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Challenging Theophrastus: A common core list of plant traits for functional ecology

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Abstract. Ecologists need a common language of plant traits in order to make comparisons across regions and scales, pool data, and maximize the utility of the data. To develop such a set of traits we began with the primary challenges faced by plants: dispersal, establishment, and persistence in order to identify fundamental traits. Most of these traits are hard to measure, but advances in comparative ecology have suggested a number of easy to measure analogs. Unfortunately, some of the fundamental traits have no simple analog. The common core list includes: seed mass, seed shape, dispersal mode, clonality, specific leaf area, leaf water content, height, aboveground biomass, life history, onset of flowering, stem density, and resprouting ability. Most of the traits can be measured quantitatively, but several traits on the list must still be measured qualitatively due to logistical problems or lack of an easy analog. Key problem areas include: dispersal ability, capacity for vegetative spread, germination, palatability, plasticity, and all the various below-ground traits. Comparative studies need to address these problem areas. The common core list is suggested as a common starting point for studies of functional ecology. The idiosyncrasies of regional floras and specific research agendas will dictate which traits can be ignored and those that need to be added.

Keywords: Dispersal; Disturbance; Establishment; Functional classification; Leaf water content; Persistence; Plant height; Seed mass; Specific leaf area.

Nomenclature: Radford et al. (1968); Bowers & Wignall (1993).

Abbreviations: LWC = Leaf Water Content; RGR = Relative Growth Rate; SLA = Specific Leaf Area.

Introduction

Natural philosophers and ecologists have long sought functional classifications of species. In his Enguiry into Plants (Historia Plantarum), Theophrastus (ca. 300 B.C.) classified plants into trees, shrubs, and herbs (literally, grasses) (Morton 1981). Theophrastus' system was primarily based on height and stem density (woody or not woody). Through the years ecologists have sought more detailed classifications (recent examples include Grime 1979; Box 1996; Lavorel et al. 1997; Gillison & Carpenter 1997; Westoby 1998). The first step in such a classification is to choose a list of key traits that are believed to be important for both understanding and prediction. In the last few years, there has been a growing list of studies where some sort of functional classification of species has been sought (e.g. Leishman & Westoby 1992; Boutin & Keddy 1992; Diaz & Cabido 1997; Reich et al. 1997). The authors of each of these studies chose an *ad hoc* set of traits that they each believed to be important. If we are to make comparisons and test for the repeatability of groups in different floras, we need to establish a common language of plant traits.

Classification is but one of many areas where plant traits are of critical interest. Other research areas that rely on traits include: dynamic global vegetation models (e.g. Woodward et al. 1995; Neilson & Running 1996), empirical landscape models (e.g. Box 1981; Woodward 1987), stand/community models (e.g. Smith & Huston 1989; Weiher & Keddy 1999), trait-environment relationships (e.g. MacGillivray & Grime 1995a, b; Silvertown et al. 1997), the search for functional groups of species that respond similarly to the environment (e.g. Diaz et al. 1992; Lavorel et al. 1997), assembly rules (e.g. Weiher et al. 1998), comparative ecology (e.g. Grime et al. 1988; Keddy 1992; Thompson et al. 1993; Westoby 1998), evolutionary approaches to comparative ecology (Silvertown & Dodd 1996; Silvertown et al. 1997), metapopulation dynamics (e.g. Eriksson 1996), the study of phenotypic plasticity within populations (e.g. Campbell et al. 1991; Aronson et al. 1992), ecophysiology and the mechanistic understanding of plant response to the environment (e.g. Lambers & Poorter 1992; van der Werf et al. 1993; Recih et al. 1997; Poorter & Garnier 1999).

In order to make comparisons among studies and foster linkages between hierarchical levels (e.g. McIntyre & Diaz 1999; this issue), we need to have some degree of standardization in the measurement of plant traits. The first goal of this paper is to suggest and justify a 'common core' list of plant traits. We are not suggesting the common core is sufficient for prediction and understanding phenomena relevant for all the abovementioned research areas. Our main goal is to identify core traits that are likely to be useful for predicting vegetation responses to disturbances that influence vegetation in large parts of the world: fire, grazing, and land use change. Whether the traits prove to be useful remains to be seen. We suggest that these core traits are indeed relevant for understanding vegetation responses to an extremely broad range of environmental factors. The list addresses the fundamentals that are common to nearly all plant species: dispersal, establishment, and persistence. Other traits will almost certainly be necessary for understanding and predicting patterns and processes in particular circumstances, but the core list will likely be of general interest and importance.

By identifying this core list, it is our hope that we can eventually build up a set of globally distributed data bases which can be used to test theories of plant distribution and biodiversity. A further goal of this paper is to address methodological issues involved in measuring these traits.

