Chapter 13

Plant Functional Types: Are We Getting Any Closer to the Holy Grail?

Sandra Lavorel · Sandra Díaz · J. Hans C. Cornelissen · Eric Garnier · Sandy P. Harrison · Sue McIntyre · Juli G. Pausas
Natalia Pérez-Harguindeguy · Catherine Roumet · Carlos Urcelay

13.1 In Search of the Holy Grail

Functional classifications have been seen as a necessary tool for the simplification of floristic complexity in global vegetation models (Neilson et al. 1992; Prentice et al. 1992; Foley et al. 1996; Woodward and Cramer 1996), for mapping vegetation patterns at key times in the past (Prentice and Webb 1998; Prentice et al. 2000), and for monitoring effects of global change or management on vegetation distribution and ecosystem processes (Díaz et al. 2002a; Cruz et al. 2002). Plant functional classifications were first designed by grouping plants a priori based on knowledge of their function, or based on observed correlations among their morphological, physiological, biochemical, reproductive or demographic characteristics (Woodward and Cramer 1996; Smith et al. 1997). It was assumed that these classifications would allow to predict changes in ecosystem processes directly from projected changes in plant species composition in response to global change. This idea was challenged by the recognition that functional effect groups (species with a similar effect on one or several ecosystem functions; e.g., primary productivity, nutrient cycling, Gitay and Noble 1997; Walker et al. 1999) and functional response groups (groups of species with a similar response to a particular environmental factor; e.g., resource availability, disturbance or CO_2; Gitay and Noble 1997; Lavorel et al. 1997) do not necessarily coincide. Although there have been sustained efforts to refine plant functional type (PFT) concepts and terminology (Gitay and Noble 1997; Lavorel et al. 1997; Lavorel and Garnier 2002), the search for a single, functionally comprehensive yet relatively parsimonious, plant functional classification has remained an elusive Holy Grail.

The Holy Grail requires to focus on functional traits of terrestrial vascular plants that (1) can together represent the key responses and effects of vegetation at various scales from ecosystems to landscapes, biomes, and continents; (2) are suitable for relatively easy, inexpensive and standardised measurement over the world; and (3) can hence be used to devise a satisfactory functional classification for global-scale modeling and mapping of the biosphere.

A large amount of research has been initiated on plant furnctional traits and PFTs since the early days of GCTE, where the Holy Grail was formulated largely by modellers. In this chapter we first summarise theoretical and empirical progress on the understanding of the response traits that are relevant to different aspects of environmental change. Recently numerous empirical studies have made considerable progress in elucidating how plant traits can be related to plant function in relation to main environmental constraints (see Sect. 13.2), and how these same traits are then relevant to the distribution of species along gradients of climate, nutrient availability, and disturbance. Additional theoretical (Ackerly 2003) and empirical (Ackerly 2004a) work has also analysed the role of phenotypic plasticity, ecological sorting and natural selection in determining present patterns of association between plant traits and environmental gradients. The correlational approach, which has formed the bulk of that research, has been quite successful in detecting significant associations between particular plant traits and environmental factors (reviewed in Sect. 13.3). Understanding how these traits may then influence biotic interactions, and eventually shape local vegetation through community assembly has however appeared to be a non-trivial scaling exercise, and we review current state of the art in Sect. 13.4. Likewise, scaling from individual plant traits that are affected by environmental changes to ecosystem effects has proved more challenging than initially anticipated because the traits that determine the response to specific environmental factors overlap directly, indirecly, or not at all with the traits that determine ecosystem functions such as biogeochemical cycling or flammability (Lavorel and Garnier 2002; reviewed in Sect. 13.5). Finally, we return to asking how these results have helped modellers working at larger scales, and what key challenges remain.

13.2 Individual Plant Structure and Function

Among all possible traits measurable on an individual plant, those of interest to global syntheses and modeling must fill four conditions: *(i)* bear some relationship to plant function; *(ii)* be relatively easy to observe and quick

In: Canadell JG, Pataki D, Pitelka L (eds) (2007) Terrestrial Ecosystems in a Changing World.
The IGBP Series, Springer-Verlag, Berlin Heidelberg

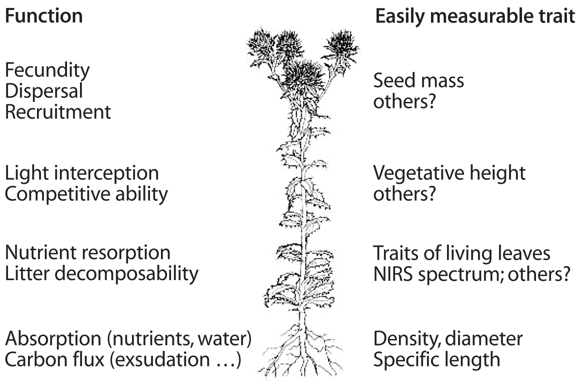

Fig. 13.1. Examples of soft traits and associated functions

to quantify ('soft' traits; Hodgson et al. 1999), *(iii)* using measurements that can be standardized across a wide range of species and growing conditions (Cornelissen et al. 2003b); *(iv)* have a consistent ranking – not necessarily constant absolute values – across species when environmental conditions vary (Garnier et al. 2001; Cornelissen et al. 2003a; Shipley and Almeida-Cortez 2003). Such traits are called 'functional traits' or 'functional markers' (Garnier et al. 2004), and can be morphological, ecophysiological, biochemical, demographical or phenomenological (Fig. 13.1). At this stage, the interest lies in the role of these traits for main plant functions, while their role in ecosystem dynamics is not specified, and they may turn to be response and/or effect traits. Information on soft traits is available for large numbers of species from all types of vegetation (see Díaz et al. 2004; Wright et al. 2004). Over the years, a consensus has been growing about which soft traits are best related to key plant functions such as resource economy or recruitment and how these then become response traits to climate and disturbances (Grime et al. 1997; Westoby et al. 2002; Cornelissen et al. 2003b) (Table 13.1). Comparability of data and global coverage must be ensured by using standardised lists of traits, which are a consensus about which traits are critical for the ecological challenges ahead (Table 13.1), and measuring them with standard methodologies (McIntyre et al. 1999; Díaz et al. 2002b; Cornelissen et al. 2003b), now freely available (Cornelissen et al. 2003b[1]).

Plant functional traits are considered as reflecting adaptations to variation in the physical environment and trade-offs (ecophysiological and/or evolutionary) among different functions within a plant. Co-varying sets of traits have been associated to 'major axes of plant specialization', that are consistent across environments, biogeographic regions and major plant taxa (Grime 1977; Chapin et al. 1993; Díaz et al. 2004). More generally, the analysis of plant functional trait responses to environmental variation, and of their effects on ecosystem function has been guided by the recognition that plants are constrained for performing alternative functions simultaneously, such as resource capture and conservation (Grime 1979; Chapin et al. 1993; Poorter and Garnier 1999), acquisition of several different resources (light and water, Smith and Huston 1989; light and nutrients, Tilman 1988), or growth and reproduction (Silvertown et al. 1993; Solbrig 1993).

A synthesis of empirical and theoretical studies proposed that at least four axes of plant specialization should be considered (Westoby et al. 2002). The first and best understood axis is represented by the specific leaf area (SLA) – leaf life span trade-off and is associated with turnover time of plant parts (including through herbivory), nutrient residence times and rate of response to favourable growth conditions. The global relevance of this axis was confirmed by an analysis across four floras from different biomes and biogeographic regions (Díaz et al. 2004). The second axis, representing the trade-off between fecundity and seed mass addresses establishment opportunities and success in the face of hazards, respectively. Seed mass and fecundity are negatively correlated, even after correcting for plant size. The third axis represented by potential plant height, carries several trade-offs and adaptive elements, and captures multiple constraints such as the density and height of shading competitors, water economy, and response to disturbance. The global relevance of plant height was confirmed by cross-continental analysis (Díaz et al. 2004). Finally, a fourth axis representing the coupled variation between twig size and leaf size determines the texture of canopies. Although a decrease in leaf size is common in dry, high light or cold conditions, the costs and benefits of small vs. large leaves remain to be formalized. Still, identifying an axis relevant to temperature variation, and especially response to extremes, stands as a challenge to ecophysiologists and ecologists.

However, the previous syntheses focused on aboveground traits, which are easily accessible. Recent studies have endeavoured to provide the same kind of information belowground, focusing on the functions of root traits, trade-offs among them, and how they relate to aboveground traits that could then be used as proxies for belowground function. Suites of correlated traits appear to also exist in roots, and represent a trade-off between root longevity and growth rate. Generally, low specific root length (SRL: ratio between root length and root biomass) is associated with thick, dense roots with low nitrogen and high lignin concentrations (Comas and Eissenstat 2004; Craine et al. 2002; Craine et al. 2003), a syndrome usually found in slow growing species or plants grown in limiting conditions (Reich et al. 1998a; Ryser 1998; Comas et al. 2002; Comas and Eissenstat 2004). Available data linking root morphology and plant functioning, and analogies to leaf traits suggest that this suite of traits reflects root longevity (Eissenstat 1991; Eissenstat

---

[1] http://www.publish.csiro.au/nid/65/paper/BT02124.htm.

In: Canadell JG, Pataki D, Pitelka L (eds) (2007) Terrestrial Ecosystems in a Changing World.
The IGBP Series, Springer-Verlag, Berlin Heidelberg

Table 13.1. Association of plant functional traits with (1) plant responses to four classes of environmental change (i.e., 'environmental filters'), (2) plant competitive strength and plant 'defense' against herbivores and pathogens (i.e., 'biological filters'), and (3) plant effects on biogeochemical cycles and disturbance regimes. See also Chapin et al. (1993), Díaz et al. (1999), Weiher et al. (1999), Lavorel (2002) and Lavorel and Garnier (2002) for details, including 'hard traits' corresponding with the soft traits given here. Soil resources include water and nutrient availability. Disturbance includes any process that destroys major plant biomass (e.g., fire, storm, floods, extreme temperatures, ploughing, landslides, severe herbivory or disease). Note that effects on disturbance regime may also result in effects on climate or atmospheric CO_2 concentration, for instance fire promotion traits may be linked with large-scale fire regimes, which in turn may affect regional climates

	Climate response	CO_2 response	Response to soil resources	Response to disturbance	Competitive strength	Plant defence/protection	Effects on biogeochemical cycles	Effects on disturbance regime
Whole-plant traits								
Growth form	*	*	*	*	*	*	*	*
Life form	*	*	*	*	*		*	*
Plant height	*	*	*	*	*	*	*	*
Clonality	*	?	*	*	*			?
Spinescence	*	?			*	*		?
Flammability		?			*	?	*	*
Leaf traits								
Specific leaf area	*	*	*		*	*	*	
Leaf size	*	?	*		*	*	*	
Leaf dry matter content	*	?	*			*	*	*
Leaf N and P concentration	*	*	*	*	*	*	*	
Physical strength of leaves	*	?	*	*		*	*	
Leaf life-span	*	*	*	*	*	*	*	*
Leaf phenology	*		*		*		*	*
Photosynthetic pathway	*	*			*			
Leaf frost resistance	*				*	*		
Stem and below-qround traits								
Stem specific density	*	?	?	*		*	*	*
Twig dry matter content	*	?	?	?		*	*	*
Twig drying time	*	?	?				?	*
Bark thickness			*	*		*		?
Specific root length	*	?	*		*	*		?
Diameter of fine root	*	?	*					
Distribution of rooting depth	*	*	*	*	*		*	*
95% rooting depth	*	?	*		*			*
Nutrient uptake strategy	*	*	*	*	*		*	
Reqenerative traits								
Dispersal mode				*				
Dispersule shape and size				*				
Seed mass			*	*	*	*		
Resprouting capacity								

et al. 2000; Ryser 1996), greater nutrient use efficiency and resistance to herbivore and physical damage (Craine et al. 2001). These traits are thought to minimize nutrient losses, allowing plants to grow larger at low nutrient supply rates. Opposite traits tend to maximize root surface area and length per unit biomass, thereby allowing quick exploration of soil resources and rapid growth. However, root traits are definitely not easily measured. Therefore, there are a number of challenges still to be resolved: *(i)* to identify traits that are closely related to key root functions such as nutrient acquisition, anchoring, rhizospheric activity, decomposition rate; *(ii)* to normalize root traits measurements for broad comparisons; *(iii)* to test relationships between leaf and root traits for

In: Canadell JG, Pataki D, Pitelka L (eds) (2007) Terrestrial Ecosystems in a Changing World.
The IGBP Series, Springer-Verlag, Berlin Heidelberg

later use of leaf traits as easier proxies. Close relationships between leaf and root nitrogen concentration have already been shown at a global scale (Craine and Lee 2003; Craine et al. 2005).

