmuth, A. and Tobias, M. 2007b, Funct. Ecol., 21, 28.

Niinemets, Ü., Díaz-Espejo, A., Flexas, J., Galmés, J. and Warren, C. R. 2009a, J. Exp. Bot., 60, 2249.

Niinemets, Ü., Wright, I. J. and Evans, J. R. 2009b, J. Exp. Bot., 60, 2433.

Niklas, K. J., Owens, T., Reich, P. B. and Cobb, E. D. 2005, Ecol. Lett., 8, 636.

Niklas, K. J., Cobb, E. D., Niinemets, Ü., Reich, P. B., Sellin, A., Shipley, B. and Wright, I. J. 2007, Proc. Natl. Acad. Sci. USA, 104, 8891.

Niu, K., Zhang, S., Zhao, B. and Du, G. 2010, Plant Soil, 330, 215.

Oyarzabal, M., Paruelo, J. M., del Pino, F., Oesterheld, M. and Lauenroth, W. K. 2008, J. Veg. Sci., 19, 183.

Pakeman, R. J. and Quested, H. M. 2009, Applied Vegetation Science, 10, 91.

Pakeman, R., Lepš, J., Kleyer, M., Lavorel, S., Garnier, E. and VISTA Consortium, 2009, J. Veg. Sci., 20, 148.

Pellissier, L., Fournier, B., Guisan, A. and Vittoz, P. 2010, Plant Ecol., 211, 351.

Pérez-Camacho, L., Rebollo, S., Hernández-Santana, V., García-Salgado, G., Pavón-García, J. and Gómez-Sal, A. 2012, Funct. Ecol., 26, 740.

Petchey, O. L., Hector, A. and Gaston, K. J. 2004, Ecology, 85, 847.

Pillar, V. D. and Sosinski Jr. E. E. 2003, J. Veg. Sci., 14, 323.

Poorter, H. and Navas, M.-L. 2003, New Phytol., 157, 175.

Poorter, L. and Bongers, F. 2006, Ecology, 87, 1733.

Premoli, A. C. and Brewer, C. A. 2007, Aus. J. Bot., 55, 585.

Press, M. C. 1999, New Phytol., 143, 213.

Price, C. A. and Enquist, B. J. 2007, Ecology, 88, 1132.

Prior, L. D., Eamus, D. and Bowman, D. 2003, Funct. Ecol., 17, 504.

Pywell, R. F., Bullock, J. M., Roy, D. B., Warman, L., Walker, K. J. and Rothery, P. 2003, J. App. Ecol., 40, 65.

Quétier, F., Thébault, A. and Lavorel, S. 2007, Ecol. Monogr., 77, 33.

Rada, F., Briceño, B. and Azócar, A. 2008, Revista chilena de historia natural, 81, 335.

Ramsay, P. M. and Oxley, E. R. B. 1997, Plant Ecol., 131, 173.

Reader, R. J. 1993, J. Ecol., 81, 169.

Řehounková, K. and Prach, K. 2010, Basic Appl. Ecol., 11, 45.

Reich, P. B., Walters, M. B. and Ellsworth, D. S. 1997, Proc. Natl. Acad. Sci. USA, 94, 13730.

Reich, P. B., Walters, M. B., Ellsworth, D. S., Vose, J. M., Volin, J. C., Gresham, C. and Bowman, W. D. 1998, Oecologia, 114, 471.

Reich, P. B., Wright, I. J., Cavender-Bares, J. C., Craine, J. M., Oleksyn, J., Westoby, M. and Walters, M. B. 2003, Int. J. Plant Sci., 164, S143.

Reich, P. B. and Oleksyn, J. 2004, Proc. Natl. Acad. Sci. USA, 101, 11001.

Rossetto, M., Crayn, D., Ford, A., Mellick, R. and Sommerville, K. 2009, Mol. Ecol., 18, 1422.

Roth-Nebelsick, A., Uhl, D., Moosbrugger, V. and Kerp, H. 2001, Ann. Bot., 87, 553.

Russell, R. B., Lei, T. T. and Nilsen, E. T. 2009, Funct. Ecol., 23, 463.

Santiago, L. S., Goldstein, G., Meinzer, F. C., Fisher, J. B., Machado, K., Woodruff, D. and Jones, T. 2004, Oecologia, 140, 543.

Santiago, L. S. and Wright, S. J. 2007, Funct. Ecol., 21, 19.

Scheepens, J. F., Frei, E. S. and Stöcklin, J. 2010, Oecologia, 164, 141.

Schoettle, A. W. and Rochelle, S. G. 2000, Am. J. Bot., 87, 1797.

Shipley, B. and Vu, T.-T. 2002, New Phytol., 153, 359.

Sieben, E. J. J., Morris, C. D., Kotze, D. C. and Muasya, A. M. 2010, Plant Ecol., 207, 107.

Sklenář, P., Kučerová, A., Macek, P. and Macková, J. 2010, Austral Ecol., 35, 929.

Smith, W. K., Germino, M. J., Johnson, D. M. and Reinhardt, K. 2009, Bot. Rev., 75, 163.

Smith, E. A., Collette, S. B., Boynton, T. A., Lilrose, T., Stevens, M. R., Bekker, M. F., Eggett, D. and St Clair, S. B. 2011, Tree Physiol., 31, 68.

Sperry, J. S. 2003, Int. J. Plant Sci., 164, S115.

Thuiller, W., Lavorel, S., Midgley, G., Lavergne, S. and Rebelo, T. 2004, Ecology, 85, 1688.

Trouwborst, G., Hogewoning, S. W., Harbinson, J. and van Ieperen, W. 2011, Physiologia plantarum, 142, 157.

Trtikova, M., Edwards, P. J. and Güsewell, S. 2010, Ecography, 33, 556.

Tsukaya, H. and Tsuge, T. 2001, Plant Biol., 3, 536.

Uhl, D. and Moosebrugger, V. 1999, Paleogeogr., Paleoclimatol., Paleoecol., 149, 15.

Ustin, S. L. and Gamon, J. A. 2010, New Phytol., 186, 795.

Vamosi, S. M. and Queenborough, S. A. 2010, J. Biogeogr., 37, 465.

Velázquez-Rosas, N., Barradas, V. L., Vázquez-Santana, S., Cruz-Ortega, R., García-Jiménez, F., Toledo-Alvarado, E. and Orozco-Segovia, A. 2010, Acta Oecol., 36, 587.

Vendramini, F., Díaz, S., Gurvich, D. E., Wilson, P. J., Thompson, K. and Hodgson, J. G. 2002, New Phytol., 154, 147.

Vernescu, C. and Ryser, P. 2009, Am. J. Bot., 96, 1068.

Vile, D., Garnier, E., Shipley, B., Laurent, G., Navas, M.-L., Roumet, C., Lavorel, S., Díaz, S., Hodgson, J. G., Lloret, F., Midgley, G. F., Poorter, H., Rutherford, M. C., Wilson, P. J. and Wright, I. J. 2005, Ann. Bot., 96, 1129.

Villar, R. and Merino, J. 2001, New Phytol., 151, 213.

Viveros-Viveros, H., Sáenz-Romero, C., Vargas-Hernández, J. J., López-Upton, J., Ramírez-Valverde, G. and Santacruz-Varela, A. 2009, Forest Ecol. Manag., 257, 836.