On the selection of plant traits

If we start with a mechanistic approach, and list the basic challenges faced by plants, then we can methodically address environmental challenges and their solutions (Noble & Slatyer 1980). Plants need to disperse to new sites, they need to become established, and once established they need to persist. Persistence is a matter of tolerating the range of biotic and abiotic conditions of a particular site. These include tolerating changes in both resource availability and non-resource stresses (e.g. pH, flooding), competing or tolerating the competitive effects of plant neighbors, and avoiding or tolerating disturbances (losses of biomass) that may be acute (e.g. fire) or chronic (e.g. herbivory).

The task is to find a list of traits that address these issues. The list of traits must also be pragmatic, in that we would prefer a set of easily measured traits. Traits that are highly desirable (e.g. competitive ability, relative growth rate, palatability) are often not measured because of the time and expense involved. Our focus therefore will be on traits that are easy to measure and can be easily incorporated into the field programs of most plant ecologists.

Another obvious place to start is with plant strategy theory (Grime 1977, 1979; Grime et al. 1997; Westoby 1998). Plants show a wide variety of trade-offs and correlations between traits and this means that we can know a lot about species' functional abilities from a small number of traits. For instance, specific leaf area (SLA, leaf area per unit leaf dry mass) is highly correlated with relative growth rate (RGR, biomass increment per unit biomass present per unit of time), maximum rate of photosynthesis per leaf dry mass, mass-based leaf N, and leaf longevity (Grime et al. 1988; Aerts & van der Peijl 1993; Poorter & van der Werf 1998; Reich 1998; van der Werf et al. 1998; Westoby 1998; Hodgson et al. 1999). At the heart of most of these trade-offs are simple biophysical limitations on organism structure and function. While many correlations have been found, vegetative traits and regenerative traits are not usually tightly coupled (Grime et al. 1988; Shipley et al. 1989; Leishman & Westoby 1992) even though dispersal modes are not randomly distributed among plant life forms (Westoby et al. 1996) or within evolutionary lineages (Venable & Levin 1983; Eriksson & Bremer 1991).

A common core of functional plant traits

Table 1 outlines the common challenges faced by plants. In the discussion that follows, we will describe the ecological challenges and identify traits that address the challenges. In most cases, the obvious and most direct traits are extremely difficult to measure. They often involve quantifying attributes over a long period of time or they involve experimental manipulations (for instance, measuring relative growth rate or competitive ability). These traits are called 'hard' because they are hard to measure. We need to recognize that it is extremely unlikely that we can measure hard traits for an entire regional flora, therefore we need traits that are easier to measure. As the search for relationships among functional traits proceeds and comparative ecology advances, we expect to find more easy analogs for hard traits.

Dispersal

Dispersal has two main components: seed dispersal in time and seed dispersal in space. Dispersal in time could be measured as mean propagule longevity in the

Challenge	Hard trait	Easy trait
1. Dispersal		2
Dispersal in space	Dispersal distance	Seed mass,
	-	Dispersal mode
Dispersal in time	Propagule longevity	Seed mass, seed shape
2. Establishment		
Seedling growth	Seed mass	Seed mass
	Relative Growth Rate	Specific Leaf Area (SLA)
		Leaf Water Content (LWC)
3. Persistence		
Seed production	Fecundity	Seed mass,
		Above-ground biomass
Competitive	Competitive	Height,
ability	effect and response	Above-ground biomass
Plasticity	Reaction norm	SLA, LWC
Holding space /	Life span	Life history
longevity		Stem density
Acquiring space	Vegetative spread	Clonality
Response to	Resprouting ability	Resprouting ability
disturbance;		
stress and	Phenology,	Onset of flowering,
disturbance	Palatability	SLA, LWC
avoidance		– –

 Table 1. The common challenges faced by plants and some suggested traits.

seed bank, or by a description of the distribution of propagule longevity, or by a longevity index (Thompson et al. 1998). Seed mass and shape (roundness) are reasonable indicators of longevity (Thompson 1993a; Thompson et al. 1993; Funes et al. in press; but see also Leishman & Westoby 1998). For example, in temperate regions small, round seeds tend to persist in the seed bank (Thompson et al. 1993). Other factors also affect seed persistence such as germination physiology and defenses against predation (Thompson et al. 1998), but these factors are difficult to quantify.