As recognised by early work (Theophrastus ca. 300 BC; Raunkiaer 1934), growth forms are one expression of trade-offs among traits and adaptation to different types of environments. As such, they provide comprehensive links between key traits, plant response to their environment and their effecs on ecosystem function (Chapin 1993), and this is why large scale dynamic models have used them as the basis for their plant functional classifications. However, there is also an important range of variation in trait values and detailed trade-offs among traits within each life form. For instance, the trade-off between leaf lifespan (and underlying protective traits) and traits that promote leaf productivity (e.g., SLA) operates both within and between life forms (Díaz et al. 2004; Wright et al. 2004), but relationships between seed dispersal syndromes and seed size depend on seed size (Westoby et al. 1990).

13.3 Traits and Environmental Gradients

The functional meaning of plant traits for response to environmental variation has been identified through observations of the variations in trait values across environments differing for one or several factors, targeted experiments and modeling. Most of our knowledge is derived from the first approach, and therefore directly applies to spatial variation. Space-for-time substitution is then used to assume that the same changes in trait values would be observed following an environmental change of the same magnitude. Growing numbers of experiments have confirmed this assumption for responses to single environmental factors such as nutrient availability (Dyer et al. 2001) or grazing (Bullock et al. 2001), as do models of community or ecosystem dynamics (Pausas 1999; Colasanti et al. 2001; Ackerly 2003; Boer and Stafford Smith 2003; Hickler et al. 2004).

This combination of approaches has advanced the understanding of the adaptive significance of traits, or combinations of traits, to predict the response of organisms to climate, nutrients and disturbance (Table 13.1). Globally, response to climate, considered in terms of response to extreme low or high temperatures, and to gradients of moisture availability, is associated with variations in life form, leaf traits, rooting depth and lateral root spread, and genome size (McGillivray 1995; Díaz and Cabido 1997; Pavón et al. 2000; Niinemets 2001; Schenk and Jackson 2002, 2005). Specific leaf area (SLA), leaf dry matter content (LDMC) and leaf chemical composition co-vary with soil resource availability (Cunningham et al. 1999; Poorter 1999) as do specific root length, tissue density and diameter (Reich et al. 2003; Robinson and Rorison 1988). Responses to CO_2 depend on life cycle, relative growth rate (RGR), photosynthetic pathway, and stochiometric relationships (Poorter et al. 1996). Response to water availability is associated with variation in SRL, root diameter and root architecture (Fitter 1991; Wright and Westoby 1999; Nicotra et al. 2002). RGR, leaf and root morphology, and seed mass determine response to shading (Leishman and Westoby 1994; Reich et al. 1998b). Response to disturbance is associated with variation in life cycle, plant height, architecture, resprouting and seed traits (McIntyre and Lavorel 2001; Bond and Migdley 2001; Pausas et al. 2004; Díaz et al. in press). Following, we summarise recent progress in the identification of plant traits associated with response to the two simple factors that vary most significantly across communities within a landscape: resource availability and disturbance.

13.3.1 Plant Functional Response to Mineral Resource Availability

Early syntheses on changes in species traits along nutrient gradients (Grime 1977; Chapin 1980) recognised that species from nutrient-rich habitats tend to be inherently fast-growing. This goes along with rapid resource capture and fast turn-over of organs leading to poor internal conservation of resources, while the reverse is true for species from nutrient-poor habitats (Tables 13.1, 13.2). More recently, a series of quantitative traits has been associated with this fundamental trade-off in plant functioning (Reich et al. 1992; Grime et al. 1997; Poorter and Garnier 1999; Díaz et al. 2004; Wright et al. 2004). Fast-growing species from nutrient-rich habitats usually have a combination of high SLA, high SRL and relatively more fine roots, high tissue nutrient (in particular nitrogen) concentration, low tissue density and cell wall content, high rates of carbon and nutrient uptake, and short-lived leaves and roots. Opposite traits characterize species from nutrient-poor habitats, in which the mean residence time of nutrients tends to be maximized through longer-lived organs and/or higher resorption of nutrients from senescing organs (Ryser 1996; Garnier and Aronson 1998; Boot 1989; Aerts and Chapin 2000; Westoby et al. 2002).

13.3.2 Plant Functional Response to Disturbance

Disturbances are defined here as natural or land use related events that remove biomass or individuals (Grime 1977). Although disturbances must be considered for relevant plant functional classifications (Lavorel et al. 1997; Lavorel and Cramer 1999; Pausas et al. 2003), a theoretical framework comparable to that developed for resource economy remains elusive. Moving beyond the well-

In: Canadell JG, Pataki D, Pitelka L (eds) (2007) Terrestrial Ecosystems in a Changing World.
The IGBP Series, Springer-Verlag, Berlin Heidelberg

Table 13.2. Summary of traits associated with contrasted environmental conditions and their feed forward effects on community structure and ecosystem processes in perennial grasslands

Level of organization	High fertility High disturbance	Low fertility Low disturbance
Individual traits	High SLA, low LDMC, low leaf C : N; allocation to leaves and stems; high plasticity	Large size, long-lived, low SLA, high LDMC, high leaf C : N; allocation to roots; low plasticity
	Numerous, persistent small seeds with high dispersal; selfing	Few larger seeds with low dispersal and no seed bank; outcrossing
Species interactions	Exploitative competitors: rapid depletion of resources; symmetric interactions	Conservative competitors: tolerance to low resource levels; asymmetric interactions
	Predominance of competition	Predominance of facilitation and allelopathy
	High herbivory	High mycorhizal associations
Community	Abundance of forbs and some stoloniferous grasses	Abundance of cespitous grasses
Ecosystem processes	Fast rates of biogeochemical cycling; rapid litter decomposition; high NPP	Slow rates of biogeochemical cycling; slow litter decomposition; low NPP
	High palatability	High fuel loads, high flammability

known ruderal syndrome (Grime 1977) requires better understanding of regeneration traits. There is good evidence that seed size has a fundamental evolutionary and ecological significance for post-disturbance colonization, competitive response and tolerance to abiotic stress (Venable et al. 1988; Westoby et al. 2002). However the role of this trait for seed persistence, dispersal or seedling growth and survival is debated (Marañon and Grubb 1993; Thompson et al. 1993; Hughes et al. 1994). Overall, traits determining population persistence have so far received limited attention in functional trait analyses (Eriksson and Ehrlén 2001). In an analysis of the sensitivity of population growth rate to species demographic parameters, Silvertown et al. (1993) found a correspondence between longevity and resource-rich environments, survival and resource shortage, and fecundity and disturbance. These patterns still need to be matched with variation in soft traits through meta-analyses of large demographic and trait data bases.

Syntheses targeted at specific disturbances organised under the banner of GCTE have highlighted recurrent patterns of plant specialization in relation to soil disturbance, grazing and fire, as well as the nuances that need to be applied to them.

Soil disturbance consistently favours plants with a suite of traits additional to the ruderal syndrome (Lavorel and McIntyre 1999c). Plant species tolerant to soil disturbance by ploughing or mammal digging are characterised by: a short and prostrate stature, with either a stoloniferous architecture in perennial grasses, or flat rosettes in forbs, high fecundity and a small dormant seed pool. Intolerant species are typically larger tussock grasses or dicotyledons, with low fecundity and no seed dormancy mechanisms, and with low plasticity in their morphology. Finally, a group of indifferent species has an architecture characterised by leafy stems, with high morphological plasticity, and high seed dormancy (Lavorel et al. 1998, 1999a,b).

There are few empirically tested generalizations about which plant traits are positively or negatively associated with ungulate grazing, and the validity of some widely recognized trait responses to grazing has remained mostly untested at the global scale. There have been suggestions in the literature, based on pair-wise regional comparisons (Díaz et al. 2001; Adler et al. 2004, 2005), that evolutionary history of grazing by ungulates, as well as habitat productivity, determine what plant traits are favoured by grazing. Díaz et al. (in press) have asked what plant traits are consistently associated with grazing at the global scale, and whether these traits varied with precipitation (a surrogate for resource availability) and evolutionary history of grazing. A quantitative analysis of 195 studies from all over the world confirmed that overall grazing favoured annuals over perennials, short-statured over tall-statured plants, prostrate over erect plants, and stoloniferous or rosette over tussock architecture. This analysis demonstrated for the first time that some of the response patterns disappeared or were substantially stronger or weaker under particular combinations of precipitation and evolutionary history of herbivory. For example, in dry regions with long evolutionary history of ungulate herbivory, grazing did not favor annual plants over perennial plants.

Pausas et al. (2004) analysed regeneration strategies worldwide for woody plant species from ecosystems that are subject to stand-replacement (crown) fires. It is commonly assumed that the main traits allowing persistence after stand-replacement fires are resprouting capacity and the ability to retain a persistent seed bank (termed 'propagule persistence capacity'). Different combinations of these two traits have been preferentially selected in floras with different evolutionary histories. Although all four possible binary combinations appear in most fire-prone ecosystems, the relative proportions of each type (and the dominant type) differ. In Australian heathlands, the proportion of resprouters and non-resprouters is rela-

In: Canadell JG, Pataki D, Pitelka L (eds) (2007) Terrestrial Ecosystems in a Changing World.
The IGBP Series, Springer-Verlag, Berlin Heidelberg

tively even, compared with other fire-prone ecosystems, though post-fire obligate resprouters (resprouters without a seed bank) are almost absent. In the Mediterranean basin, most resprouters are obligate, while in California shrubs resprouters are evenly segregated among those having propagules that persist after fire (facultative species) and those without propagule persistence capacity (obligate resprouters). Species with neither persistence mechanism are rare in most fire-prone shrublands. Although data was limited, the review also highlighted some clear trade-offs with other traits (e.g., height), as well as the importance of considering the phylogenetic relatedness for a proper understanding of functional traits and trade-offs. For instance, in the Mediterranean basin flora, most resprouters have fleshy fruits and most non-resprouters have dry fruits. However, this pattern is not due to an ecological trade-off, but to a common lineage, as demonstrated by a phylogenetically controlled analysis (Pausas and Verdú 2005).

The data syntheses relating response traits to fire and grazing have still only dealt with individual disturbances. A further challenge lies in the understanding of disturbance regimes. For example, in many grasslands of the world disturbance regimes combine fire, grazing and/or mowing, fertilization and soil disturbance. Because regimes represent fixed combinations of disturbances that recur on the landscape, they can mask the interactions between the individual disturbances within that structure plant communities (Collins 1987). Woodlands and savannas are often shaped by the combination of grazing by wild and domestic herbivores, together with intentional or unintentional fire (Bond et al. 2003). Additional disturbances associated with farming and forestry can co-occur with grazing and fire to structure woodlands and forests (McIntyre and Martin 2001; McIntyre et al. 2002; Dale et al. 2001). Grazing tolerance of a number of species from Australian subtropical grasslands was found to covary with other disturbances (McIntyre et al. 2003), with the grazing tolerance of native species tending to decline in the presence of soil disturbance or water enrichment. Novel combinations of human-induced and natural disturbances are already widespread and are expected to be features of the future. Their effects can range from changes in dominance of different PFTs to dramatic shifts associated to plant invasions (D'Antonio and Vitousek 1992).