Walls, R. L. 2011, Am. J. Bot., 98, 244.

Watkins, J. E. Jr., Kawahara, A. Y., Leicht, S. A., Auld, J. R., Bicksler, A. J. and Kaiser, K. 2006, Am. Fern J., 96, 83.

Weiher, E., Werf, A. V. D., Thompson, K., Roderick, M., Garnier, E. and Werf, V. D. 1999, J. Veg. Sci., 10, 609.

Westoby, M. and Wright, I. J. 2006, Trends Ecol. Evol., 21, 261.

Wilson, P. J., Thompson, K., Hodgson, J. G. and Hodgson, G. 1999, New Phytol., 143, 155.

Woodward, F. I. 1987, Nature, 327, 617.

Wright, I. J., Reich, P. B., Westoby, M., Ackerly, D. D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J. H. C., Diemer, M., Flexas, J., Garnier, E., Groom, P. K., Gulias, J., Hikosaka, K., Lamont, B. B., Lee, T., Lee, W., Lusk, C., Midgley, J. J., Navas, M.-L., Niinemets, Ü., Oleksyn, J., Osada, N., Poorter, H., Poot, P., Prior, L., Pyankov, V. I., Roumet, C., Thomas, S. C., Tjoelker, M. G., Veneklaas, E. J. and Villar, R. 2004, Nature, 428, 821.

Yang, D., Li, G. and Sun, S. 2009, J. Veg. Sci., 20, 359.

Yang, D., Niklas, K. J., Xiang, S. and Sun, S. 2010, Ann. Bot., 105, 71.

Zhang, S.-B., Guan, Z.-J., Chang, W., Hu, H., Yin, Q. and Cao, K-F. 2011, Physiol. Plant., 142, 118.

Zhu, Y., Jiang, Y., Liu, Q., Kang, M., Spehn, E. M. and Körner, C. 2009, Plant Ecol., 205, 273.

Zhu, Y., Siegwolf, R. T. W., Durka, W. and Körner, C. 2010, Oecologia, 162, 853.

Table S2. References used for values on Table 2.

Trait	**# cit**	**References**
LMA/SLA	96	Albert *et al.* 2010a,b; Ansquer *et al.* 2009; Bansal and Germino 2010; Baptist and Choler 2008; Baptist *et al.* 2009; Baptist *et al.* 2010; Bernhardt-Romermann *et al.* 2008; Bonser *et al.* 2010; Ceriani *et al.* 2009; Chu *et al.* 2009; Cornelissen *et al.* 2003; Cornwell and Ackerly 2009; Craine *et al.* 2001; Craine and Towne 2010; Diaz *et al.* 1998; Diaz *et al.* 2001; Doležal *et al.* 2011; Donovan *et al.* 2011; Duckworth *et al.* 2000; Evju *et al.* 2010; Fajardo and Piper 2010; Funk *et al.* 2008; Garnier *et al.* 2001; Gonzalo-Turpin and Hazard 2009; Grime *et al.* 1997; Hallik *et al.* 2009a; Hallik *et al.* 2009b; Hattenschwiler 2001; Hoch and Körner 2005; Hodgson *et al.* 2005; Hodgson *et al.* 2011; Hulshof and Swenson 2010; Jung *et al.* 2010; Kamiyama *et al.* 2010; Kessler *et al.* 2007; Kitajima and Poorter 2010; van Kleunen *et al.* 2010; Kraft *et al.* 2008; Lachapelle and Shipley 2012; Lavorel and Garnier 2002; Lavorel *et al.* 2010; Leishman *et al.* 2007; Li *et al.* 2004; Louault *et al.* 2005; Lusk *et al.* 2008; Ma *et al.* 2010; Macek *et al.* 2009; Milla *et al.* 2009; Milla and Reich 2011; Mommer *et al.* 2006; Niinemets 1999; Niinemets 2001; Niinemets *et al.* 2007a; Niinemets *et al.* 2009a; Niklas *et al.* 2007; Niu *et al.* 2010; Oyarzabal *et al.* 2008; Pakeman and Quested 2007; Pakeman *et al.* 2009; Paz and Martinez-Ramos 2003; Pellissier *et al.* 2010; Petchey *et al.* 2004; Poorter and Navas 2003; Poorter and Bongers 2006; Poorter *et al.* 2009; Preston *et al.* 2006; Price and Enquist 2007; Prior *et al.* 2003; Quétier *et al.* 2007; Reich *et al.* 1997; Reich *et al.* 1998; Reich *et al.* 2003; Santiago *et al.* 2004; Santiago and Wright 2007; Scheepens *et al.* 2010; Shipley 2006; Shipley and Vu 2002; Smith *et al.* 2011; Trouwborst *et al.* 2011; Trtikova *et al.* 2010; Ustin and Gamon 2010; Velazquez-Rosas *et al.* 2010; Vendramini *et al.* 2002; Vernescu and Ryser 2009; Vile *et al.* 2005; Villar and Merino 2001; Voesenek *et al.* 2006; Walls 2011; Weiher *et al.* 1999; Westoby 1998; Westoby *et al.* 2002; Wilson *et al.* 1999; Wright and Cannon 2001; Wright *et al.* 2004; Yang *et al.* 2009; Yang *et al.* 2010
Plant height	59	Ackerly 2009; Acosta *et al.* 2008; Albert *et al.* 2010a,b; Alexander *et al.* 2009; Ansquer *et al.* 2009; Aryal and Neuner 2010; Bernhardt-Romermann *et al.* 2008; Ceriani *et al.* 2009; Chu *et al.* 2009; Cierjacks *et al.* 2008; Cornelissen *et al.* 2003; Dirnbock and Dullinger 2004; Diaz *et al.* 2001; Diaz *et al.* 2004; Diaz *et al.* 2007; Duckworth *et al.* 2000; Evju *et al.*

Table S2 continued..