Seed dispersal in space could be measured as mean dispersal distance (Willson 1993) or by describing a probability distribution of dispersal distances, but this would be practically impossible for most species. Seed mass is also associated with dispersal ability (Leishman et al. 1995; Thompson et al. 1998) in that wind dispersed seeds tend to be light in mass. In addition, small seeds are associated with large seed production, which in itself enhances dispersal. However, the relationships between seed size and other dispersal modes are complex and are not easily simplified (Hughes et al. 1994). The distinction of dispersal modes - anemochory, endozoochory, exozoochory, myrmecochory, 'ballistichory', and 'unassisted' - is important and the types are worthwhile traits (van der Pijl 1982), however they are qualitative. Terminal velocity is a quantitative trait that is potentially useful for estimating dispersal distance for wind and ballistically dispersed seeds but for other dispersal syndromes there is no simple quantitative trait that expresses seed dispersal efficiency.

Establishment

After seeds arrive in a new location, they must become established, i.e. they must deploy into a new seedling. While the regeneration niche (Grubb 1977) is of considerable interest, we see no simple way of measuring it. In addition to the germination characteristics of the seeds, seedling size is thought to be critical for successful establishment. The latter depends on the pattern in which seed size and relative growth rate combine (e.g. Jurado & Westoby 1992; Swanborough & Westoby 1996; Leishman 1999).

Germination is largely a matter of specific physiological tolerances which are not likely to be related to any simple trait. However, Shipley & Parent (1991) found that germination attributes were negatively related to relative growth rate, and positively related to minimum time to reproduction (annuals and facultative annuals). Seed mass was unrelated to germination. Seedling establishment is however often positively associated with seed mass, but the evidence is not unequivocal (Westoby et al. 1996). Species with heavy seeds tend to have better establishment when competing with neighbors (Grime & Jeffery 1965; Gross & Werner 1982; Gross 1984; Reader 1993; Leishman & Westoby 1994; Osunkoya et al. 1994; Burke & Grime 1996). Seed mass may also be important for establishment along soil fertility gradients (Lee & Fenner 1989; Jurado & Westoby 1992), but no clear general trend has emerged (Westoby et al. 1996).

Seedling establishment is also affected by relative growth rate (Grime & Hunt 1975; Poorter & Remkes 1990; van der Werf et al. 1993a). Although there are numerous counter-examples, large-seeded species tend to have low RGR (reviewed in Shipley & Peters 1990). The relative impacts of seed size and RGR on seedling size must therefore be carefully assessed (see Jurado & Westoby 1992 for an example in the Australian flora). According to Leishman (1999) these are likely to differ substantially among environments (e.g. under a forest canopy or in an abandoned agricultural field) and with the identity of neighboring plants. Leishman (1999) thus concluded that the relationships between plant traits and establishment ability were likely to be context-dependent.

More generally, relative growth rate is linked to a wide variety of other plant traits and functions and is therefore also related to persistence. In fact, the consequences of high RGR versus low RGR and the trade-offs associated with them make RGR one of the most fundamental plant traits (Hodgson et al. 1999). Easy analogs for RGR include specific leaf area, as species with high SLA-leaves have larger RGR (Garnier 1992; Lambers & Poorter 1992; Reich et al. 1992; van der Werf et al. 1993a). Another correlate of RGR is leaf water content (Garnier 1992; Poorter & Bergkotte 1992; Hodgson et

al. 1999). Specific leaf area and leaf water content are also strongly correlated with other morphological and operational traits that measure stress tolerance (Grime et al. 1988; MacGillivray & Grime 1995a; Ryser 1996; Poorter & Garnier 1999).

Persistence

After an individual becomes established, it must persist. There are many traits that enhance population persistence, but the most basic trait is the life span of the individual. The range of life spans among plants is tremendous, from some annuals living just a few weeks to nearly immortal clonal plants that live for centuries or even millennia (Cook 1985). The potential for a long life span in many plants implies that populations may be persistent for extended periods of time even where recruitment is no longer occurring (Eriksson 1996). Such remnant populations may have a great significance for the vegetation response to environmental factors such as a change in land use. Life span is of broad interest, and in our discussions, we came upon an interesting and humorous observation: immortality is good. Many clonal perennials are effectively immortal and this increases the difficulty in measuring life span. Life span can be approximated by scoring species life history as either: annual, biennial, or perennial. Biennials are distinctive and warrant status equal to short-lived semelparous annuals and long-lived iteroparous perennials (de Jong et al. 1987).

Because plants are not truly immortal, they must produce seeds (or spores) if they are to persist. Fecundity is largely dependent on seed mass and aboveground vegetative biomass (Shipley & Dion 1992; Weiher unpubl.).