Pausas and Lavorel (2003) proposed a unifying framework that may apply to a variety of disturbance types. This framework is based on the recognition that plants can have persistence strategies at different levels of organisation and provides an understanding of the order in which different mechanisms act on plant persistence in disturbed systems. The main parameters to determine persistence in chronically disturbed ecosystems are those related to: **I**ndividual-persistence capacity, **P**ropagule-persistence capacity (persistence at the population level), **C**ompetitive capacity (persistence at the community level) and **D**ispersal capacity (persistence at the landscape level). The approach by Pausas et al. (2004) is a special case of this approach. Much remains to be done to identify traits relevant to different levels of response, and how these may vary depending on context. Nevertheless, sixteen possible functional types could be obtained by assuming a simple binary classification of the four levels of persistence.

13.3.3 Projecting Changes in Plant Functional Traits in Response to Global Change

Natural gradients usually combine variations in climate, resource availability, and disturbance regimes. These underlying simple gradients may be explicit for analyses of plant response to altitude (Pavón et al. 2000) or agricultural disturbance (Kleyer 1999), though again these combinations are likely to not be stable in the future. In many other instances however, the nature and amount of environmental variation underlying complex gradients (*sensu* Austin and Smith 1989) along which traits are studied has not been quantified or formalized. For instance, this is the case of successional gradients (Bazzaz 1996; Prach et al. 1997; Garnier et al. 2004; Richardson et al. 2005) or ecotones (Dodd et al. 2002) which are prime opportunities to obtain time series of plant functional traits.

Interpretation and projections of plant distributions along complex gradients are problematic because traits associated with different factors, such as water and nutrient stress, can overlap (Díaz et al. 2004) or be independent (Cunningham et al. 1999; Dyer et al. 2001). Non-overlapping trait responses are commonly observed when one environmental factor involves adult traits (e.g., nutrient availability) and other regeneration traits (e.g., disturbance) (Shipley et al. 1989; Leishman and Westoby 1992; Thompson et al. 1996; Lavorel et al. 1999b). In addition, the role of genetically-based plasticity of traits in response to environmental changes has largely been ignored from analyses, though it may contribute to population persistence (Strand and Weisner 2004; Stanton et al. 2000). Attempts to understand linkages, trade-offs and dependency among traits based on basic ecophysiological and evolutionary mechanisms, as reviewed in Sect. 13.2, are the way forward to address these complex responses (Ackerly et al. 2000; Westoby et al. 2002). In the context of global change, our ability to generate reliable projections of future vegetation is further limited by the fact that different combinations of climatic factors could occur in the future, as they have in the past (Jackson and Williams 2004), as will novel combinations of atmospheric CO_2 concentration, climate and distur-

In: Canadell JG, Pataki D, Pitelka L (eds) (2007) Terrestrial Ecosystems in a Changing World.
The IGBP Series, Springer-Verlag, Berlin Heidelberg

bance regimes. Our ability to apply plant functional responses to generate future vegetation projections must therefore rely on more experimental and modeling work. One remaining challenge for modeling, however, lies in the construction of PFTs from analyses of continuous plant traits. This methodological challenge can be solved with statistical approaches (Pillar and Sosinsky 2003; Nygaard and Erjnaes 2004), but is also a more fundamental issue because of the assumption that future responses to multiple factors will be stable within groups.

13.4 Scaling from Individual Plants to Communities: from Response Traits to Community Assembly

Having learned how populations of individual species respond to environmental variation across landscapes, understanding how communities assemble remains a significant challenge (Weiher and Keddy 1999; Ackerly 2003; Suding et al. 2003). This challenge is particularly significant when novel environmental conditions and landscape fragmentation by land use may lead to entirely new assemblages, as have different environmental conditions in the past (Jackson and Williams 2004). Effects of changes in climate or land use might be modeled as changes in the strength of different abiotic (climatic, atmospheric CO_2 concentration, resource availability, disturbance) and biotic (competition, predation, mutualisms) filters that successively constrain which species and traits, from a regionally available pool, can persist at a site (Woodward and Diament 1991; Díaz et al. 1999; Naeem and Wright 2003; see also Díaz et al. 2007, Chap. 7 of this volume). We should then be able to predict the trait composition of communities by combining knowledge of (1) the regional species pool, (2) the nature and strength of different filters, (3) the response traits associated with each filter and (4) the rules that shape assembly (Campbell et al. 1999).

Attempts to predict interspecific competition from plant traits have had mixed success (Keddy et al. 1998; Wardle et al. 1998), in particular because species competitive rankings are sensitive to nutrient availability (Keddy et al. 2000), disturbance (Suding and Goldberg 2001), and to mycorrhizal associations (van der Heijden et al. 1998; Wardle et al. 1998). A reasonable consensus has been reached regarding tolerance of competition by neighbours (competitive response) where plant height and seed mass are positively associated with greater tolerance (Goldberg 1991). However, the attributes that determine competitive effects of plants upon their neighbours, and how these may vary with resources and disturbance, remain to be elucidated. Grime's competitive syndrome (1977, 2001) includes attributes such as tall stature, wide spread, nutrient monopolization and abundant litter production. Tilman (1988) also emphasised the importance of height in productive conditions, but in nutrient-poor environments leaf and root attributes associated with nutrient uptake are those expected to confer competitive effects (Craine et al. 2001, 2005). Further, Goldberg and Novoplansky (1997) proposed that competitive effects of species may depend on whether nutrients or water is most limiting. Relating this idea to the strategy model by Ackerly (2004b) in the case of nutrient limitation, a 'conservative competitor' strategy, with leaf traits promoting resource conservation, such as a low SLA, high tissue density and long life span, is expected. Otherwise an 'exploitative competitor' strategy, with opposite leaf traits, is expected (Michalet 2001; Liancourt et al. 2005). In addition, other types of plant-plant interactions such as facilitation and allelopathy may gain importance in either resource-poor and physically stressful, or resource-rich and physically benign environments (Bertness and Callaway 1994; Pellissier 1998; Bruno et al. 2003). Which plant traits are conducive to these other mechanisms remains to be elucidated, but are most likely related to the nutrient and water acquisition vs. conservation syndromes (Liancourt et al. 2005), including their effects on herbivory.

Another fundamental interaction structuring communities is herbivory (Crawley 1992). There is good evidence that structural and chemical traits known to be associated with nutrient or climatic gradients influence patterns of herbivory by generalist invertebrates (Grime et al. 1996; Wardle et al. 1998; Cornelissen et al. 1999; Pérez-Harguindeguy et al. 2003) and vertebrates (McKey et al. 1978; Bryant et al. 1991). Nutrient and/or water limitation tends to select for conservative strategies which result in low attractiveness to these herbivores due for example, to leaf high tensile strength (toughness) and low nutritive value (e.g., high C/N ratio) (Bryant et al. 1983; Coley et al. 1985; Cebrían 1998; Díaz et al. 2004). The opposite applies to resource-rich environments. How antiherbivore defences may then feedback to ecosystem productivity *via* the soil is discussed in Sect. 13.5.

Finally, the strength of interactions among plants is also expected to co-vary with other key traits along environmental gradients. This is because the nature and the quantity of the production of secondary biochemical compounds involved in anti-herbivore defense, litter decomposition, or allelopathy (Pellissier and Souto 1999) can also be affected by microclimate and resource availability (Herms and Mattson 1992; Hartley and Jones 1997).

Other types of trophic interactions that influence community structure and ecosystem processes are associations with soil microbes, for instance mycorrhizae (van der Heijden et al. 1998; Klironomos et al. 2000; Langley and Hungate 2003; Read et al. 2004; Rillig 2004). Cornelissen et al. (2001) revealed consistent large and significant differences in inherent relative growth rate (RGR), foliar chemistry and leaf litter decomposability

In: Canadell JG, Pataki D, Pitelka L (eds) (2007) Terrestrial Ecosystems in a Changing World.
The IGBP Series, Springer-Verlag, Berlin Heidelberg

among plants with mycorrhizal association strategies. This results in slow carbon cycling in ericoid and ectomycorrhizal plant species from temperate ecosystems with low pH, vs. low nitrogen availability and fast carbon cycling in arbuscular and non-mycorrhizal species, found in more nitrogen-rich ecosystems with higher pH. The relative abundance of dependent and non-dependent species in a community will determine the importance of this plant-fungus interaction (Urcelay and Díaz 2003). All together, these findings support Read's (1991) hypothesis that mycorrhizal type is an important component of a plant's strategy in the context of nutrient availability. However, at a global scale we still know little about links between plant-associated microbes and plant traits, or about belowground plant traits in general. Recent efforts in this field are promising (Jackson et al. 1996; Ryser 1996; Craine et al. 2003; Craine and Lee 2003; Wardle 2002).

In order to better capture the complexities of community assembly, and how these may link to individual plant traits, Suding et al. (2003) proposed that trade-offs among species traits (e.g., ability to capture and cycle resources quickly vs. leaf toughness) determine community structure through the nature and intensity of competition and other interspecific interactions depending on environmental conditions. Our current knowledge, as summarised above, highlights a number of these linkages. For instance, we expect that nutrient-poor environments will select for species with leaf traits promoting resource conservation, such as low SLA, high tissue density and long life span. As a consequence of these primary traits, predominant plants in such environments will compete with their neighbours by sequestering nutrients – possibly with the help of mycorrhizal associations, by accumulating poorly degradable litter (Berendse 1994), and sometimes through allelopathy or nutrient immobilization (Michelsen et al. 1995; Hättenschwiller and Vitousek 2000); while also facilitating subordinates by herbivore protection. The converse would be expected in nutrient-rich environments (Table 13.2).

13.5 Scaling from Communities to Ecosystems: from Response Traits to Effect Traits

The 'Holy Grail' hypothesis states that environmental changes will lead to changes in community composition and thus in plant traits, and these in turn will affect ecosystem functioning. This hypothesis was first approached by matching lists of response attributes with known effects of some of these attributes (or their correlates) on ecosystem processes (Díaz et al. 1999; Walker et al. 1999; Eviner and Chapin 2003; see also Díaz et al. 2007, Chap. 7 of this volume; see Tables 13.1 and 13.2 and Table 1 *in* Lavorel and Garnier 2002). Inspections of these lists have revealed that the resource axis has maximum overlap between response and effect traits, whereas overlaps are few in the case of disturbance. One essential step to understanding the causes of these differing degrees of overlap has been the analysis of the specific functions of the traits involved in either response or effect (Lavorel and Garnier 2002; see Table 13.1). For the resource axis it showed that responses to resource availability and effects on biogeochemistry are jointly constrained by the trade-off between acquisition and conservation strategies, and their characteristic traits (Chapin et al. 1993; Grime 2001). For example, plants growing in adverse environments have low specific leaf area, high C/N ratio, and high tensile strength. These traits make them less palatable to generalist herbivores (see above), and persist in litter, thereby strongly influencing decomposition (Wardle et al. 1998; Cornelissen et al. 1999; Pérez Harguindeguy et al. 2000). This way, herbivore-induced changes in the balance of palatable and unpalatable species lead to changes in the net litter quality and therefore in decomposer activity (Wardle et al. 1998; Cebrían et al. 1998; Wardle 2002). Association with N_2 fixing bacteria is another trait that provides feedback on ecosystem productivity *via* N-rich litter. This mechanism is in particular a recurrent one underlying the impacts of invasive species on nutrient cycling (D'Antonio and Corbin 2003). On the other hand, regeneration and demographic traits associated with response to disturbance (e.g., fire, grazing) are known to have little direct relation with adult ecophysiological traits, and would therefore be of little relevance to biogeochemistry.