		2010; Fajardo and Piper 2010; Funk *et al.* 2008; Gonzalo-Turpin and Hazard 2009; Grime *et al.* 1997; Hills *et al.* 1994; Hoch and Körner 2005; Hodgson *et al.* 1999; Hodgson *et al.* 2005; Jung *et al.* 2010; Kitajima and Poorter 2010; Lavorel and Garnier 2002; Lavorel *et al.* 2010; Li *et al.* 2004; Macek *et al.* 2009; Mathisen and Hofgaard 2011; Milla and Reich 2011; Moles *et al.* 2007; Mommer *et al.* 2006; Montalvo *et al.* 1991; Niu *et al.* 2010; Oyarzabal *et al.* 2008; Pakeman *et al.* 2009; Pellissier *et al.* 2010; Pérez-Camacho *et al.* 2012; Petchey *et al.* 2004; Pillar and Sosinski 2003; Poorter and Bongers 2006; Pywell *et al.* 2003; Quétier *et al.* 2007; Reich *et al.* 2003; Rossetto *et al.* 2009; Thuiller *et al.* 2004; Totland and Birks 1996; Trtikova *et al.* 2010; Vesk *et al.* 2004; Viveros-Viveros *et al.*, 2009; Voesenek *et al.* 2006; Weiher *et al.* 1999; Westoby 1998; Westoby *et al.* 2002; Zhu *et al.* 2010
Leaf N content	57	Albert *et al.* 2010a,b; Ansquer *et al.* 2009; Baptist and Choler 2008; Baptist *et al.* 2009; Baptist *et al.* 2010; Bussotti 2008; Ceriani *et al.* 2009; Cornelissen *et al.* 2003; Doležal *et al.* 2011; Donovan *et al.* 2011; Evans and Poorter 2001; Evju *et al.* 2010; Funk *et al.* 2008; Garnier *et al.* 2001; Givnish *et al.* 2004; Grime *et al.* 1997; Grulke 2010; Hallik *et al.* 2009a; Hallik *et al.* 2009b; Hattenschwiler 2001; Hoch and Körner 2005; Hodgson *et al.* 2005; Kraft *et al.* 2008; Lachapelle and Shipley 2012; Lavorel and Garnier 2002; Lavorel *et al.* 2010; Leishman *et al.* 2007; Louault *et al.* 2005; Lusk *et al.* 2008; Macek *et al.* 2009; Milla *et al.* 2009; Milla and Reich 2011; Niinemets 1999; Niinemets *et al* 2006; Niinemets *et al.* 2007a; Niinemets *et al* 2007b; Niinemets *et al.* 2009a; Niklas *et al.* 2007; Oyarzabal *et al.* 2008; Pakeman *et al.* 2009; Poorter and Bongers 2006; Prior *et al.* 2003; Quétier *et al.* 2007; Reich *et al.* 1997; Reich *et al.* 1998; Reich *et al.* 2003; Santiago *et al.* 2004; Santiago and Wright 2007; Smith *et al.* 2011; Trouwborst *et al.* 2011; Ustin and Gamon 2010; Velazquez-Rosas *et al.* 2010; Villar and Merino 2001; Walls 2011; Westoby *et al.* 2002; Wright *et al.* 2004
Leaf area	45	Ackerly 2004; Ackerly 2009; Acosta *et al.* 2008; Baptist *et al.* 2010; Ceriani *et al.* 2009; Chu *et al.* 2009; Cornelissen *et al.* 2003; Diaz *et al.* 2001 Evju *et al.* 2010; Givnish 1987; Grubb 1977; Harrison *et al.* 2010; Hattenschwiler 2001; Hodgson *et al.* 2005; Hodgson *et al.* 2011; Hulshof and Swenson 2010; Kamiyama *et al.* 2010; Kessler *et al.* 2007; Kitajima and Poorter 2010; Kraft *et al.* 2008; Li *et al.* 2004; Ma *et al.* 2010; Macek *et al.* 2009; Martorell and Ezcurra 2007; Milla and Reich 2011; Montalvo *et al.* 1991; Niinemets *et al.* 2006; Niinemets *et al.* 2007a; Niinemets *et al.* 2007b; Niklas *et al.* 2007; Niu *et al.* 2010; Oyarzabal *et al.* 2008; Petchey *et al.* 2004; Pickup *et al.* 2005; Rossetto *et al.* 2009; Royer *et al.* 2005; Tanner 1980; Thuiller *et al.* 2004; Trtikova *et al.* 2010; Villar and Merino 2001; Westoby *et al.* 2002; Westoby and Wright 2006; Wilson *et al.* 1999; Wright and Cannon 2001; Yang *et al.* 2010
Leaf lifespan/phenol	36	Bernhardt-Romermann *et al.* 2008; Box 1995; Bussotti 2008; Coley 1983; Cornelissen *et al.* 2003; Diaz and Cabido 1997; Diaz *et al.* 2004; Donovan *et al.* 2011; Duckworth *et al.* 2000; Givnish 1987; Garnier *et al.* 2001; Hallik *et al.* 2009a; Harrison *et al.* 2010; Iversen *et al.* 2009; Kamiyama *et al.* 2010; Kitajima and Poorter 2010; Lavorel and Garnier 2002;

Table S2 continued..

		Lusk *et al.* 2008; Niinemets *et al.* 2007b; Niinemets *et al.* 2009b; Pellissier *et al.* 2010; Pérez-Camacho *et al.* 2012; Poorter and Bongers 2006; Prior *et al.* 2003; Reich *et al.* 1997; Reich *et al.* 1998; Reich *et al.* 2003; Santiago and Wright 2007; Ustin and Gamon 2010; Villar and Merino 2001; Walls 2011; Westoby *et al.* 2002; Wright and Cannon 2001; Wright *et al.* 2004; Westoby and Wright 2006; Yang *et al.* 2009
Leaf thickness	31	Barrington 1993; Brodribb *et al.* 2007; Bussotti 2008; Ceriani *et al.* 2009; Craine *et al.* 2001; Craine and Towne 2010; Diaz *et al.* 2004; Fahn and Cutler 1992; Givnish 1987; Guy 1990; Hattenschwiler 2001; Hodgson *et al.* 2005; Hodgson *et al.* 2011; Jin *et al.* 2011; Kessler *et al.* 2007; Macek *et al.* 2009; Niinemets 1999; Niinemets 2001; Niklas 1996; Niklas 1999; Niklas *et al.* 2007; Petchey *et al.* 2004; Price and Enquist 2007; Prior *et al.* 2003; Velazquez-Rosas *et al.* 2010; Vendramini *et al.* 2002; Vernescu and Ryser 2009; Vile *et al.* 2005; Wilson *et al.* 1999; Wolfe 1993; Wright and Cannon 2001
LDMC	30	Albert *et al.* 2010a,b; Ansquer *et al.* 2009; Baptist *et al.* 2009; Baptist *et al.* 2010; Ceriani *et al.* 2009; Cornelissen *et al.* 2003; Doležal *et al.* 2011; Garnier *et al.* 2001; Gonzalo-Turpin and Hazard 2009; Hodgson *et al.* 2005; Hodgson *et al.* 2011; Jung *et al.* 2010; Kitajima and Poorter 2010; Lavorel and Garnier 2002; Lavorel *et al.* 2010; Louault *et al.* 2005; Oyarzabal *et al.* 2008; Pakeman *et al.* 2009; Pakeman and Quested 2007; Petchey *et al.* 2004; Quetier *et al.* 2007; Roche *et al.* 2004; Shipley and Vu 2002; Velazquez-Rosas *et al.* 2010; Vernescu and Ryser 2009; Vile *et al.* 2005; Weiher *et al.* 1999; Wilson *et al.* 1999; Wright and Cannon 2001
Photosynthetic rate/capac/net	30	Brodribb *et al.* 2007; Donovan *et al.* 2011; Feild *et al.* 2009; Feild *et al.* 2011; Givnish 1987; Grulke 2010; Hallik *et al.* 2009a; Hattenschwiler 2001; Koh *et al.* 2009; Lachapelle and Shipley 2012; Leishman *et al.* 2007; Lusk *et al.* 2008; Niinemets *et al.* 2007a; Niinemets *et al.* 2007b; Niinemets *et al.* 2009a; Poorter and Bongers 2006; Premoli and Brewer 2007; Prior *et al.* 2003; Reich *et al.* 1997; Reich *et al.* 1998; Reich *et al.* 2003; Santiago *et al.* 2004; Santiago and Wright 2007; Smith *et al.* 2009; Smith *et al.* 2011; Trouwborst *et al.* 2011; Ustin and Gamon 2010; Walls 2011; Wright *et al.* 2004; Zhang *et al.* 2011
Seed mass	29	Bernhardt-Romermann *et al.* 2008; Blionis and Vokou 2005; Ceriani *et al.* 2009; Cierjacks *et al.* 2008; Cornelissen *et al.* 2003; Diaz *et al.* 2004; Doležal *et al.* 2011; Duckworth *et al.* 2000; Evju *et al.* 2010; Fernández Alés *et al.* 1993; Funk *et al.* 2008; Garnier *et al.* 2001; Kraft *et al.* 2008; Lavorel and Garnier 2002; Moles *et al.* 2007; Pakeman and Quested 2007; Pakeman *et al.* 2009; Paz and Martinez-Ramos 2003; Pellissier *et al.* 2010; Pérez-Camacho *et al.* 2012; Petchey *et al.* 2004; Pluess *et al.* 2005; Quétier *et al.* 2007; Reich *et al.* 2003;Totland and Birks 1996; Trtikova *et al.* 2010; Weiher *et al* 1999; Westoby 1998; Westoby *et al.* 2002
Wood density	24	Ackerly 2004; Bucci *et al.* 2004; Chave *et al.* 2009; Cornwell and Ackerly 2009; Enquist *et al.* 1999; Fajardo and Piper 2010; Hacke and Sperry 2001; Hacke *et al.* 2001; King *et al.* 2005; Kraft *et al.* 2008; Lavorel and Garnier 2002; Loehle 1988; Meinzer 2003; Muller-Landau 2004; Poorter *et al.* 2010; Preston *et al.* 2006; Reich *et al.* 2003; Roderick 2000; Sack *et al.* 2003; Santiago *et al.* 2004; Sperry 2003; Swenston and Enquist 2007; Westoby and Wright 2006; Zanne and Falster 2010