Individual plants must also face competition by neighbors and so some measure of competitive ability is necessary. It has been suggested that under nutrient-rich conditions fast growth is a prerequisite for a high competitive ability (Grime et al. 1997, but see van der Werf et al. 1998), therefore, SLA could be an indicator of competitive ability. Others (e.g. Gaudet & Keddy 1988) have shown that height and above-ground biomass are associated with competitive ability, measured as competitive effect (sensu Goldberg & Landa 1991). In other cases, one might expect slow growing, shade tolerant species to have the strongest competitive response to neighbors (Smith & Huston 1989), and therefore have greater competitive ability. Under nutrient poor conditions, efficient nutrient conservation has been proposed as a key element for the success of slowgrowing species (Chapin 1980; Berendse & Aerts 1987; Aerts & van der Peijl 1993; Schläpfer & Ryser 1996; Berendse 1998). This primarily involves a long life span of organs, and of leaves in particular (Aerts 1995; Garnier & Aronson 1998; Eckstein et al. 1999).

Goldberg (1997) recently reviewed the expected relationships between traits and competitive ability in terms of both effect and response at both early and late succession. Among the 22 traits listed were height, RGR, lateral spread, and both plant and tissue longevity. Whether the association between competitive ability and the trait was positive or negative was dependent on the environmental conditions and the type of competitive ability. Furthermore, competitive effect (ability to suppress neighbors) and competitive response (ability to tolerate suppressive effect from neighbors) are not necessarily correlated (Keddy et al. 1994). In a recent study of 48 wetland species, Keddy et al. (1998) found that the former was positively correlated with RGR, while the latter was not. Goldberg also found that in general, competitive hierarchies are not contingent on the identity of the species in question, and this means that competitive ability is a species trait that we can indeed measure. However, competitive hierarchies were contingent on the environmental conditions about half the time. This means that competitive abilities can vary along environmental gradients and so we cannot say that a certain trait confers high competitive ability in all situations. However, we do know that certain traits are associated with competitive ability, whether the trait is positively associated with competitive ability may be dependent on what kind of competitive ability one is interested in and it may be dependent on resource availability or on successional age of the stand.

The most compelling traits that address competitive ability remain RGR, seed mass and plant height (e.g. Gross 1984; Gaudet & Keddy 1988; Goldberg & Landa 1991; Reader 1993; Westoby 1998; Hodgson et al. 1998).

Plants must be able to tolerate changes in their surroundings and they must be able to make use of this heterogeneity in both space and time (Grime 1994). Plasticity may be defined as the ability to alter allocation patterns, morphology, or physiology in response to environmental variation. Even though the adaptive significance of phenotypic plasticity has long been recognized (Bradshaw 1965; Schlichting 1986), the role of plasticity in competition and response to disturbance is poorly understood. Plasticity in relative growth rate is correlated with maximum relative growth rate (Shipley & Keddy 1988; Campbell et al. 1991; Garnier 1998), but this does not seem to be the case for the plasticity of other plant traits such as the root: shoot ratio (see Reynolds & D'Antonio 1996; Garnier 1998 for recent meta-analyses dealing with nitrogen supply). This suggests that plasticity in RGR is positively associated with specific leaf area and leaf water content, but whether this is also true for other plant traits remains to be established. Furthermore, we know very little about plastic responses to disturbance.

Plasticity is difficult to measure, especially in the field. Plasticity is a measure of response to change, therefore, measuring plasticity requires a manipulative experiment. Transplant experiments and common gardens have been used to assess plasticity and local adaptation (e.g. Turesson 1922; Clausen et al. 1940). Campbell et al. (1991) screened species in the laboratory. Non-manipulative, empirical studies that attempt to quantify the amount of variation within a trait will tend to confuse real plasticity with both genotypic variation and maternal effects. These alternative sources of variation, coupled with the logistical problems associated with screening large numbers of species, suggest that plasticity will remain a difficult trait to quantify.

Some species avoid or reduce competition by growing in the off season. In temperate regions, there are numerous spring ephemerals and winter annuals. In order to generalize this idea, we might call such species ephemerals or phenological avoiders. In order to quantify this we suggest the mean flowering start date be used.

Adult plants also persist by acquiring space through vegetative reproduction. Clonality and the capacity to spread laterally are difficult to measure. One impediment is the time and effort required to excavate and carefully follow rhizomes through the soil. In measuring clonality, we need to measure such problematic traits as distance, angle, and longevity of the connection between ramets and the frequency and angle of branching (van Groenendael et al. 1997, see also Klimeš et al. 1997). Another difficulty is the number of ramets produced in a growing season. Some species can quickly produce a series of ramets, so methods that simply measure from ramet to ramet are inaccurate (e.g. Weiher et al. 1998). In our discussions, we could find no simple solution for quantifying clonality and we were left with a simple binary trait: clonal or non-clonal. More detailed qualitative groupings have also been suggested. For instance, van Groenendael et al. (1997) suggested four basic forms of plant clonality (+/- splitting, combined with +/- spreading) which are subdivided into a total of 16 general forms. Such classifications have strong heuristic value, but the ease with which misclassifications can occur and the large number of potential intermediates make such classifications difficult to implement.