The ultimate goal of response-effect analyses should be the formulation of parsimonious quantitative relationships expressing the different components of each ecosystem function in relation to particular traits (Lavorel and Garnier 2002; Eviner and Chapin 2003). These relationships would make it possible to use traits to scale from individual plants and the communities they form to the ecosystem level (Dawson and Chapin 1993). Such formulations have been proposed for aboveground primary productivity (Chapin 1993 and further modifications by Lavorel and Garnier 2002 and Garnier et al. 2004). Specific annual net primary productivity (SANPP; "ecosystem efficiency", Reich et al. 1997) expresses ANPP per gram of green biomass, and can be written as:

$$\mathrm{SANPP} = \frac{\log_e\left[\sum_{i=1}^{n\,\mathrm{species}} p_i x e^{\mathrm{RGR}_i x (tf-to)_i}\right]}{\Delta T}$$

where p_i is the relative contribution of species i to the biomass of the community, RGR_i and $(tf–to)_i$ are the aboveground relative growth rate and period of active growth of species i, respectively, and ΔT is the period over which SANPP is assessed. Garnier et al. (2004)

In: Canadell JG, Pataki D, Pitelka L (eds) (2007) Terrestrial Ecosystems in a Changing World.
The IGBP Series, Springer-Verlag, Berlin Heidelberg

tested this relationship against independent measurements of leaf traits and productivity and showed that specific leaf area, LDMC, and leaf nitrogen concentration are indeed correlated with SANPP due to the well-established links between these traits and RGR (Reich et al. 1992; Poorter and Garnier 1999). In this equation, contributions of individual species to ecosystem function are proportional to their abundance in the community. Díaz et al. (this volume) further discuss the role of dominant species in functional diversity – ecosystem function relationships.

Correlations have also been established between rates of litter decomposition and leaf traits (SLA, LDMC and leaf tensile strength) of individual species (Cornelissen et al. 1999) and over communities (Garnier et al. 2004). However, in contrast to the case of ANPP there is no mechanistic model available. Empirical relationships between response and effects have been proposed for several other environmental factors and ecosystem functions (Chapin 2003; Eviner and Chapin 2003; Diaz et al. 2007, Chap. 7 of this volume), but developing formal models must be the next step.

Our understanding remains even more limited when attempting to link disturbance response and effect traits. Lavorel and Garnier (2002) showed that the list of traits relevant to ecosystem flammability has in fact minimal *direct* overlap with traits relating to fire response. When functional linkages between traits promoting fire tolerance and those involved in ecosystem flammability exist (Bond and Midgley 1995), even once phylogeny has been accounted for (Schwilk and Ackerly 2001), they result from associations or trade-offs between fire response traits and the actual traits that determine flammability, and are therefore *indirect*. For instance, a high growth rate is required to increase the success of seed regeneration after fire, and is also often associated with canopy architectures with many thin stems and high surface/volume ratios, which promote fire. Large underground structures allow resprouting, which increases fire survival, and drought tolerance, which allows low water potential and hence increases flammability. Closer investigations using phylogenetically independent analyses across floras evolved in high vs. low fire regimes, or sites with high vs. low resources, are needed to explore this issue further. Further knowledge will also be gained by analysing trait and ecosystem processes for cases of invasions that trigger positive fire feedback loops (D'Antonio 2000; Grigulis et al. 2005). Likewise, formal analyses and models linking grazing response strategies and palatability along resource gradients are still needed to build on the abundant but dispersed grazing literature (Landsberg et al. 1999; Adler et al. 2004). Pasture agronomists have shown that patterns of pastoral value (i.e., biomass quantity and quality over the growing season) along gradients of nutrient availability can be related to response traits such as LDMC (Cruz et al. 2002; Duru et al. 2004).

13.6 So, Are We Getting Closer to the Holy Grail? Scaling beyond Ecosystems

13.6.1 Plant Functional Traits and Landscape Dynamics

Plant functional types have been for a long time 'building blocks' of models of patch and landscape dynamics. At the landscape scale their most widespread use has been in models that couple successional dynamics as represented by applications of the Vital Attributes (VA) model (Noble and Slatyer 1980) with sub-models of lateral processes such as seed dispersal and disturbance propagation. These applications have been particularly successful in the case of 'Landscape Fire Succession Models' (*sensu* Keane et al. 2007, Chap. 12 of this volume), probably because the VA scheme was first designed to capture plant response to fire, and represents an intermediate level of complexity that is amenable to sophisitication by addition of new processes. Examples include applications to Australian wet sclerophyllous forest (Noble and Gitay 1996), Mediterranean shrublands (Pausas 2003) and of coniferous-dominated forests of northwestern America (Roberts and Betz 1997).

More complex versions of VA, such as the FATE model (Moore and Noble 1990) have been adapted to model landscape-fire interactions (LAMOS, Grigulis et al. 2005; FATELAND, Pausas and Ramos 2005) and responses to other disturbances such as grazing (Cousins et al. 2003) by including a series of semi-quantitative traits (e.g., for shade tolerance, recruitment). The latest developments of VA-based landscape models can take into account continuous traits and processes e.g., for biomass production and the dispersal phase (Grigulis et al. 2005). Current challenges lie in including biogeochemical processes, as captured by plant effect traits into the current models that simulate responses to changing soil resources, disturbances and their modifications by climate. Such models will make it possible to better capture important non-linearities associated with landscape dynamics (Reynolds et al. 1997; Boer and Stafford Smith 2003).

13.6.2 Regional to Global Models – Revisiting the Early Functional Classifications

Dynamic Global Vegetation Models (DGVMs: Foley et al. 1996; Friend et al. 1997; Woodward et al. 1998; Potter and Klooster 1999; Sitch et al. 2003; Gerten et al. 2004) simulate natural vegetation distribution and terrestrial carbon cycling in response to atmospheric and soil environment, disturbance and their interactions. The properties of the vegetation system arise out of competition between a limited number of PFTs whose behavior is, in turn, determined by basic physiological constraints.

In: Canadell JG, Pataki D, Pitelka L (eds) (2007) Terrestrial Ecosystems in a Changing World.
The IGBP Series, Springer-Verlag, Berlin Heidelberg

DGVMs can be used with some confidence to predict the broad-scale behavior of terrestrial vegetation in response to observed climate changes in the recent past, and have been used to explore the consequences of past climate changes and future climate scenarios for the functioning of terrestrial ecosystems (Cramer et al. 2001; Prentice et al. 2007, Chap. 15 of this volume). Plant functional classification is central to all current approaches to modeling the response of vegetation to a changing environment at regional to global scales. However, even state-of-the-art DGVMs only use a relatively small number (<10) of PFTs. While the bioclimatic limits of these PFTs are explicit, their characterization in terms of observable traits are sketchy, or at best defined from a small set of postulated characteristics (based on life form or leaf form) and descriptions of function (phenology, photosynthetic pathway, life cycle, bioclimatic tolerance).

Two approaches to improving the representation of biospheric complexity in DGVMs have been advocated. The first approach is simply to increase the number of PFTs, perhaps by incorporating functional types that have been identified as important for some specific ecological function or are responsive to specific aspects of climate. There are more complex PFT classification schemes (Box 1981) that would be candidates for such a model expansion. Increasing the number of PFTs could improve modeling of the response to both disturbance and of migration. The IPCD approach (see Sect. 13.3) could provide a generic framework for modeling vegetation dynamics in chronically disturbed systems. Ongoing analyses of how long distance dispersal is distributed across life forms and in relation to other traits may inform the development of new classifications (Higgins et al. unpublished, Midgley et al. 2007, Chap. 11 of this volume). Increasingly detailed classifications (recognising up to 100 different PFTs) have been devised. However, it remains to be examined whether and how these 'top-down' schemes can be matched with 'bottom-up' classifications obtained from empirical work, and the degree to which they are useful for predicting changes in community composition and ecosystem functioning in response to scenarios of changes in multiple environmental drivers. In addition, to be able to simulate the behavior of a given PFT, it is necessary to provide quantitative values for a number of parameters relating to plant physiology, phenology, allocation strategy and response to disturbance (Prentice et al. 2007, Chap. 15 of this volume). Thus, data availability is a key limitation on the number of PFTs that could usefully be included in DGVMs. The statistical analysis of field measurements of trait abundance along climatic, nutrient and/or disturbance gradients (see Sect. 13.3), and resulting data bases, may go some way to providing these quantitative estimates but does not provide information on absolute physiological limits. Additional work in comparative ecophysiology and modeling is required to establish robust relationships between 'soft' traits that are routinely measured over a diversity of ecosystems, and the 'hard' traits used by models (see e.g., Arora and Boer 2005).

An alternative approach to increasing biotic complexity in models is to simulate traits explicitly. This avoids the classification problems inherent in defining discrete plant functional types from trait assemblages, but still raises the need for explicit, quantitative information for each trait. It also requires a fundamental rearrangement in the structure of current models. Some continental-scale models are using continuous traits rather than a discrete classification. For example, Berry and Roderick (2002a,b) used two fundamental leaf traits, leaf surface area to volume ratio and leaf thickness, to capture the combined response to water and mineral resource availability and CO_2. This classification was sufficient to describe current distribution of vegetation types on the Australian continent and to investigate historical and palaeoenvironmental changes. This plant functional scheme is also a functional effects scheme, and can be applied to modeling the carbon cycle at continental scale (Berry and Roderick 2004). Continuous response traits may also be used to capture other land-atmosphere feedbacks, such as effects on climate (Chapin 2003; Díaz et al. 2007, Chap. 7 of this volume).

13.6.3 Validation: the Contribution of Paleo-Data

Palaeoecology provides insights into how vegetation has responded to global changes in the past (Overpeck et al. 2003). Although the causes of these changes are not identical to the causes of expected future changes, our confidence in the ability of models (of climate and/or ecosystems) to make future projections can only be assured by demonstrating that these models are capable of reproducing the range of conditions that are documented from different periods during the recent geological period (Harrison and Foley 1995; Grassl 2000; Joussaume and Taylor 2000). The ability to test models under past conditions depends, in part, on palaeodata being represented in a form compatible with global model outputs (Prentice and Webb 1998; Kohfeld and Harrison 2000; Prentice et al. 2000). The desire for such a representation motivated the GAIM/GCTE-sponsored Palaeovegetation Mapping Project (BIOME 6000: Prentice and Webb, 1998 ; Prentice et al. 2000), which used pollen and plant macrofossil data to produce vegetation maps for the last glacial maximum and the mid-Holocene. To reduce the taxonomic diversity of the fossil data to a manageable level, BIOME 6000 adopted a method that relied on the allocation of pollen and plant macrofossil taxa from different floras to a common global suite of PFTs. Recent regional reconstructions (Harrison et al. 2001; Bigelow et al. 2003) have converged on a scheme which recognises a suite of 99 climatically-diagnostic PFTs based on combination of traits

In: Canadell JG, Pataki D, Pitelka L (eds) (2007) Terrestrial Ecosystems in a Changing World.
The IGBP Series, Springer-Verlag, Berlin Heidelberg

describing life form, leaf morphology, phenology and bioclimatic tolerances (principally related to cold tolerance mechanisms in woody plants). Together, the BIOME 6000 data set (Prentice et al. 2000) along with more recent updates (Harrison et al. 2001 ; Harrison and Prentice 2003 ; Bigelow et al. 2003; Pickett et al. 2004), and the global PFT-scheme which underlies it suggest one route for continuing improvement of the representation of PFTs in DGVMs.

13.7 Summary and Conclusions

Plant functional type research has soared for over ten years under the impetus of GCTE. The requirement from large scale ecosystem models to group plants according to similarity in response to changes in their environment *and* effects on ecosystem structure and processes has proved to be the 'Holy Grail' of plant functional type research.