Full references for Table S2

Ackerly, D. 2004, Ecol. Monogr., 74, 25.

Ackerly, D. 2009, Proc. Natl. Acad. Sci. USA, 106(Suppl.), 19699.

Acosta, B., Sánchez-Jardón, L., del Pozo, A., García-Ibáñez, E., Casado, M. A., Montalvo, J. and Pineda, F. D. 2008, Acta Oecol., 34, 26.

Albert, C. H., Thuiller, W., Yoccoz, N. G., Soudant, A., Boucher, F., Saccone, P. and Lavorel, S. 2010a, J. Ecol., 98, 604.

Albert, C. H., Thuiller, W., Yoccoz, N. G., Douzet, R., Aubert, S. and Lavorel, S. 2010b, Funct. Ecol., 24, 1192.

Alexander, J. M., Edwards, P. J., Poll, M., Parks, C. G. and Dietz, H. 2009, Ecology, 90, 612.

Ansquer, P., Duru, M., Theau, J. P. and Cruz, P. 2009, Ecol. Indic., 9, 1020.

Aryal, B. and Neuner, G. 2010, Oecologia, 162, 1.

Bansal, S. and Germino, M. J. 2010, J. Veg. Sci., 21, 133.

Baptist, F. and Choler, P. 2008, Ann. Bot., 101, 549.

Baptist, F., Yoccoz, N. G. and Choler, P. 2009, Plant Soil, 328, 397.

Baptist, F., Flahaut, C., Streb, P. and Choler, P. 2010, Plant Biol., 12, 755.

Barrington, D. S. 1993, J. Biogeogr., 20, 275.

Bernhardt-Romermann, M., Romermann, C., Nuske, R., Parth, A., Klotz, S., Schmidt W. and Stadler, J. 2008, Oikos, 117, 1533.

Blionis, G. J. and Vokou, D. 2005, Plant Ecol., 178, 77.

Bonser, S. P., Ladd, B., Monro, K., Hall, M. D. and Forster, M. A. 2010, Ann. Bot., 106, 979.

Box, E. O. 1995, Vegetation, 121, 101.

Brodribb, T. J., Field, T. S. and Jordan, G. J. 2007, Plant Physiol., 144, 1890.

Bucci, S. J., Goldstein, G., Meinzer, F. C., Scholz, F. G., Franco, A. C. and Bustamante, M. 2004, Tree Physiol., 24, 891.

Bussotti, F. 2008, Glob. Change Biol., 14, 2727.

Ceriani, R. M., Pierce, S. and Cerabolini, B. 2009, Plant Ecol., 204, 1.

Chave, J., Coomes, D., Jansen, S., Lewis, S. L., Swenson, N. G. and Zanne, A. E. 2009, Ecol. Lett., 12, 351.

Chu, C., Wang, Y., Li, Q., Zhao, L., Ren, Z., Xiao, S., Yuan, J. and Wang, G 2009, J. Plant Ecol., 2, 135.

Cierjacks, A., Rühr, N. K., Wesche, K. and Hensen, I. 2008, Plant Ecol., 194, 207.

Coley, P. D. 1983, Ecol. Monogr., 53, 209.

Cornelissen, J. H. C. A., Lavorel, S. B., Garnier, E. B., Díaz, S., Buchmann, N., Gurvich, D. E., Reich, P. B., ter Steege, H., Morgan, H. D., van der Heijden, M. G. A., Pausas, J. G. and Poorter, H. 2003, Aus. J. Bot., 51, 335.

Cornwell, W. K. and Ackerly, D. D. 2009, Ecol. Monogr., 79, 109.

Craine, J. M., Froehle, J., Tilman, D. G., Wedin, D. A. and Chapin III, F. S. 2001, Oikos, 93, 274.

Craine, J. M. and Towne, E. G. 2010, Plant Soil, 337, 193.

Díaz, S., Cabido, M. and Casanoves, F. 1998, J. Veg. Sci., 9, 113.

Díaz, S., Noy-Meir, I. and Cabido, M. 2001, J. App. Ecol., 38, 497.

Díaz, S., Hodgson, J. G., Thompson, K., Cabido, M., Cornelissen, J. H. C., Jalili, A., Montserrat-Martí, G., Grime, J. P., Zarrinkamar, F., Asri, Y., Band, S. R., Basconcelo, S., Castro-Díez, P., Funes, G., Hamzehee, B., Khoshnevi, M., Pérez-Harguindeguy, N., Pérez-Rontomé, M. C., Shirvany, F. A., Vendramini, F., Yazdani, S., Abbas-Azimi, R., Bogaard, A., Boustani, S., Charles, M., Dehghan, M., de Torres-Espuny, L., Falczuk, V., Guerrero-Campo, J., Hynd, A., Jones, G., Kowsary, E., Kazemi-Saeed, F., Maestro-Martínez, M., Romo-Díez, A., Shar, S., Siavash, B., Villar-Salvador, P. and Zak, M. R. 2004, J. Veg. Sci., 15, 295.

Díaz, S., Lavorel, S., McIntyre, S., Falczuk, V., Casanoves, F., Milchunas, D. G., Skarpe, C., Rusch, G., Sternberg, M., Noy-Meir, I., Landsberg, J., Zhang, W., Clark, H. and Campbell, B. D. 2007, Glob. Change Biol., 13, 313.

Dirnkbock, T. and Dullinger, S. 2011, J. Veg. Sci., 15, 77.

Doležal, J., Mašková, Z., Lepš, J., Steinbachová, D., de Bello, F., Klimešová, J., Tackenberg, O., Zemek, F. and Kvet, J. 2011, Agr. Ecosyst. Env., 145, 10.

Donovan, L. A., Maherali, H., Caruso, C. M., Huber, H. and de Kroon, H. 2011, Trends Ecol. Evol., 26, 88.