Plants must also be able to tolerate disturbances. Some species avoid disturbances through phenology, by having an annual life history. The most general and fundamental trait for disturbance tolerance is the ability to resprout following a disturbance (Noble & Slatyer 1980). We know of no easy morphological analog and therefore we must rely on knowledge of individual species natural history.

Trait	Function	
Seed mass	Dispersal distance, longevity in seed bank, establishment success, fecundity	
Seed shape	Longevity in seed bank	
Dispersal type	Dispersal distance, longevity in seed bank	
Clonality	Space acquisition	
LWC, SLA	RGR, plasticity, stress tolerance, evergreenness, leaf longevity	
Height	Competitive ability	
Above-ground biomass	Competitive ability, fecundity	
Life history	Pant longevity, space-holding ability, disturbance tolerance	
Onset of flowering	Stress avoidance, disturbance avoidance	
Resprouting ability	Disturbance tolerance	
Stem density	Plant longevity, carbon storage	

Table 2. The common core traits and functions.

Stem density (as a measure of 'woodyness') is related to plant height, allocation to support structure, and stem palatability. The most important reason for including stem density is that it facilitates the ability to scale up from local to global models. Many dynamic global vegetation models use woodyness and SLA as key vegetation parameters which makes them crucial in data collection.

Table 2 reviews the common core traits and their ecological functions. Some of the common core traits are highly correlated, but we suggest that there is not yet enough evidence to choose between some of the similar traits. For instance, height and above-ground biomass are highly correlated, but biomass is also related to fecundity and this makes both traits valuable. Similarly, leaf water content may be a better general indicator of relative growth rate than specific leaf area (Wilson et al. 1999), but there are more SLAdata and it is an important component of many largescale vegetation models.

The other main observation from Table 2 is that some traits are related to many aspects of plant function. If we were asked for a minimal list of plant traits we would suggest: (1) a leaf measurement, either specific leaf area or leaf water content, (2) seed mass, and (3) adult size, measured as either above-ground biomass or height. We strongly agree with Westoby's (1998) recent suggestion that SLA, canopy height, and seed mass are the most fundamental functional plant traits that can be identified. Westoby's goal was to define a set of simple axes for determining the strategy of any plant species. Our main goal, to define a set of core traits that will help us predict species responses to disturbances and perhaps other environmental factors, is a much more specific goal. It is interesting to also note that although our respective goals were different, we converged on similar traits. This suggests that a consensus is developing.

Methodological guidelines

There are a number of important issues and logistical problems that relate to measurement methods. Many of us have participated in discussions on such topics as how to choose a plant to measure and exactly how to measure plant height. In general, we have converged on similar methods or at least we have largely agreed on the most logical and pragmatic choices. In order to maximize our ability to make comparisons and pool data sets, we must agree on methods and communicate them clearly.

The first problem is defining an individual. We must recognize that the fundamental unit is the ramet. This choice is both pragmatic, as genets would be impossible to identify in the field; and ecologically sound, as the ramet is sensibly the functional unit of most interest. We define a ramet as an iteration of the basic form of the plant without obvious connections to other ramets that would clearly unify the parts into one iteration. With this definition we should be able to identify the following examples as individuals: multiple stemmed shrubs and trees (e.g. Vaccinium corymbosum, Magnolia virginiana), ramets of clonal species with stolons (e.g. Agrostis stolonifera) or rhizomes (e.g. Typha latifolia), ramets of clonal species with root sprouting ability (e.g. Fagus grandifolia), and ramets of tussock-forming graminoids (e.g. Carex cherokeensis, Schizachyrium scoparium). Tussockforming graminoids pose somewhat of a problem in that the tussock acts as a functional unit in terms of holding space. Therefore, one might find it necessary to also collect traits on a tussock.