One first achievement has been the production of standardised lists of the most significant and easily measurable and well understood traits. Based on these and large data bases, and on large efforts to synthesise the literature, it has been possible to identify and explain plant functional response traits associated with response to resource gradients (esp. nutrients) and widespread disturbances such as grazing and fire. Current research is focusing on the links between these and effects on biogeochemistry, confirming the relevance of fundamental trade-offs that constrain the way plants manage their resources (Grime 2001). This progress and the remaining challenges for ecosystem level plant functional research can be summarised in a series of confirmed or hypothetical linkages between individual plant traits and processes at different levels of organisation (Table 13.2). Significant remaining challenges not only concern further understanding the significance of particular traits, fundamental trade-offs among them, or how short a minimal trait list can be. First, understanding the mechanisms through which species traits, as determined by environmental factors, determine community structure is a priority that will require theoretical, experimental and modeling approaches. Second, our understanding of how these response traits also determine (or not) effects on ecosystems, remains very preliminary. Significant challenges to be addressed regard effects of plant disturbance response on biogeochemical cycles and on disturbance regimes. For this, and also to further resolve the effects of plant resource response on biogeochemistry, it is essential to recognize that simultaneous effects on multiple, linked ecosystem processes are involved (Chapin 2003). Progress in this area will call upon multi-factorial manipulations (see Norby et al. 2007, Chap. 3 of this volume), biodiversity experiments (Hooper et al. 2005; Naeem et al. 2003 and the further development of ecosystem models that directly use those plant traits that can be easily measured for large numbers of species.

Current approaches to defining PFTs that emphasize the importance of classifying plants according to well-defined, readily observable and usually continuous plant traits with known responses to particular environmental factors (CO_2 concentration, soil resources, climate, and different types of disturbances) should encourage the development of a new generation of DGVMs that explicitly represent key features of this global classification. Model development, however, needs to be paralleled by the global collection of trait data following unified protocols, and by the development of an internally-consistent modern (actual) vegetation map explicitly based on plant functional properties (Nemani and Running 1996).

"The same happens to all of us. One hears about the Grail and one thinks one is the only one who will find it" (U. Eco, Baudolino). Rather, the last decade of plant functional research has taught us that, if "There is much to be done. There is also a real hope that we may be getting somewhere" (Westoby et al. 2002), getting somewhere will require continued collaboration across those multiple fields that span from ecophysiology to global modeling.

Acknowledgments

We thank the members and Task leaders of the GCTE PFT network for their continued contribution to the development of the ideas presented here, and the relentless efforts in data collection around the world. Special Acknowledgments are made for initial ideas and continued support over the years to: Terry Chapin, Wolfgang Cramer, Phil Grime, Ian Noble, Colin Prentice and Will Steffen. Sandra Lavorel is supported by the CNRS ATIP project and group members 'Functional traits and dynamics of alpine ecosystems'.

References

Ackerly DD (2003) Community assembly, niche conservatism, and adaptive evolution in changing environments. International Journal of Plant Sciences 164:S165–S184

Ackerly DD (2004a) Adaptation, niche conservatism, and convergence: Comparative studies of leaf evolution in the California chaparral. American Naturalist 163:654–671

Ackerly DD (2004b) Functional strategies of chaparral shrubs in relation to seasonal water deficit and disturbance. Ecological Monographs 74:25–44

Ackerly DD, Dudley SA, Sultan SE, Schmitt J, Coleman JS, Linder CR, Sandquist DR, Geber MA, Evans AS, Dawson TE, Lechowicz MJ (2000) The evolution of plant ecophysiological traits: recent advances and future directions. Bioscience 50:979–995

Adler PB, Milchunas DG, Lauenroth WK, Sala OE, Burke IC (2004) Functional traits of graminoids in semi-arid steppes: a test of grazing histories. Journal of Applied Ecology 41:653–663

Adler PB, Milchunas DG, Sala OE, Burke IC, Lauenroth WK (2005) Plant traits and ecosystem grazing effects: Comparison of U.S. sagebrush steppe and Patagonian steppe. Ecological Applications 15:774–792

In: Canadell JG, Pataki D, Pitelka L (eds) (2007) Terrestrial Ecosystems in a Changing World.
The IGBP Series, Springer-Verlag, Berlin Heidelberg

D'Antonio CM (2000) Fire, plant invasions, and global changes. In: Mooney HA, Hobbs RJ (eds) Invasive species in a changing world. Island Press, Covela, pp 65–94

D'Antonio CM, Corbin JD (2003) Effects of plant invaders on nutrient cycling – Exploring the link between invasion and development of species effects. In: Canham C, Cole JJ, Lauenroth WK (eds) Models in Ecosystem Ecology. Princeton University Press, Princeton, pp 363–384

D'Antonio CM, Vitousek PM (1992) Biological invasions by exotic grasses, the grass/fire cycle, and global change. Annual Review of Ecology and Systematics 23:63–87

Dale VH, Joyce LA, McNulty S, Neilson RP, Ayres MP, Flannigan MD, Hanson PJ, Irland LC, Lugo AE, Peterson CJ, Simberloff D, Swanson FJ, Stocks BJ, Wotton BM (2001) Climate change and forest disturbances. Bioscience 51:723–734

Danell K, Bergström R (2002) Mammalian herbivory in terretrial environments. In: Herrera CMP, O. (ed) Plant-animal interactions. Blackwell Publishing, Oxford, pp 107–131

Dawson TE, Chapin III FS (1993) Grouping plants by their form – Function characteristics as an avenue for simplification in scaling between leaves and landscapes. In: Field CB, Ehleringer JR (eds) Scaling physiological processes from the leaf to the globe. Academic Press, pp 313–319

Díaz S, Cabido M (1997) Plant functional types and ecosystem function in relation to global change. Journal of Vegetation Science 8:463–474

Díaz S, Cabido M, Casanoves F (1999) Functional implications of trait-environment linkages in plant communities. In: Weiher E, Keddy P (eds) Ecological assembly rules – Perspectives, advances, retreats. Cambridge University Press, Cambridge, pp 338–362

Díaz S, Noy-Meir I, Cabido M (2001) Can grazing response of herbaceous plants be predicted from simple vegetative traits ? Journal of Applied Ecology 38:497–508

Díaz S, Briske D, McIntyre S (2002a) Range management and plant functional types. In: Hodkingson K, Grice AC (eds) Global Rangelands: Progress and Prospects. CAB International, Wallingford, pp 81–100

Díaz S, McIntyre S, Lavorel S, Pausas J (2002b) Does hairiness matter in Harare? – Global comparisons of plant trait responses to disturbance. New Phytologist 154:7–9

Díaz S, Hodgson JG, Thompson K, Cabido M, Cornelissen JHC, Jalili A, Montserrat-Martí G, Grime JP, Zarrinkamar F, Asri Y, Band SR, Basconcelo S, Castro-Diez P, Funes G, Hamzehee B, Khoshnevi M, Pérez-Harguindeguy N, Pérez-Rontomé MC, Shirvany FA, 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, Shaw S, Siavash B, Villar-Salvador P, Zak MR (2004) The plant traits that drive ecosystems: Evidence from three continents. Journal of Vegetation Science 15:295–304

Díaz S, Lavorel S, Chapin III FS, Tecco PA, Gurvich DE, Grigulis K (2007) Functional diversity – at the crossroads between ecosystem functioning and environmental filters. In: Canadell J, Pitelka LF, Pataki D (eds) Terrestrial Ecosystems in a Changing World. Springer-Verlag, this volume

Díaz S, Lavorel S, McIntyre S, Falczuk V, Casanoves F, Milchunas D, Skarpe C, Rusch G, Sternberg M, Noy-Meir I, Landsberg J, Zangh W, Clark H, Campbell BD (in press) Grazing and plant traits – A global synthesis. Global Change Biology

Dodd MB, Lauenroth WK, Burke IC, Chapman PR (2002) Associations between vegetation patterns and soil texture in the shortgrass steppe. Plant Ecology 158:127–137

Duru M, Cruz P, Magda D (2004) Using plant traits to compare sward structure and composition of grass species across environmental gradients. Applied Vegetation Science 7:11–18

Dyer AR, Goldberg DE, Turkington R, Sayre C (2001) Effects of growing conditions and source habitat on plant traits and functional group definition. Functional Ecology 15:85–95

Eissenstat DM (1991) The ecology of root lifespan. Advances in Ecological Research 27:1–60

Eissenstat DM, Wells CE, Yanai RD, Whitbeck JL (2000) Building roots in a changing environment: implications for root longevity. New Phytologist 147:33–42

Eriksson O, Ehrlén J (2001) Landscape fragmentation and the viability of plant populations. In: Silvertown J, Antonovics J (eds) Integrating ecology and evolution in a spatial context. Blackwell Science, Oxford, pp 157–175

Eviner VT, Chapin III FS (2003) Functional matrix: a conceptual framework for predicting multiple plant effects on ecosystem processes. Annual Review of Ecology and Systematics 34: 455–485

Fitter A, Stickland TR (1991) Architectural analysis of plant root systems. 2. Influence of nutrient supply on architecture in contrasting plant species. New Phytologist 118:383–389

Foley JA, Prentice IC, Ramankutty S, Levis S, Pollard D, Sitch S, Haxeltine A (1996) An integrated biosphere model of land surface processes, terrestrial carbon balance and vegetation dynamics. Global Biogeo-chemical Cycles 10:603–628

Friend AD, Stevens AK, Knox RG, Cannell MGR (1997) A process-based, terrestrial biosphere model of ecosystem dynamics (Hybrid v3.0). Ecological Modelling 95:249–287

Garnier E, Aronson J (1998) Nitrogen-use efficiency from leaf to stand level: clarifying the concept. In: Lambers H, Poorter H, Van Vuuren MMI (eds) Inherent variation in plant growth. Physiological mechanisms and ecological consequences. Backhuys Publishers, Leiden, The Netherlands, pp 515–538

Garnier E, Cortez J, Billès G, Navas M-L, Roumet C, Debussche M, Laurent G, Blanchard A, Aubry D, Bellmann A, Neill C, Toussaint J-P (2004) Plant functional markers capture ecosystem properties during secondary succession. Ecology 85: 2630–2637

Garnier E, Laurent G, Bellmann A, Debain S, Berthelier P, Ducout B, Roumet C, Navas M-L (2001) Consistency of species ranking based on functional leaf traits. New Phytologist 152:69–83

Gerten D, Schaphoff S, Haberlandt U, Lucht W, Sitch S (2004) Terrestrial vegetation and water balance: hydrological evaluation of a dynamic global vegetation model. Journal of Hydrology 286:249–270

Gitay H, Noble IR (1997) What are functional types and how should we seek them? In: Smith TM, Shugart HH, Woodward FI (eds) Plant Functional Types. Their Relavance to Ecosystem Properties and Global Change. Cambridge University Press, Cambridge, pp 3–19

Goldberg DE (1991) Competitive effect and response: hierarchies and correlated traits in the early stages of competition. Journal of Ecology 79:1013–1030

Goldberg DE, Novoplansky A (1997) On the relative importance of competition in unproductive environments. Journal of Ecology 85:409–418

Grassl H (2000) Status and improvements of coupled general circulation models. Science 288:1991–1997

Grigulis K, Lavorel S, Davies ID, Dossantos A, Lloret F, Vilà M (2005) Landscape-scale positive feedbacks between fire and expansion of the large tussock grass, *Ampelodesmos mauritanica*, in Catalan shrublands. Global Change Biology 11:1042–1053

Grime JP (1977) Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. The American Naturalist 111:1169–1194

Grime JP (1979) Plant strategies and vegetation processes. John Wiley and Sons, Chichester