Duckworth, J. C., Kent, M. and Ramsay, P. M. 2000, Prog. Phys. Geog., 4, 515.

Enquist, B. J., West, G. B., Charnov, E. L. and Brown, J. H. 1999, Nature, 401, 907.

Evju, M., Austrheim, G., Halvorsen, R. and Mysterud, A. 2009, Oecologia, 161, 77.

Fahn, A. and Cutler, D. F. 1992, Handbuch der Pflanzenanatomie, 13, 1.

Fajardo, A. and Piper, F. I. 2011, New Phytol., 189, 259.

Feild, T. S., Chatelet, D. S. and Brodribb, T. J. 2009, Geobiology, 7, 237.

Feild, T. S., Upchurch, G. R., Chatelet, D. S, Brodribb, T. J., Grubbs, K. C., Samain, M-S. and Wanke, S. 2011, Paleobiology, 37, 195.

Fernández Alés, R., Laffraga, J. M. and Ortega, F. 1993, J. Veg. Sci., 4, 313.

Funk, J. L., Cleland, E. E., Suding, K. N. and Zavaleta, E. S. 2008, Trends Ecol. Evol., 23, 695.

Garnier, E., Laurent, G. and Bellmann, A. 2001, New Phytol., 152, 69.

Givnish, T. J. 1987, New Phytol., 106, 131.

Gonzalo-Turpin, H. and Hazard, L. 2009, J. Ecol., 97, 742.

Grime, J. P., Thompson, K., Hunt, R., Hodgson, J. G., Cornelissen, J. H. C., Rorison, I. H., Hendry, G. A. F., Ashenden, T. W., Askew, A. P., Band, S. R., Booth, R. E., Bossard, C. C., Campbell, B. D., Cooper, J. E. I., Davison, A. W., Gupta, P. L., Hall, W., Hand, D. W., Hannah, M. A., Hillier, S. H., Hodkisnon, D. J., Jalili, A., Liu, Z., Mackey, J. M. L., Matthews, N., Mowforth, M. A., Neal, A. M., Reader, R. J., Reiling, K., Ross-Fraser, W., Spencer, R. E., Sutton, F., Tasker, D. E., Thorpe, P. C. and Whitehouse, J. 1997, Oikos, 79, 259.

Grubb, P. J. 1977, Annu. Rev. Ecol. Syst., 8, 83.

Grulke, N. E. 2010, Environ. Pollut., 158, 2032.

Guy, C. L. 1990, Annu. Rev. Plant Phys., 41, 187.

Hacke, U. G. and Sperry, J. S. 2001, Perspect. Plant Ecol., 4, 97.

Hacke, U. G., Sperry, J. S., Pockman, W. T., Davis, S. D. and Mcculloch, K. A. 2001, Oecologia, 126, 457.

Hallik, L., Niinemets, Ü. and Wright, I. J. 2009a, New Phytol., 184, 257.

Hallik, L., Kull, O., Niinemets, Ü. and Aan, A. 2009b, Basic Appl. Ecol., 10, 309.

Harrison, S. P., Prentice, I. C., Barboni, D., Kohfeld, K. E., Ni, J. and Sutra, J-P. 2010, J. Veg. Sci., 21, 300.

Hättenschwiler, S. 2001, Oecologia, 129, 31.

Hills, J. M., Murphy, K. J., Pulford, I. D. and Flowers, T. H. 1994, Funct. Ecol., 8, 242.

Hoch, G. and Körner, C. 2005, Funct. Ecol., 19, 941.

Hodgson, J. G., Wilson, P. J., Hunt, R., Grime, J. P. and Thompson, K. 1999, Oikos, 83, 282.

Hodgson, J. G., Montserrat-Martí, G., Cerabolini, B., Ceriani, R. M., Maestro-Martínez, M., Peco, B., Wilson, P. J., Thompson, K., Grime, J. P., Band, S. R., Bogard, A., Castro-Díez, P., Charles, M., Jones, G., Pérez-Rontomé, M. C., Caccianiga, M., Alard, D., Bakker, J. P., Cornelissen, J. H. C., Dutoit, T., Grootjans, A. P., Guerrero-Campo, J., Gupta, P. L., Hynd, A., Kahmen, S., Poschold, P., Romo-Díez, A., Rorison, I. H., Rosén, E., Schreiber, K-F., Tallowin, J., de Torres Espuny, L. and Villar-Salvador, P. 2005, Basic Appl. Ecol., 6, 119.

Hodgson, J. G., Montserrat-Martí, G., Charles, M., Jones, G., Wilson, P., Shipley, B., Sharafi, M., Cerabolini, B. E. L., Cornelissen, J. H. C., Band, S. R., Bogard, A., Castro-Díez, P., Guerrero-Campo, J., Palmer, C., Pérez-Rontomé, M. C., Carter, G., Hynd, A., Romo-Díez, A., de Torres Espuny, L. and Royo Pla, F. 2011, Ann. Bot., 108, 1337.

Hulshof, C. M. and Swenson, N. G. 2010, Funct. Ecol., 24, 217.

Iversen, M., Bråthen, K. A., Yoccoz, N. G. and Ims, R. A. 2009, J. Veg. Sci., 20, 903.

Jin, B., Wang, L., Wang, J., Jiang, K-Z., Wang, Y., Jiang, X-X., Ni, C-Y., Wang, Y-L. and Teng, N-J. 2011, BMC Plant Biol., 11, 35.

Jung, V., Violle, C., Mondy, C., Hoffmann, L. and Muller, S. 2010, J. Ecol., 98, 1134.

Kamiyama, C., Oikawa, S., Kubo, T. and Hikosaka, K. 2010, Oecologia, 164, 591.

Kessler, M., Siorak, Y., Wunderlich, M. and Wegner, C. 2007, Funct. Plant Biol., 34, 963.

King, D. A., Davies, D. J., Supardi, M. N. N. and Tan, S. 2005, Funct. Ecol., 19, 445.

Kitajima, K. and Poorter, L. 2010, New Phytol., 186, 708.

van Kleunen, M., Weber, E. and Fischer, M. 2010, Ecol. Lett., 13, 235.

Koh, S. C., Demmig-Adams, B. and Adams, W. W. 2009, Arct. Antarct. Alp. Res., 41, 317.

Kraft, N. J. B., Valencia, R. and Ackerly, D. D. 2008, Science, 322, 580.

Lachapelle, P. and Shipley, B. 2012, Ann. Bot., 109, 1149.

Lavorel, S. and Garnier, E. 2002, Funct. Ecol., 16, 545.

Lavorel, S., Grigulis, K. and Lamarque, P. 2010, J. Ecol., 99, 135.

Leishman, M. R., Haslehurst, T., Ares, A. and Baruch, Z. 2007, New Phytol., 176, 635.

Li, C., Liu, S. and Berninger, F. 2004, Trees - Struct. Funct., 18, 277.

Loehle, C. F. 1988, Can. J. Forest Res., 18, 209.

Louault, F., Pillar, V. D., Garnier, E. and Soussana, J. F. 2005, J. Veg. Sci., 16, 151.

Lusk, C. H., Reich, P. B., Montgomery, R. A., Ackerly, D. D. and Cavender-Bares, J. 2008, Trends Ecol. Evol., 23, 299.