The second problem is choosing individuals for measurement. Should one choose individuals that express the potential of the species, i.e., should they be well-grown plants from an ungrazed, reasonably fertile, unshaded site? Should one collect traits in each site where the species is found and then should one keep track of how the traits of each species varies with environmental conditions (cf. Diaz et al. 1992)? Should one collect traits in each site where the species is found and should one then determine a regional mean? In our opinion, the last alternative is the least desirable. At the minimum, one should collect traits on individuals that are growing in the most benign conditions in which the species is observed (i.e., well-grown plants). Well-grown plants should give us the best point estimate of the potential each species has in expressing each trait. Depending on the research questions, it may be extremely important to link the traits with the sites in which they are found (Diaz et al. 1999; this issue). Therefore, one should also be prepared to collect traits in each location where a species is found. Doing so may also give some indication of species plasticity (but of course one cannot measure plant traits in all possible environments). In general, individuals should be chosen to represent the median individual in each particular location. Extremes should be avoided, unless one is interested in knowing what the extremes are.

We do not yet know if sampling should be uniform, random, or haphazard, or what the costs and benefits of each approach would be. Logistically, it is clear that uncommon species will be sampled haphazardly. If quadrat samples are being collected, then individuals should be collected from within, or adjacent to, the quadrat.

Most plant traits vary more or less continuously in nature, therefore continuous traits should be preferred over categorical or qualitative traits.

Seed mass and shape

Plants should be collected when seeds become mature. When measuring seed shape, the dispersule is of primary interest, therefore, seeds should not be rigorously cleaned of accessories (Hodgson & Thompson 1993). In the case of fleshy fruits however, seeds should be removed (Thompson et al. 1993). Seed shape should be measured as the variance of the seed's length, width, and breadth after the axes have been standardized to one by dividing by the largest of the three values (Thompson 1993b; Thompson et al. 1993). When measuring seed dimensions, accessories that easily fall off (e.g. pappus) should not be included in the measurements. A minimum of five seeds per species is recommended (Thompson 1993b).

The intact dry mass of a dispersule may be of interest, but establishment ability is more closely related to actual seed mass. Therefore, seeds should be cleaned of their accessories (e.g. pappuses, comas) prior to weighing (Westoby 1998). The seed coat should not be removed. In practice, we may need to recognize that the logistical problems associated with cleaning large numbers of seeds could prove overwhelming. In all likelihood, intact seeds will provide a fairly good estimate of mean seed mass. Seeds, achenes, and indehiscent, singleseeded fruits should be dried to a constant mass at 80° C, weighed, and counted. Because seed mass is variable, between 50 and 100 seeds should be counted for each ramet, when possible, and the mean seed mass for each ramet should be determined. The mean seed mass for a species is then the mean of the ramet seed masses.

Dispersal mode

Dispersal mode is a set of qualitative categories: anemochory (wind-dispersed, with obvious pappus or coma), exozoochory (with obvious barbs for attaching to animals), endozoochory (with fleshy fruit), myrmechochory (with elaisomes), 'ballistichory' (ballistic dispersal), and 'unassisted' (van der Pijl 1982). Finer categories may be necessary in some circumstances (e.g. where hydrochory is important, or when the specific animal disperser is of interest). Ideally, quantitative versions of these categories would be used. For anemochory, seed terminal velocity could be used (Askew et al. 1997). Ballistic dispersal is also related to seed mass and terminal velocity. The other dispersal syndromes pose problems for quantitative measurement. Dispersal distance for exozoochorous species is not a simple function of the size and number of barbs (Kiviniemi 1996), nor would we necessarily expect that the size of a fleshy fruit would be associated with dispersal distance.

Clonality

Clonality is most simply measured using binary categories: clonal or non-clonal. Quantifying clonality is extremely problematic and time consuming. The capacity for lateral spread has previously been estimated as the number of connections to other ramets or meristems multiplied by the maximum distance to the next ramet and the degree to which a species forms a tussock was estimated by the number of ramets within a prescribed distance (Weiher et al. 1998). These methods suffer from underestimating clonal spread in species that produce a series of ramets per rhizome or stolon (e.g. *Agrostis stolonifera*) and in species that produce very large tussocks. Because there seems to be no simple solution to this problem, we suggest scoring clonality as a binomial trait, at least until a reasonable easy trait is found.