Grime JP (2001) Plant strategies, vegetation processes and ecosystem properties, 2nd edn. John Wiley and Sons, Chichester

Grime JP, Corneliessen HJC, Thompson K, Hodgson JG (1996) Evidence of a causal connection between anti-herbivore defence and the decomposition rate of leaves. Oikos 77:489–494

Grime JP, Thompson K, Hunt R, Hodgons JG, Cornelissen JHC, Rorison IH, Hendry GAF, Ashenden TW, Askew AP, Band SR, Booth RE, Bossard CC, Campbell BD, Cooper JEL, Davison AW, Gupta PL, Hall W, Hand DW, Hannah MA, Hillier SH, Hodkinson DJ, Jalili A, Liu Z, Mackey JML, Matthews N, Mowforth MA, Neal AM, Reader RJ, Reiling K, Ross-Fraser W, Spencer RE, Sutton F, Tasker DE, Thorpe PC, Whitehouse J (1997) Integrated screening validates primary axis of specialisation in plants. Oikos 79:259–281

Hanley M, Lamont B (2002) Relationships between physical and chemical attributes of congeneric seedlings: how important is seedling defence? FUNCTIONAL ECOLOGY 16:216–222

In: Canadell JG, Pataki D, Pitelka L (eds) (2007) Terrestrial Ecosystems in a Changing World.
The IGBP Series, Springer-Verlag, Berlin Heidelberg

Harrison SP, Foley JA (1995) General circulation models, climate change and ecological impact studies. In: Pernetta J, Leemans R, Elder D, Humphrey S (eds) The Impact of Climate Change on Ecosystems and Species: Environmental Context. IUCN, Gland, Switzerland, pp 9–26

Harrison SP, Prentice IC (2003) Climate and CO_2 controls on global vegetation distribution at the last glacial maximum: analysis based on palaeovegetation data, biome modelling and palaeoclimate simulations. Global Change Biology 9:983–1004

Harrison SP, Yu G, Takahara H, Prentice IC (2001) Plant diversity and palaeovegetation in East Asia. Nature 413:129–130

Hartley SE, Jones CG (1997) Plant chemistry and herbivory, or why the world is green. In: Crawley JM (ed) Plant ecology. Blackwell Science Ltd., Oxford, pp 284–335

Hättenschwiller S, Vitousek PM (2000) The role of polyphenols in terrestrial ecosystem nutrient cycling. Trends in Ecology and Evolution 15:238–243

Herms DA, Mattson WJ (1992) The dilemma of plants: to grow or defend. Quaterly Review of Biology 67:293–335

Hickler T, Smith B, Sykes MT, Davis MB, Sugita S, Walker K (2004) Using a general vegetation model to simulate vegetation dynamics in northeastern U.S.A. Ecology 85:519–530

Hodgson JG, Wilson PJ, Hunt R, Grime JP, Thompson K (1999) Allocating C-S-R plant functional types: a soft approach to a hard problem. Oikos 85:282–294

Hooper DU, Ewel JJ, Hector A, Inchausti P, Lavorel S, Lodge D, Loreau M, Naeem S, Schmid B, Setälä H, Symstad AJ, Vandermeer J, Wardle DA (2005) Effects of biodiversity on ecosystem functioning: a consensus of current knowledge and needs for future research. Ecological Monographs 75:3–35

Hughes L, Dunlop M, French K, Leishman MR, Rice B, Rodgerson L, Westoby M (1994) Predicting dispersal spectra: a minimal set of hypotheses based on plant attributes. Journal of Ecology 82:933–950

Jackson ST, Williams JW (2004) Modern analogs in Quaternary paleoecology: here today, gone yesterday, gone tomorrow? Annual Review of Planetary Science 32:495–530

Jackson RB, Canadell J, Ehleringer JR, Mooney HA, Sala OE, Schulze ED (1996) A global analysis of root distribution for terrestrial biomes. Oecologia 108:389–411

Joussaume S, Taylor KE (2000) The Paleoclimate Modeling Intercomparison Project. In: Braconnot P (ed) Paleoclimate Modelling Intercomparison Project (PMIP). Proceedings of the third PMIP workshop, vol. WCRP-111; WMO/TD-No. 1007, La Huardière, Canada, pp 9–24

Keane RE, Cary GJ, Davies ID, Flannigan MD, Gardner RH, Lavorel S, Lenihan JM, Li C, Rupp TS (2007) Understanding global fire dynamics by classifying and comparing spatial models of vegetation and fire dynamics. In: Canadell J, Pitelka LF, Pataki D (eds) Terrestrial Ecosystems in a Changing World. Springer-Verlag, this volume

Keddy PA (1992) Assembly and response rules: two goals for predictive community ecology. Journal of Vegetation Science 3:157–164

Keddy PA, Fraser LH, Wisheu IC (1998) A comparative approach to examine competitive response of 48 wetland plant species. Journal of Vegetation Science 9:777–786

Keddy P, Gaudet C, Fraser LH (2000) Effects of low and high nutients on the competitive hierarchy of 26 shoreline plants. Journal of Ecology 88:413–423

Kleyer M (1999) Distribution of plant functional types along gradients of disturbance intensity and resource supply in an agricultural landscape. Journal of Vegetation Science 10:697–708

Klironomos JN (2003) Variation in plant response to native and exotic arbuscular mycorrhizal fungi. Ecology 84:2292–2301

Klironomos JN, McCune J, Hart MM, Neville J (2000) The influence of arbuscular mycorrhizae on the relationship between plan biodiversity and productivity. Ecology Letters 3:137–141

Kohfeld KE, Harrison SP (2000) How well can we simulate past climates? Evaluating the models using global palaeoenvironmental datasets. Quaternary Science Review 19:321–346

Landsberg J, O'Connor T, Freudenberger D (1999) The impacts of livestock grazing on biodiversity in natural ecosystems. In: Jung HG, Fahey GC (eds) Nutritional Ecology of Herbivores. Proc. Vth International Symposium on the Nutrition of Herbivores. American Soc. Anim. Sci., Savoy, Illinois, pp 752–777

Langley JA, Hungate B (2003) Mycorrhizal controls on belowground litter quality. Ecology 84:2302–2312

Lavorel S, Cramer W (eds) (1999) Plant functional response to land use and natural disturbance

Lavorel S, Garnier E (2002) Predicting the effects of environmental changes on plant community composition and ecosystem functioning: revisiting the Holy Grail. Functional Ecology 16:545–556

Lavorel S, McIntyre S (1999c) Plant functional types: is the real world too complex ? In: Proceedings of the VIth International Rangelands Congress, Townsville, Australia, pp 905–911

Lavorel S, McIntyre S, Landsberg J, Forbes D (1997) Plant functional classifications: from general groups to specific groups based on response to disturbance. Trends in Ecology and Evolution 12:474–478

Lavorel S, Touzard B, Lebreton J-D, Clément B (1998) Identifying functional groups for response to disturbance in an abandonned pasture. Acta Oecologica 19:227–240

Lavorel S, McIntyre S, Grigulis K (1999a) Plant response to disturbance in a Mediterranean grassland: how many functional groups ? Journal of Vegetation Science 10:661–672

Lavorel S, Rochette C, Lebreton J-D (1999b) Functional groups for response to disturbance in Mediterranean old fields. Oikos 84:480–498

Leishman MR, Westoby M (1992) Classifying plants into groups on the basis of associations of individual traits – evidence from Australian semi-arid woodlands. Journal of Ecology 80:417–424

Leishman MR, Westoby M (1994) The role of seed size in seedling establishment in dry soil conditions-experimental evidence from semi-arid species. Journal of Ecology 82:249–258

Liancourt P, Callaway RM, Michalet R (2005) Stress tolerance and competitive response ability determine the outcome of biotic interactions. Ecology 86:1611–1618

Marañon T, Grubb PJ (1993) Physiological basis and ecological significance of the seed size and relative growth rate relationship in Mediterranean annuals. Functional Ecology 7:591–599

McGillivray CW (1995) Testing predictions of the resistance and resilience of vegetation subjected to extreme events. Functional Ecology 9:640–649

McIntyre S, Lavorel S (2001) Livestock grazing in sub-tropical pastures: steps in the analysis of attribute response and plant functional types. Journal of Ecology 89:209–226

McIntyre S, Martin TG (2001) Biophysical and human influences on plant species richness in grasslands – comparing variegated landscapes in sub-tropical and temperate regions. Austral Ecology 26:233–245

McIntyre S, Martin TG (2002) Managing intensive and extensive land uses to conserve grassland plants in sub-tropical eucalypt woodlands. Biological Conservation 107:241–252

McIntyre S, Lavorel S, Landsberg J, Forbes TDA (1999) Disturbance response in vegetation – towards a global perspective on functional traits. Journal of Vegetation Science 10:621–630

McIntyre S, Heard KM, Martin TG (2002) How grassland plants are distributed over five human-created habitats typical of eucalypt woodlands in a variegated landscape. Pacific Conservation Biology 7:274–285

McIntyre S, Heard KM, Martin TG (2003) The relative importance of cattle grazing in sub-tropical grasslands – does it reduce or enhance plant diversity? Journal of Applied Ecology 40:445–457

McKey D, Waterman PG, Gartlan JS, Struhsacker TT (1978) Phenolic content of vegetation in two African rainforests: ecological implications. Science 202:61–64

Michalet R (2001) Facteurs abiotiques et traits biologiques déterminant les interactions biotiques, la répartition des populations dominantes et la structuration des communautés terrestres: Application à quelques écosystèmes de l'Arc Alpin. In. Université J. Fourier, Grenoble

Michelsen A, Schmidt IK, Dighton J, Jones HE, Callaghan TV (1995) Inhibition of growth and effects on nutrient uptake of arctic graminoids by leaf extracts – allelopathy or resource competition between plants and microbes. Oecologia 103:407–418

Midgley GF, Thuiller W, Higgins SI (2007) Plant species migration as a key uncertainty in predicting future impacts of climate change on ecosystems: progress and challenges. In: Canadell J, Pitelka LF, Pataki D (eds) Terrestrial Ecosystems in a Changing World. Springer-Verlag, this volume

In: Canadell JG, Pataki D, Pitelka L (eds) (2007) Terrestrial Ecosystems in a Changing World.
The IGBP Series, Springer-Verlag, Berlin Heidelberg

Moore AD, Noble IR (1990) An individualistic model of vegetation stand dynamics. Environmental Management 31:61–81

Naeem S, Wright JP (2003) Disentangling biodiversity effects on ecosystem functioning: deriving solutions to a seemingly insurmontable problem. Ecology Letters 6:567–579

Neilson RP, King GA, DeVelice RL, Lenihan JM (1992) Regional and local vegetation patterns: the responses of vegetation diversity to subcontinental air masses. In: Hansen AJ, di Castri F (eds) Landscape Boundaries. Springer-Verlag, pp 129–149

Nicotra AB, Babicka N, Westoby M (2002) Seedling root anatomy and morphology: an examination of ecological differentiation with rainfall using phyllogenetically independent contrasts. Oecologia 130:136–145

Niinemets Ü (2001) Global-scale climatic controls of leaf dry mass per area, density, and thickness in trees and shrubs. Ecology 82:453–469

Noble IR, Gitay H (1996) A functional classification for predicting the dynamics of landscapes. J Vegetat Sci 7:329–336

Noble IR, Slatyer RO (1980) The use of vital attributes to predict successional changes in plant communities subject to recurrent disturbances. Vegetatio 43:5–21

Norby RJ, Rustad LE, Dukes JS, Ojima DS, Parton WJ, Del Grosso SJ, McMurtrie RE, Pepper DA (2007) Multiple factor interactions on ecosystem function. In: Canadell J, Pitelka LF, Pataki D (eds) Terrestrial Ecosystems in a Changing World. Springer-Verlag, this volume