Ma, W., Shi, P., Li, W., He, Y., Zhang, X., Shen, X. and Chai, S. 2010, Science China, 53, 1142.

Macek, P., Macková, J. and de Bello, F. 2009, Acta Oecol., 35, 778.

Mathisen, I. E. and Hofgaard, A. 2011, Plant Ecol. Divers., 4, 1.

Martorell, C. and Ezcurra, E. 2007, Oecologia, 151, 561.

Meinzer, F. C. 2003, Oecologia, 134, 1.

Milla, R., Giménez-Benavides, L., Escudero, A. and Reich, P. B. 2009, Funct. Ecol., 23, 111.

Milla, R. and Reich, P. B. 2011, Ann. Bot., 107, 455.

Moles, A. T., Ackerly, D. D., Tweddle, J. C., Dickie, J. B., Smith, R., Leishman, M. R., Mayfield, M. M., Pitman, A., Wood, J. T. and Westoby, M. 2007, Global Ecol. Biogeogr., 16, 109.

Mommer, L., Lenssen, J. P. M., Huber, H., Visser, E. J. W. and de Kroon, H. 2006, J. Ecol., 94, 1117.

Montalvo, J., Casado, M. A., Levassor, C. and Pineda, F. D. 1991, J. Veg. Sci., 2, 655.

Muller-Landau, H. C. 2004, Biotropica, 36, 20.

Niinemets, Ü. 1999, New Phytol., 144, 35.

Niinemets, Ü. 2001, Ecology, 82, 453.

Niinemets, Ü., Portsmuth, A. and Tobias, M. 2006, New Phytol., 171, 91.

Niinemets, Ü., Portsmuth, A., Tena, D., Tobias, M., Matesanz, S. and Valladares, F. 2007a, Ann. Bot., 100, 283.

Niinemets, Ü., Portsmuth, A. and Tobias, M. 2007b, Funct. Ecol., 21, 28.

Niinemets, Ü., Díaz-Espejo, A., Flexas, J., Galmés, J. and Warren, C. R. 2009a, J. Exp. Bot., 60, 2249.

Niinemets, Ü., Wright, I. J. and Evans, J. R. 2009b, J. Exp. Bot., 60, 2433.

Niklas, K. J. 1996, Ann. Bot., 78, 61.

Niklas, K. J. 1999, New Phytol., 143, 19.

Niklas, K. J., Cobb, E. D., Niinemets, Ü., Reich, P. B., Sellin, A., Shipley, B. and Wright, I. J. 2007, Proc. Natl. Acad. Sci. USA, 104, 8891.

Niu, K., Zhang, S., Zhao, B. and Du, G. 2010, Plant Soil, 330, 215.

Oyarzabal, M., Paruelo, J. M., del Pino, F., Oesterheld, M. and Lauenroth, W. K. 2008, J. Veg. Sci., 19, 183.

Pakeman, R. J. and Quested, H. M. 2009, Applied Vegetation Science, 10, 91.

Pakeman, R., Lepš, J., Kleyer, M., Lavorel, S., Garnier, E. and VISTA Consortium, 2009, J. Veg. Sci., 20, 148.

Paz, H. and Martínez-Ramos, M. 2003, Ecology, 84, 439.

Pellissier, L., Fournier, B., Guisan, A. and Vittoz, P. 2010, Plant Ecol., 211, 351.

Pérez-Camacho, L., Rebollo, S., Hernández-Santana, V., García-Salgado, G., Pavón-García, J. and Gómez-Sal, A. 2012, Funct. Ecol., 26, 740.

Petchey, O. L., Hector, A. and Gaston, K. J. 2004, Ecology, 85, 847.

Pickup, M., Westoby, M. and Basden, A. 2005, Funct. Ecol.,19, 88.

Pillar, V. D. and Sosinski, Jr. E. E. 2003, J. Veg. Sci., 14, 323.

Pluess, A. R., Schütz, W. and Stöcklin, J. 2005, Oecologia, 144, 55.

Poorter, H. and Navas, M.-L. 2003, New Phytol., 157, 175.

Poorter, L. and Bongers, F. 2006, Ecology, 87, 1733.

Poorter, H., Niinemets, Ü., Poorter, L., Wright, I. J. and Villar, R. 2009, New Phytol., 182, 565.

Poorter, L., McDonald, I., Alarcón, A., Fichtler, E., Licona, J-C., Peña-Claros, M., Sterck, F., Villegas, Z. and Sass-Klaassen, U. 2010, New Phytol., 185, 481.

Premoli, A. C. and Brewer, C. A. 2007, Aus. J. Bot., 55, 585.

Preston, K. A., Cornwell, W. K. and DeNoyer, J. L. 2006, New Phytol., 170, 807.

Price, C. A. and Enquist, B. J. 2007, Ecology, 88, 1132.

Prior, L. D., Eamus, D. and Bowman, D. 2003, Funct. Ecol., 17, 504.

Pywell, R. F., Bullock, J. M., Roy, D. B., Warman, L., Walker, K. J. and Rothery, P. 2003, J. App. Ecol., 40, 65.

Quétier, F., Thébault, A. and Lavorel, S. 2007, Ecol. Monogr., 77, 33.

Reich, P. B., Walters, M. B. and Ellsworth, D. S. 1997, Proc. Natl. Acad. Sci. USA, 94, 13730.

Reich, P. B., Walters, M. B., Ellsworth, D. S., Vose, J. M., Volin, J. C., Gresham, C. and Bowman, W. D. 1998, Oecologia, 114, 471.

Reich, P. B., Wright, I. J., Cavender-Bares, J. C., Craine, J. M., Oleksyn, J., Westoby, M. and Walters, M. B. 2003, Int. J. Plant Sci., 164, S143.

Roche, P., Díaz-Burlinson, N. and Gachet, S. 2004, Plant Ecol., 174, 37.

Roderick, M. L. 2000, Funct. Ecol., 14, 244.

Rossetto, M., Crayn, D., Ford, A., Mellick, R. and Sommerville, K. 2009, Mol. Ecol., 18, 1422.

Royer, D. L., Wilf, P., Janesko, D. A., Kowalski, E. A. and Dilcher, D. L. 2005, Am. J. Bot., 92, 1141.

Sack, L., Cowan, P. D., Jaikumar, N. and Holbrook, N. M. 2003, Plant Cell Env., 26, 1343.

Santiago, L. S., Goldstein, G., Meinzer, F. C., Fisher, J. B., Machado, K., Woodruff, D. and Jones, T. 2004, Oecologia, 140, 543.

Santiago, L. S. and Wright, S. J. 2007, Funct. Ecol., 21, 19.

Scheepens, J. F., Frei, E. S. and Stöcklin, J. 2010, Oecologia, 164, 141.

Shipley, B. 2006, Funct. Ecol., 20, 565.

Shipley, B. and Vu, T.-T. 2002, New Phytol., 153, 359.

Smith, W. K., Germino, M. J., Johnson, D. M. and Reinhardt, K. 2009, Bot. Rev., 75, 163.

Smith, E. A., Collette, S. B., Boynton, T. A., Lilrose, T., Stevens, M. R., Bekker, M. F., Eggett, D. and St Clair, S. B. 2011, Tree Physiol., 31, 68.

Sperry, J. S. 2003, Int. J. Plant Sci., 164, S115.

Swenson, N. G. and Enquist, B. J. 2007, Am. J. Bot., 94, 451.