Specific leaf area and leaf water content

Specific Leaf Area (SLA) is the area of one side of a single leaf divided by its dry mass. Leaf area should be measured on fresh, mature leaves using a leaf area meter, image analysis software, or planimeter. Specific leaf area may be highly variable, depending on environmental conditions (Poorter & van der Werf 1998). Therefore, it is particularly important to standardize this measurement. We suggest following many of the recommendations given by Westoby (1998), i.e., measure SLA on the youngest fully grown leaf in the light. To estimate variation in SLA, the oldest still green leaf could also be sampled. Leaf water content is the difference between the fresh mass of a fully turgid leaf and its dry mass, divided by its fresh mass (e.g. Garnier & Laurent 1994; Shipley 1995). Leaf water content should be determined on leaves that have been rehydrated for at least one night, preferably with deionized or distilled water. Leaves should be dried at a temperature between 60 and 80°C until at constant mass, and they should be handled with forceps. The measurement of leaf area is not straightforward for some species. The question of whether petioles should be removed is an important issue. Westoby (1998) suggested that the petiole should not be removed because it is an integral part of the leaf and because the petiole has the same characteristic longevity as the leaf lamina. The petiole also has the same functional value as the central vein of sessile leaves. Others have removed the petiole (e.g. Shipley 1995). Because there is a continuum of leaf form, from compound leaves with completely separate leaflets (e.g. legumes) to simple sessile leaves in which the central vein is embedded in the lamina to the stem (e.g. many Asteraceae), we suggest leaving the petiole attached. This allows for the relatively simple rule that leaves should be removed at the point of normal abscission (Westoby 1998) An alternative to leaving the petiole would be to cut disks from the lamina of each leaf. However, these two approaches will clearly lead to different values for SLA.

Some species do not have true leaves, such as species that are reduced to a photosynthetic stem (e.g. Eleocharis erythropoda, Euphorbia antisyphilitica). For these species, the functional equivalent of a leaf should be used (e.g. a stem or a portion of the stem). In the case of stem succulents, disks or sections can be cut along a rib. Because SLA is intended to measure the ratio of light capturing area to dry biomass of the functional leaf, there is the question of whether one should measure the entire light capturing surface area of the functional leaf or the one-sided area. This question will apply to species with oddly-shaped leaves (e.g. the erect conical leaves of Sarracenia alata) and some equitant species with leaves that have no lower surface, but rather a left side and a right side (e.g. the Iridaceae and Juncaceae). Leaf area should not include the non-light gathering underside of 'normal' leaves, but non-standard leaves require special considerations.

Westoby (1998) suggested that all leaf areas should be measured on a one-sided basis. If the intention with SLA is to measure the ratio of light-capturing area to dry mass, then the SLA of non-standard species may be underestimated. However, it can also be argued that although two sides of some leaves (and green stems) can potentially be light-capturing surfaces, they do not perform this function at the same time. This temporal dissociation of light capture would suggest that the onesided measurement of leaf area is appropriate. In all likelihood, the one-sided area has been measured and used in most cases, and so we may need to defer to historical precedent and use the measurement that has yielded a large number of strong relationships.

The proportion of species with non-standard leaves is quite small in most floras, therefore it may be useful to measure leaf area using both one-sided and two-sided methods in order to investigate which measure is more useful. Most of us would agree that results and strong relationships are the true test of the utility of the traits. This discussion on leaf area suggests that leaf water content may be a better trait than SLA simply because it seems to be measured more simply. With LWC one can avoid all the arguments about how to measure leaf area. The simplicity of LWC also suggests that it can be measured with less error. Recent work shows that SLA is much more variable between samples than LWC, and suggests that much of this extra variability can be attributed to errors in measurement of leaf area (Wilson et al. 1999). Its high correlation with SLA (Shipley 1995) means that much of the information in SLA is also in LWC (see also Garnier & Laurent 1994).

We have not included a measurement of leaf shape in the core list because there was no clear need for it. Leaf length and width are important for parameterizing climate models, and they can be used to calculate a variety of shape indices which may be useful for predicting community composition (e.g. Weiher & Keddy 1999). Leaf length and -width are easily measured and should be noted as high-value secondary traits.

Height and above-ground biomass

Plant height should be measured near the end of the growing season. Height should be measured as the difference between the elevation of the highest photosynthetic tissue in the canopy and the base of the plant. In general, scapes and peduncles should not be included as photosynthetic tissue (e.g. Gaudet & Keddy 1988), because we are interested in canopy height, not inflorescence height. Westoby (1998) suggested that height should be measured as "the top of the general canopy of the species, discounting any exceptional individuals or branches ... the height recorded should correspond to the upper 20 % of the leaf display". Measuring which amounts to the average height of the unself-shaded canopy is a good idea, but the 20 % value seems somewhat arbitrary. It will also require estimations and will therefore lead to increased measurement error. We suggest that it is much simpler and clearer to measure height as the higest point of the plant canopy. As long as one is clear about how height was measured, the difference between the two methods will be small.

Above-ground biomass (dry matter) is the oven-dry mass of the entire above-ground portion of the ramet (80 °C for 24 h). In general, the above-ground biomass will include all living portions of the plant (i.e., stem, leaves, fruits, seeds), but dead material (leaves) should be removed. The relative allocation to seeds and fruits versus vegetative biomass is also of general interest (e.g. Shipley & Dion 1992), and when possible, vegetative biomass should also be determined.