Nygaard B, Erjnaes R (2004) A shortcut around the fourth corner – a new approach to functional interpretation of vegetation data. Journal of Vegetation Science 15:49–56

Overpeck J, Whitlock C, Huntley B (2003) Terrestrial biosphere dynamics in the climate system: past and future. In: Alverson KD, Bradley RS, Pedersen T (eds) Paleoclimate, Global Change and the Future. Springer-Verlag, Berlin-Heidelberg-New York, pp 81–103

Pausas JG (1999) Response of plant functional types to changes in the fire regime in Mediterranean ecosystems: a simulation approach. Journal of Vegetation Science 10:717–722

Pausas JG (2003) The effect of landscape pattern on Mediterranean vegetation dynamics: A modelling approach using functional types. Journal of Vegetation Science 14:365–374

Pausas J, Lavorel S (2003) A hierarchical deductive approach for functional types in disturbed ecosystems. Journal of Vegetation Science 14:409–416

Pausas JG, Ramos JI (2005) Landscape Analysis and Simulation Shell (LASS). Environmental Modelling and Software in press

Pausas JG, Verdú M (2005) Plant persistence traits in fire-prone ecosystems of the Mediterranean Basin: A phylogenetic approach. Oikos 109:196–202

Pausas JG, Rusch GM, Leps J (eds) (2003) Plant Functional Types in relation to disturbance and land use

Pausas JG, Bradstock RA, Keith DA, Keeley JE, Network tGF (2004) Plant functional traits in relation to fire in crown-fire ecosystems. Ecology 85:1085–1100

Pavón N, Hernández-Trejo H, Rico-Gray V (2000) Distribution of plant life forms along an altitude gradient in the semi-arid valley of Zapoltitlán, Mexico. Journal of Vegetation Science 11: 39–42

Pellissier F (1998) The role of soil community in plant population dynamics: is allelopathy a key component? Trends in Ecology and Evolution 13:407–407

Pellissier F, Souto XC (1999) Allelopathy in northern temperate and boreal semi-natural woodland. Critical Reviews in Plant Sciences 18:637–652

Pérez-Harguindeguy N, Díaz S, Cornelissen JHC, Vendramini F, Cabido M, Castellanos A (2000) Chemistry and toughness predict leaf litter decomposition rates over a wide spectrum of functional types and taxa in central Argentina. Plant and Soil 218:21–30

Pérez-Harguindeguy N, Díaz S, Vendramini F, Cornelissen JHC, Gurvich DE, Cabido M (2003) Leaf traits and herbivore selection in the field and in cafeteria experiments. Austral Ecol 28:642–650

Pickett EJ, Harrison SP, Hope G, Harle K, Dodson JR, Kershaw AP, Prentice IC, Backhouse J, Colhoun EA, D'Costa D, Flenley J, Grindrod J, Haberle S, Hassell C, Kenyon C, Macphail M, Martin H, Martin AH, McKenzie M, Newsome JC, Penny D, Powell J, Raine JI, Southern W, Stevenson J, Sutra JP, Thomas I, van der Kaars S, Ward J (2004) Pollen-based reconstructions of biome distributions for Australia, Southeast Asia and the Pacific (SEAPAC region) at 0, 6000 and 18000 ^{14}C yr B.P. Journal of Biogeography 31:1–65

Pillar VD, Sosinsky EJ (2003) An improved method for searching plant functional types by numerical analysis. Journal of Vegetation Science 14:323–332

Poorter L (1999) Growth responses of 15 rain-forest tree species to a light gradient: the relative importance of morphological and physiological traits. Functional Ecology 13:396–410

Poorter H, Garnier E (1999) Ecological significance of inherent variation in relative growth rate and its components. In: Pugnaire FI, Valladares F (eds) Handbook of Functional Plant Ecology. Marcel Dekker INC., New-York, pp 81–120

Poorter H, Roumet C, Campbell BD (1996) Interspecific variation in the growth response of plants to elevated CO_2: a search for functional types. In: Körner C, Bazzaz FA (eds) Carbon dioxyde, populations, and communities. Academic Press, San Diego, California, pp 375–412

Potter CS, Klooster SA (1999) Dynamic global vegetation modelling for prediction of plant functional types and biogenic trace gas fluxes. Global Ecology and Biogeography 8:473–488

Prach K (1997) Changes in species traits during succession: a search for pattern. Oikos 79:201–205

Prentice IC, Cramer W, Harrison SP, Leemans R, Monserud RA, Solomon AM (1992) A global biome model based on plant physiology and dominance, soil properties and climate. Journal of Biogeography 19:117–134

Prentice IC, Jolly D, participants B (1998) Mid-Holocene and glacial-maximum vegetation geography of the northern continents and Africa. Journal of Biogeography 25:997–1005

Prentice IC, Heimann M, Sitch S (2000) The carbon balance of the terrestrial biosphere: Ecosystem models and atmospheric observations. Ecological Applications 10:1553–1573

Prentice IC, Bondeau A, Cramer W, Harrison SP, Hickler T, Lucht W, Sitch S, Smith B, Sykes M (2007) Dynamic global vegetation models: tools to understand the biosphere. In: Canadell J, Pitelka LF, Pataki D (eds) Terrestrial Ecosystems in a Changing World. Springer-Verlag, this volume

Raunkiaer C (1934) The life forms of plants and statistical plant geography. Oxford University Press, Oxford

Read DJ (1991) Mycorrhizas in ecosystems. Experientia 47:376–391

Read DJ, Leake JR, Perez-Moreno J (2004) Mycorrhizal fungi as drivers of ecosystem processes in heathland and boreal forest biomes. Canadian Journal of Botany 82:1243–1263

Reich PB, Walters MB, Ellsworth DS (1992) Leaf lifespan in relation to leaf, plant and stand characteristics among diverse ecosystems. Ecological Monographs 62:356–392

Reich PB, Walters MB, Ellsworth DS (1997) From tropics to tundra: a global convergence in plant functioning. Proceedings of the National Academy of Sciences, USA 94:13730–13734

Reich PB, Tjoelker MG, Walters MB, Vanderklein DW, Buschena C (1998a) Close association of RGR, leaf and root morphology, seed mass and shade tolerance in seedlings of nine boreal tree species grown in high and low light. Functional Ecology 12:337–338

Reich PB, Walters MB, Tjoelker MG, Vanderklein DW, Buschena C (1998b) Photosynthesis and respiration rates depend on leaf and root morphology and nitrogen concentration in nine boreal species differing in relative growth rate. Functional Ecology 12:337–338

Reich PB, Wright IJ, Cavender-Bares J, Craine JM, Oleksyn J, Westoby M, Walters MB (2003) The evolution of plant functional variation: traits, spectra, and strategies. International Journal of Plant Sciences 164:143–164

Richardson SJ, Peltzer DA, Allen RB, McGlone MS (2005) Resorption proficiency along a chronosequence: Responses among communities and within species. Ecology 86:20–25

Rillig MC (2004) Arbuscular mycorrhizae and terrestrial ecosystem processes. Ecology Letters 7:740–754

Roberts DW, Betz DW (1997) Simulating landscape vegetation dynamics of Bryce Canyon National Park with the vital attributes/fuzzy systems model VAFS/LANDSIM. In: Mladenoff DJ, Baker WL (eds) Spatial modeling of forest landscape change: approaches and applications. Cambridge University Press, Cambridge, pp 99–124

Robinson D, Rorison IH (1988) Plasticity in grass species in relation to nitrogen supply. Functional Ecology 2:249–257

Ryser P (1996) The importance of tissue density for growth and life span of leaves and roots: a comparison of five ecologically contrasting grasses. Functional Ecology 10:717–723

In: Canadell JG, Pataki D, Pitelka L (eds) (2007) Terrestrial Ecosystems in a Changing World.
The IGBP Series, Springer-Verlag, Berlin Heidelberg

Ryser P (1998) Intra- and interspecific variation in root length, root turnover and the underlying parameters. In: Lambers H, Poorter H, Van Vuuren MMI (eds) Inherent variation in plant growth. Physiological mechanisms and ecological consequences. Backhuys Publishers, Leiden, The Netherlands, pp 441–465

Schenk HJ, Jackson RB (2002) Rooting depths, lateral root spreads and below-ground / above-ground allometries of plants in water-limited ecosystems. Journal of Ecology 90:480–494

Schenk HJ, Jackson RB (2005) Mapping the global distribution of deep roots in relation to climate and soil characteristics. Geoderma 126:129–140

Schwilk DW, Ackerly DD (2001) Flammability and serotiny as strategies: correlated evolution in pines. Oikos 94:326–336

Shipley B, Almeida-Cortez J (2003) Interspecific consistency and intraspecific variability of specific leaf area with respect to irradiance and nutrient availability. Ecoscience 10:74–79

Shipley B, Keddy PA, Moore DRJ, Lemky K (1989) Regeneration and establishment strategies of emergent macrophytes. Journal of Ecology 77:1093–1110

Silvertown J, Franco M, Pisanty I, Mendoza A (1993) Comparative plant demography – relative importance of life-cycle components to the finite rate of increase in woody and herbaceous perennials. Journal of Ecology 81:465–476

Sitch S, Smith B, Prentice IC, Arneth A, Bondeau A, Cramer W, Kaplan JO, Levis S, Lucht W, Sykes MT, Thonicke K, Venevsky S (2003) Evaluation of ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ dynamic global vegetation model. Global Change Biology 9:161–185

Smith T, Huston M (1989) A theory of the spatial and temporal dynamics of plant communities. Vegetatio 83:49–69

Smith TM, Shugart HH, Woodward FI (eds) (1997) Plant functional types, their relevance to ecosystem properties and global change. Cambridge University Press, Cambridge

Solbrig OT (1993) Plant traits and adaptative strategies: their role in ecosystem function. In: Schulze ED, Mooney HA (eds) Biodiversity and ecosystem function, vol 99. Springer-Verlag, Berlin, pp 97–116

Stanton ML, Roy BA, Thiede DA (2000) Evolution in stressful environments. I. Phenotypic variability, phenotypic selection, and response to selection in five environmental stresses. Evolution 54:93–111

Strand JA, Weisner SEB (2004) Phenotypic plasticity – contrasting species-specific traits induced by identical environmental constraints. New Phytologist 163:449–451

Suding KN, Goldberg DE (2001) Do disturbances alter competitive hierarchies? Mechanisms of change following gap creation. Ecology 82:2133–2149

Suding KN, Goldberg DE, Hartman KM (2003) Relationships among species traits: separating levels of response and identifying linkages to abundance. Ecology 84:1–16

Thompson K, Band SR, Hodgson G (1993) Seed size and shape predict persistence in soil. Functional Ecology 7:236–241

Thompson K, Hillier SH, Grime JP, Bossard CC, Band SR (1996) A functional analysis of a limestone grassland community. Journal of Vegetation Science 7:371–380

Tilman D (1988) Plant strategies and the dynamics and structure of plant communities. Princeton University Press, Princeton

Urcelay C, Díaz S (2003) The mycorrhizal dependence of subordinates determines the effect of arbuscular mycorrhizal fungi on plant diversity. Ecology Letters 6:388–391

van der Heijden MGA, Boller T, Wiemken A, Sanders IR (1998a) Different arbuscular mycorrhizal fungal species are potential determinants of plant community structure. Ecology 79: 2082–2091

van der Heijden MGA, Klironomos JN, Ursic M, Mouroglis P, Striwolf-Engel R, Boller T, Wiemken A, Sanders I (1998b) Mycorrhizal fungal diversity determines plant biodiversity, ecosystem variability and productivity. Nature 396:69–72

Venable DL, Brown JS (1988) The selective interaction of dispersal, dormancy, and seed size as adaptations for reducing risk in variable environments. American Naturalist 131:361–384