Tanner, E. V. J. 1980, J. Ecol., 68, 573.

Thuiller, W., Lavorel, S., Midgley, G., Lavergne, S. and Rebelo, T. 2004, Ecology, 85, 1688.

Totland, O. and Birks, H. 1996, Ecography, 19, 269.

Trouwborst, G., Hogewoning, S. W., Harbinson, J. and van Ieperen, W. 2011, Physiol. Plant., 142, 157.

Trtikova, M., Edwards, P. J. and Güsewell, S. 2010, Ecography, 33, 556.

Ustin, S. L. and Gamon, J. A. 2010, New Phytol., 186, 795.

Velázquez-Rosas, N., Barradas, V. L., Vázquez-Santana, S., Cruz-Ortega, R., García-Jiménez, F., Toledo-Alvarado, E. and Orozco-Segovia, A. 2010, Acta Oecol., 36, 587.

Vendramini, F., Díaz, S., Gurvich, D. E., Wilson, P. J., Thompson, K. and Hodgson, J. G. 2002, New Phytol., 154, 147.

Vernescu, C. and Ryser, P. 2009, Am. J. Bot., 96, 1068.

Vesk, P. A., Leisham, M. R. and Westoby, M. 2004, J. App. Ecol., 41, 22.

Vile, D., Garnier, E., Shipley, B., Laurent, G., Navas, M.-L., Roumet, C., Lavorel, S., Díaz, S., Hodgson, J. G., Lloret, F., Midgley, G. F., Poorter, H., Rutherford, M. C., Wilson, P. J. and Wright, I. J. 2005, Ann. Bot., 96, 1129.

Villar, R. and Merino, J. 2001, New Phytol., 151, 213.

Viveros-Viveros, H., Sáenz-Romero, C., Vargas-Hernández, J. J., López-Upton, J., Ramírez-Valverde, G. and Santacruz-Varela, A. 2009, Forest Ecol. Manag., 257, 836.

Voesenek, L. A. C. J., Colmer, T. D., Pierik, R., Millenaar, F. F. and Peeters, A. J. M. 2006, New Phytol., 170, 213.

Walls, R. L. 2011, Am. J. Bot., 98, 244.

Weiher, E., Werf, A. V. D., Thompson, K., Roderick, M., Garnier, E. and Werf, V. D. 1999, J. Veg. Sci., 10, 609.

Westoby, M. 1998, Plant Soil, 199, 213.

Westoby, M., Falster, D. S., Moles, A. T., Vesk, P. A. and Wright, I. J. 2002, Annu. Rev. Ecol. Syst., 33, 125.

Westoby, M. and Wright, I. J. 2006, Trends Ecol. Evol., 21, 261

Wilson, P. J., Thompson, K., Hodgson, J. G. and Hodgson, G. 1999, New Phytol., 143, 155.

Wolfe, J. A. 1993, US Geological Survey Bulletin, 2040.

Wright, I. J. and Cannon, K. 2001, Funct. Ecol., 15, 351.

Wright, I. J., Reich, P. B., Westoby, M., Ackerly, D. D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J. H. C., Diemer, M., Flexas, J., Garnier, E., Groom, P. K., Gulias, J., Hikosaka, K., Lamont, B. B., Lee, T., Lee, W., Lusk, C., Midgley, J. J., Navas, M.-L., Niinemets, Ü., Oleksyn, J., Osada, N., Poorter, H., Poot, P., Prior, L., Pyankov, V. I., Roumet, C., Thomas, S. C., Tjoelker, M. G., Veneklaas, E. J. and Villar, R. 2004, Nature, 428, 821.

Yang, D., Li, G. and Sun, S. 2009, J. Veg. Sci., 20, 359.

Yang, D., Niklas, K. J., Xiang, S. and Sun, S. 2010, Ann. Bot., 105, 71.

Zanne, A. E. and Falster, D. 2010, New Phytol., 185, 348.

Zhang, S.-B., Guan, Z.-J., Chang, W., Hu, H., Yin, Q. and Cao, K-F. 2011, Physiol. Plant., 142, 118.

Zhu, Y., Siegwolf, R. T. W., Durka, W. and Körner, C. 2010, Oecologia, 162, 853.

ACKNOWLEDGEMENTS

We acknowledge gratefully the Research Coordinating Networks and the Physiological Systems and Structure programs, US National Science Foundation, for financial support.

REFERENCES

1. Reich, P. B., Walters, M. B. and Ellsworth, D. S. 1997, Proc. Natl. Acad. Sci. USA, 94, 13730.
2. Reich, P. B., Wright, I. J., Cavender-Bares, J. C., Craine, J. M., Oleksyn, J., Westoby, M. and Walters, M. B. 2003, Int. J. Plant Sci., 164, S143.
3. Duckworth, J. C., Kent, M. and Ramsay, P. M. 2000, Prog. Phys. Geog., 4, 515.
4. Meinzer, F. C. 2003, Oecologia, 134, 1.
5. Lavorel, S., Díaz, S., Cornelissen, J. H. C., Garnier, E., Harrison, S. P., McIntyre, S., Pausas, J. G., Pérez-Harguindeguy, N., Roumet, C. and Urcelay, C. 2007, Plant functional types: are we getting any closer to the holy grail? Terrestrial Ecosystems in a Changing World, J. G. Canadell, D. Pataki and L. Pitelka L (Eds.), Springer-Verlag, Berlin, 149.
6. Ansquer, P., Duru, M., Theau, J. P. and Cruz, P. 2009, Ecol. Indic., 9, 1020.
7. Monson, R. K. 2003, Int. J. Plant Sci., 164, S43.
8. Ackerly, D. 2009, Proc. Natl. Acad. Sci. USA, 106(Suppl.), 19699.
9. Smith, W. K., Vogelmann, T. M. and Critchley, C. 2004, Photosynthetic Adaptation: Chloroplast to Landscape, Springer, New York.
10. Violle, C., Navas, M.-L., Vile, D., Kazakou, E., Fortunel, C., Hummer, I. and Garnier, E. 2007, Oikos, 116, 882.
11. Poorter, H. and Navas, M.-L. 2003, New Phytol., 157, 175.
12. Nicotra, A. B., Atkin, O. K., Bonser, S. P., Davidson, A. M., Finnegan, E. J., Mathesius, U., Poot, P., Purugganan, M. D., Richards, C. L., Valladares, F. and van Kleunen, M. 2010, Trends Plant Sci., 15, 684.
13. Ackerly, D. D. and Monson, R. 2003, Int. J. Plant Sci., 164, S1.
14. Chapin III, F. S., Autumn, K. and Pugnaire, F. 1993, Am. Nat., 142, S78.
15. Hodgson, J. G., Wilson, P. J., Hunt, R., Grime, J. P. and Thompson, K. 1999, Oikos, 83, 282.
16. Grime, J. P. 2001, Plant strategies, vegetation processes and ecosystem properties, Wiley, Chichester.
17. Valladares, F. and Niinemets, Ü. 2008, Ann. Rev. Ecol. Evol. S., 39, 237.
18. Poorter, H., Niinemets, Ü., Poorter, L., Wright, I. J. and Villar, R. 2009, New Phytol., 182, 565.
19. Lachapelle, P. and Shipley, B. 2012, Ann. Bot., 109, 1149.