Life history, onset of flowering and resprouting ability

Life history should be qualitatively scored as annual (a species that produces seeds and dies within one growing season), biennial (a species that grows vegetatively for more than one growing season, then flowers and dies), or perennial (a species that grows vegetatively for more than one growing season and flowers more than once before dying). It would be useful to subdivide perennials into longevity categories, but in practice this is very difficult, especially for herbs. There is probably little to be gained by subdividing perennials into Raunkiaer life forms (but at high latitudes, bud location is related to cold tolerance, Raunkiaer 1937).

The onset of flowering should be measured by field observations. The mean date of anthesis should be scored for a sample of ramets. In the Northern hemisphere, we suggest scoring the date as the number of days from January 1, and in the Southern Hemisphere the number of days from July 1 could be used. We recognize that these traits will be useful in predictable seasonal climates, but their utility and importance will decline in climates where plants respond to unpredictable events (e.g. rainfall in semi-arid climates) and in tropical climates with little seasonality.

Resprouting ability is a categorical trait that relies on our natural history knowledge of each species. Plants that can regrow after the above-ground portion has been destroyed (due to grazing, fire, erosion, or other disturbance) have resprouting ability. A quantitative measure would again be desirable.

Stem density

Stem density can be assigned a binary trait: woody or not woody. Ideally, stem density should be measured quantitatively by dividing the dry mass of a portion of a stem by its fresh volume. We tentatively suggest investigating the utility of stem water content as an index of stem density (in order to avoid the difficulty of measuring volume).

Hard traits in need of easy analogs

While searching for and identifying a common core list of plant traits, it became apparent that we need to develop more easy analogs for many of the functional traits in which many ecologists are interested. Within the common core, seed dispersal, clonality, seedling establishment, plasticity, and resprouting ability clearly need better analogs either in terms of finding simple quantitative traits or easier measurement.

Several other traits have high functional interest, but are logistically impossible to measure in a large number of species. These traits might be high priority traits to consider in future comparative studies. It would be useful to find easy analogs or to simply show that much of their variation is captured indirectly through tradeoffs and correlations with other core traits. The list includes: photosynthesis (are SLA and leaf nitrogen sufficient?), plasticity in allocation patterns due to changes in either resources or disturbance (is SLA or leaf water content sufficient?), rooting depth, leaf life span (is SLA sufficient?), palatability (again, is SLA, leaf water content, or leaf toughness, sensu Hendry & Grime 1993, sufficient?), cold tolerance and genome size (is stomatal size or cell size sufficient? see Bennett 1987, MacGillivray & Grime 1995b), the presence of secondary compounds, litter decomposition rate (is ash content sufficient? see Cornelissen & Thompson 1997), and pollination vector. This list could easily be expanded, but our point is that we need more comparative studies that seek relationships between difficult to quantify functional traits and simple, pragmatic, easy traits. This is especially true for below-ground traits.

Conclusions

In order to make comparisons and build bridges across hierarchical levels, we need a common language, a common core of plant traits. The list presented here is by no means exhaustive, but it does capture a biologically significant proportion of functional plant attributes. The common core is meant to be a starting point from which each of us can tailor our own list of traits by adding details specific to our own region and research agenda (e.g. McIntyre et al. this issue). The common core supports Westoby's leaf-height-seed strategy (Westoby 1998), by placing a high priority on leaves (LWC, SLA), size (height, above-ground biomass), and seed mass. The common core is also a starting point for the future. As comparative ecology advances we expect that easy traits will be found for some of the harder traits, such as capacity for vegetative spread and dispersal ability, and thus we may be able to add or replace traits as new data become available.

When Theophrastus first classified plants according to their traits, he recognized the importance of height and woodyness as fundamental plant traits. These two traits remain fundamental. However, they are but two of about a dozen traits related to the fundamental challenges faced by plants. It seems very unlikely that we could once again be content with Theophrastus' system. Perhaps with time, our list will collapse into an equally elegant classification, but nature may not be that accommodating. Acknowledgements. We would like to thank Ian Noble for repeatedly questioning whether we can do any better than Theophrastus. This paper is the result of a workshop organized by Sue McIntyre, Sandra Lavorel, and Sandra Diaz; their organization, vision, demands, and trust were essential to our efforts. Thanks also go to Wolfgang Cramer and Sandra Lavorel for editing the special issue and Terry Chapin, Lauchlan Fraser, and Bill Shipley for their helpful comments. The workshop was sponsored by the International Geosphere-Biosphere Program - Global Change and Terrestrial Ecosystems project, C.N.R.S. and Région Languedoc Roussillon, and is a contribution to GCTE task 2.2.1.

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