Walker B, Kinzig A, Langridge J (1999) Plant attribute diversity, resilience and ecosystem function: the nature and significance of dominant and minor species. Ecosystems 2:95–113

Wardle DA (2002) Communities and ecosystems. Linking the aboveground and belowground components. Princeton University Press, Princeton

Wardle DA, Barker GM, Bonner KI, Nicholson KS (1998) Can comparative approaches based on plant ecophysiological traits predict the nature of biotic interactions and individual plant species effects in ecosystems? J Ecology 86:405–420

Wardle DA, Baker GM, Yeattes GW, Bonner KI, Ghani A (2001) Impacts of introduced browsing mammals in New Zealand forest on decomposer communities,soil biodiversity and ecosystem properties. Ecological Monographs 71:587–614

Wardle DA, Bardgett RD, Klironomos JN, Setälä H (2004) Ecological linkages between aboveground and belowground biota. Science 304:1629–1633

Weiher E, Keddy P (eds) (1999) Ecological assembly rules – Perspectives, advances, retreats. Cambridge University Press, Cambridge

Weiher E, van der Werf A, Thompson K, Roderick M, Garnier E, Eriksson O (1999) Challenging Theophrastus: A common core list of plant traits for functional ecology. Journal of Vegetation Science 10:609–620

Westoby M (1998) A leaf-height-seed (LHS) plant ecology strategy scheme. Plant and Soil 199:213–227

Westoby M, Rice B, Howell J (1990) Seed size and plant growth form as factors in dispersal spectra. Ecology 71:1307–1315

Westoby M, Falster DS, Moles AT, Vesk PA, Wright IJ (2002) Plant ecological strategies: come leading dimensions of variation between species. Annual Review of Ecology and Systematics 33: 125–159

Woodward FI, Cramer W (1996) Plant functional types and climatic changes: introduction. Journal of Vegetation Science 7:306–308

Woodward FI, Lomas MR, Betts AK (1998) Vegetation-climate feedbacks in a greenhouse world. Philisophical Transactions of the Royal Society of London, Series B 353:29–38

Wright IJ, Westoby M (1999) Differences in seedling growth behaviour among species: trait correlations across species, and trait shifts along nutrient compared to rainfall gradients. Journal of Ecology 87:85–97

Wright IJ, Reich PB, Westoby M, Ackerly DD, Baruch Z, Bongers F, Cavender-Bares J, Chapin FSI, Cornelissen JHC, Diemer M, Flexas J, Garnier E, Groom PK, Gulias J, Hikosaka K, Lamont BB, Lee T, Lee W, Lusk C, Midgley JJ, Navas M-L, Niinemets Ü, Oleksyn J, Osada N, Poorter H, Poot P, Prior L, Pyankov VI, Roumet C, Thomas SC, Tjoelker MG, Veneklaas E, Villar R (2004) The worldwide leaf economics spectrum. Nature 428:821–827

In: Canadell JG, Pataki D, Pitelka L (eds) (2007) Terrestrial Ecosystems in a Changing World.
The IGBP Series, Springer-Verlag, Berlin Heidelberg

Aerts R, Chapin III FS (2000) The mineral nutrition of wild plants revisited: a re-evaluation of processes and patterns. Advances in Ecological Research 30:1–67

Arora VK, Boer GJ (2005) A parameterization of leaf phenology for the terrestrial ecosystem component of climate models. Global Change Biology 11:39–59

Austin MP, Smith TM (1989) A new model for the continuum concept. Vegetatio 83:35–47

Bazzaz FA (1996) Plants in Changing Environments – Linking physiological, population and community ecology. Cambridge University Press, Cambridge

Berendse F (1994) Litter decomposability – a neglected component of plant fitness. Journal of Ecology 82:187–190

Berry SL, Roderick ML (2002a) CO_2 and land-use effects on Australian vegetation over the last two centuries. Australian Journal of Botany 50:511–531

Berry SL, Roderick ML (2002b) Estimating mixtures of leaf functional types using continental-scale satellite and climate data. Global Ecology and Biogeography 11:23–39

Berry SL, Roderick ML (2004) Gross primary productivity and transpiration flux of the Australian vegetation from 1788 to 1988 AD: effects of CO_2 and land use change. Global Change Biology 10:1884–1898

Bertness MD, Callaway R (1994) Positive interactions in communities. Trends in Ecology and Evolution 9:191–193

Bigelow NH, Brubaker LB, Edwards ME, Harrison SP, Prentice IC, Anderson PM, Andreev AA, Bartlein PJ, Christensen TR, Cramer W, Kaplan JO, Lozhkin AV, Matveyeva NV, Murray DF, McGuire AD, Razzhivin VY, Rtchie JC, Smith B, Walker DA, Gajewski K, Wolf V, Holmqvist BH, Igarashi Y, Kremenetskii K, Paus A, Pisaric MFJ, Volkova VS (2003) Climate change and Arctic ecosystems: 1. Vegetation changes north of 55°N between the last glacial maximum, mid-Holocene and present. Journal of Geophysical Research 108:8170, doi: 8110.1029/2002JD002558

Boer M, Stafford Smith M (2003) A plant functional approach to the prediction of changes in Australian rangeland vegetation under grazing and fire. Journal of Vegetation Science 14: 333–344

Bond WJ, Midgley JJ (1995) Kill thy neighbour: an individualistic argument for the evolution of flammability. Oikos 73:79–85

Bond WJ, Midgley JJ (2001) Ecology of sprouting in woody plants: the persistence niche. Trends in Ecology and Evolution 16: 45–51

Bond WJ, Midgley GF, Woodward FI (2003) The importance of low atmospheric CO_2 and fire in promoting the spread of grasslands and savannas. Global Change Biology 9:973–982

Boot RGA (1989) The significance of size and morphology of root systems for nutrient acquisition and competition. In: Lambers H, Cambridge ML, Konings H, Pons TL (eds) Causes ans consequences of variation in growth rate and productivity of higher plants. SPB Academic Publishing, The Hague, pp 299–311

Box EO (1981) Macroclimate and Plant Forms:An Introduction to Predictive Modelling in Phytogeography. Junk, The Hague

Brant SP, Chapin III FS, Klein DR (1983) Carbon/nutrient balance of boreal plants in relation to vertebrate herbivory. Oikos 40: 357–368

Bruno JF, Stachowicz JJ, Bertness MD (2003) Inclusion of facilitation into ecological theory. Trends in Ecology and Evolution 18: 119–125

Bryant JP, Provenza FD, Pastor J, Reichardt PB, Clausen TP, du Toit JT (1991) Interactions between woody plants and browsing mammals mediated by secondary metabolites. Annual Review of Ecology and Systematics 22:431–446

Bullock JM, Franklin J, Stevenson MJ, Silvertown J, Coulson SJ, Gregory SJ, Tofts R (2001) A plant trait analysis of responses to grazing in a long-term experiment. Journal of Applied Ecology 38:253–267

Campbell C, Stafford Smith DM, Ash JE (1999) A rule-based model for the functional analysis of vegetation change in Australasian grasslands. Journal of Vegetation Science 10:723–730

Cebrian J, Williams M, McClelland J, Valiela I (1998) The dependence of heterotrophic consumption and C accumulation on autotrophic nutrient content in ecosystems. Ecology Letters 1:165–170

Chapin III FS (1993) Functional role of growth forms in ecosystem and global processes. In: Ehrlinger JR, Field CB (eds) Scalling physiological processes: leaf to globe. Academic press, San Diego, pp 287–312

Chapin III FS (2003) Effects of plant traits on ecosystem and regional processes: a conceptual framework for predicting the consequences of global change. Annals of Botany 91:1–9

Chapin III STA, Autumn K, Pugnaire F (1993) Evolution of suites of traits in response to environmental stress. The American Naturalist 142:578–592

Colasanti RL, Hunt R, Askew AP (2001) A self-assembling model of resource dynamics and plant growth incorporating plant functional types. Functional Ecology 15:676–687

Coley PD, Bryant JP, Chapin III S (1985) Resource availability and plant antiherbivore defense. Science 230:895–899

Collins SC (1987) Interaction of disturbances in a tallgrass prairie: a field experiment. Ecology 68:1243–1250

Comas LH, Eissenstat DM (2002) Linking root traits to potential growth rate in six temperate tree species. Oecologia 132:34–43

Comas LH, Eissenstat DM (2004) Linking fine root traits to maximum potential growth rate among 11 mature temperate tree species. Functional Ecology 18:388–397

Cornelissen JHC, Pérez-Harguindeguy N, Díaz S, Grime JP, Marzano B, Cabido M, Vendramini F, Cerabolini B (1999) Leaf structure and defence control litter decomposition rate across species and life forms in regional flora on two continents. New Phytologist 143:191–200

Cornelissen HJC, Aerts R, Cerabolini B, Werger MJA, van der Heijden MGA (2001) Carbon cycling traits of plant species are linkedwith mycorrhizal strategy. Oecologia 129:611–619

Cornelissen JHC, Cerabolini B, Castro-Díez P, Villar-Salvador P, Montserrat-Martí G, Puyravaud JP, Maestro M, Werger MJA, Aerts R (2003a) Functional traits of woody plants: correspondence of species rankings between field adults and laboratory-grown seedlings? Journal of Vegetation Science 14:311–322

Cornelissen JHC, Lavorel S, Garnier E, Díaz S, Buchmann N, Gurvich DE, Reich PB, ter Steege H, Morgan HD, van der Heijden MGA, Pausas JG, Poorter H (2003b) Handbook of protocols for standardised and easy measurement of plant functional traits worldwide. Australian Journal of Botany 51:335–380

Cousins S, Lavorel S, Davies ID (2003) Modelling the effects of landscape pattern and grazing regimes on the persistence of plant species with high conservation value in grasslands in south-eastern Sweden. Landscape Ecology 18:315–332

Craine JM, Lee WG (2003) Covariation in leaf and root traits for native and non-native grasses along an altitudinal gradient in New Zealand. Oecologia 134:471–478

Craine JM, Froehle J, Tilman DG, Wedin DA, Chapin III FS (2001) The relationships among root and leaf traits of 76 grassland species and relative abundance along fertility and disturbance gradients. Oikos 93:274–285

Craine JM, Tilman D, Wedin D, Reich PB, Tjoelker MG, Knops J (2002) Functional traits, productivity and effects on nitrogen cycling in 33 grassland species. Functional Ecology 16:585–595

Craine JM, Wedin DA, Chapin FSI, Reich PB (2003) Relationship between the structure of root systems and resource use for 11 North American grassland plants. Plant Ecology 165:85–100

Craine JM, Lee WG, Bond WJ, Williams RJ, Johnson LC (2005) Environmental constraints on a global relationship among leaf and root traits of grasses. Ecology 86:12–19

Cramer W, Bondeau A, Woodward FI, Prentice IC, Betts RA, Brovkin V, Cox PM, Fisher V, Foley J, Friend AD, Kucharik C, Lomas MR, Ramankutty N, Sitch S, Smith B, White A, Young-Molling C (2001) Dynamic responses of global terrestrial ecosystems to changes in CO_2 and climate. Global. Change Biology 7:357–374

Crawley MJ (ed) (1992) Natural Enemies. Blackwell Scientific Publications, Oxford

Cruz P, Duru M, Therond O, Theau JP, Ducourtieux C, Jouany C, Al Haj Khaled R, Ansquer P (2002) Une nouvelle approche pour caractériser la valeur d'usage des prairies naturelles et semi-naturelles. Fourrages 172:335–354

Cunningham SA, Summerhayes B, Westoby M (1999) Evolutionary divergences of leaf structure and chemistry, comparing rainfall and soil nutrient gradients. Ecological Monographs 69:569–588

In: Canadell JG, Pataki D, Pitelka L (eds) (2007) Terrestrial Ecosystems in a Changing World.
The IGBP Series, Springer-Verlag, Berlin Heidelberg