20. Montalvo, J., Casado, M. A., Levassor, C. and Pineda, F. D. 1991, J. Veg. Sci., 2, 655.
21. Grime, J. P., Thompson, K., Hunt, R., Hodgson, J. G., Cornelissen, J. H. C., Rorison, I. H., Hendry, G. A. F., Ashenden, T. W., Askew, A. P., Band, S. R., Booth, R. E., Bossard, C. C., Campbell, B. D., Cooper, J. E. I., Davison, A. W., Gupta, P. L., Hall., W., Hand, D. W., Hannah, M. A., Hillier, S. H., Hodkisnon, D. J., Jalili, A., Liu, Z., Mackey, J. M. L., Matthews, N., Mowforth, M. A, Neal, A. M., Reader, R. J., Reiling, K., Ross-Fraser, W., Spencer, R. E., Sutton, F., Tasker, D. E., Thorpe, P. C. and Whitehouse, J. 1997, Oikos, 79, 259.
22. Weiher, E., Werf, A. V. D., Thompson, K., Roderick, M., Garnier, E. and Werf, V. D. 1999, J. Veg. Sci., 10, 609.
23. Cornelissen, J. H. C. A., Lavorel, S. B., Garnier, E. B., Díaz, S., Buchmann, N., Gurvich, D. E., Reich, P. B., ter Steege, H., Morgan, H. D., van der Heijden, M. G. A., Pausas, J. G. and Poorter, H. 2003, Aust. J. Bot., 51, 335.
24. Díaz, S., Hodgson, J. G., Thompson, K., Cabido, M., Cornelissen, J. H. C., Jalili, A., Montserrat-Martí, G., Grime, J. P., Zarrinkamar, F., Asri, Y., Band, S. R., Basconcelo, S., Castro-Díez, P., Funes, G., Hamzehee, B., Khoshnevi, M., Pérez-Harguindeguy, N., Pérez-Rontomé, M. C., Shirvany, F. A., Vendramini, F., Yazdani, S., Abbas-Azimi, R., Bogaard, A., Boustani, S., Charles, M., Dehghan, M., de Torres-Espuny, L., Falczuk, V., Guerrero-Campo, J., Hynd, A., Jones, G., Kowsary, E., Kazemi-Saeed, F., Maestro-Martínez, M., Romo-Díez, A., Shar, S., Siavash, B., Villar-Salvador, P. and Zak, M. R. 2004, J. Veg. Sci.,15, 295.
25. Lavorel, S. and Garnier, E. 2002, Funct. Ecol., 16, 545.
26. Wright, I. J., Reich, P. B., Westoby, M., Ackerly, D. D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J. H. C., Diemer, M., Flexas, J., Garnier, E., Groom, P. K., Gulias, J., Hikosaka, K., Lamont, B. B., Lee, T., Lee, W., Lusk, C., Midgley, J. J., Navas, M.-L., Niinemets, Ü., Oleksyn, J., Osada, N., Poorter, H., Poot, P., Prior, L., Pyankov, V. I., Roumet, C., Thomas, S. C., Tjoelker, M. G., Veneklaas, E. J. and Villar, R. 2004, Nature, 428, 821.
27. Bernhardt-Romermann, M., Romermann, C., Nuske, R., Parth, A., Klotz, S., Schmidt W. and Stadler, J. 2008, Oikos, 117, 1533.
28. Smith, W. K. and Hughes, N. M. 2009, Castanea, 74, 1.
29. Westoby, M., Falster, D. S., Moles, A. T., Vesk, P. A. and Wright, I. J. 2002, Annu. Rev. Ecol. Syst., 33, 125.
30. Niinemets, Ü. 1999, New Phytol., 144, 35.
31. Roderick, M. L. and Cochrane, M. L. 2002, Ann. Bot., 89, 537.
32. Wilson, P. J., Thompson, K. and Hodgson J. G. 1999, New Phytol., 143, 155.
33. Nobel, P. S. 2009, Physicochemical and Environmental Plant Physiology. Academic Press, Oxford.
34. Vile, D., Garnier, E., Shipley, B., Laurent, G., Navas, M.-L., Roumet, C., Lavorel, S., Díaz, S., Hodgson, J. G., Lloret, F., Midgley, G. F., Poorter, H., Rutherford, M. C., Wilson, P. J. and Wright, I. J. 2005, Ann. Bot., 96, 1129.
35. Shipley, B. 2006, Funct. Ecol., 20, 565.
36. Tosens, T., Niinemets, Ü., Westoby, M. and Wright, I. J. 2012, J. Exp. Bot., 63, 5105.
37. Smith, W. K., Vogelmann, T. C., Bell, D. T., DeLucia, E. H. and Shepherd, K. A. 1997, BioScience, 47, 785.
38. Brodribb, T. J. and Field, T. S. 2010, Ecol. Lett., 13, 175.
39. Perry, G. L. W., Enright, N. J., Miller, B. P. and Lamont, B. B. 2012, J. Veg. Sci., 23.
40. Paulsen, J., Weber, U. M. and Körner, C. 2000, Arct. Antarct. Alp. Res., 32, 14.
41. Hofgaard, A. and Wilmann, B. 2002, Ecoscience, 9, 375.
42. Smith, W. K., Germino, M. J. and Johnson, D. M. 2003, Tree Physiol., 23, 1101.
43. Smith, W. K., Germino, M. J., Johnson, D. M. and Reinhardt, K. 2009, Bot. Rev., 75, 163.
44. Körner, C. 2012, Alpine treelines. Springer, Basel.

45. Wieser, G., Holtmeier, F.-K. and Smith, W. K. 2012, Trees in a changing environment: Ecophysiology, adaptation and future survival. Plant Ecophysiology Series, M. Tausz and N. E. Grulke (Eds.), Springer, in press.
46. Cavieres, L. A., Badano, E. I., Sierra-Almeida, A. and Molina-Montenegro, M. A. 2007, Arct. Antarct. Alp. Res., 39, 229.
47. Smith, W. K. and Brewer, C. A. 1994, Am. Nat., 143, 528.
48. Smith, W. K. and Carter, G. A. 1988, Am. J. Bot., 75, 496.
49. Carlsson, B. A. and Callaghan, T. V. 1991, J. Ecol., 79, 973.
50. Battlori, E., Camarero, J. J., Ninot, J. M. and Gutiérrez, E. 2009, Global Ecol. Biogeogr., 18, 460.
51. Gitay, H. and Noble, I. R. 1997, What are functional types and how should we seek them? T. M. Smith, H. H. Shugart, F. I. Woodward (Eds.) Cambridge University Press, Cambridge, 3.
52. McIntyre, S., Lavorel, S., Landsberg, J. and Forbes, T. D. A. 1999, J. Veg. Sci. 10, 621.
53. Westoby, M. and Wright, I. J. 2006, Trends Ecol. Evol., 21, 261.
54. Brodribb, T. J., Feild, T. S. and Jordan, G. J. 2007, Plant Physiol., 144, 1890.
55. Niklas, K. J., Cobb, E. D., Niinemets, Ü., Reich, P. B., Sellin, A., Shipley, B. and Wright, I. J. 2007, Proc. Natl. Acad. Sci. USA, 104, 8891.
56. Niinemets, Ü., Díaz-Espejo, A., Flexas, J., Galmés, J. and Warren, C. R. 2009, J. Exp. Bot., 60, 2249.