Functional Ecology 2002
16, 545–556

ESSAY REVIEW

Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail

S. LAVOREL* and E. GARNIER

Centre d' Ecologie Fonctionnelle et Evolutive, CNRS UPR 9056, 1919 route de Mende, 34293 Montpellier Cedex 5, France

Summary

1. The concept of plant functional type proposes that species can be grouped according to common responses to the environment and/or common effects on ecosystem processes. However, the knowledge of relationships between traits associated with the *response* of plants to environmental factors such as resources and disturbances (response traits), and traits that determine *effects* of plants on ecosystem functions (effect traits), such as biogeochemical cycling or propensity to disturbance, remains rudimentary.

2. We present a framework using concepts and results from community ecology, ecosystem ecology and evolutionary biology to provide this linkage. Ecosystem functioning is the end result of the operation of multiple environmental filters in a hierarchy of scales which, by selecting individuals with appropriate responses, result in assemblages with varying trait composition. Functional linkages and trade-offs among traits, each of which relates to one or several processes, determine whether or not filtering by different factors gives a match, and whether ecosystem effects can be easily deduced from the knowledge of the filters.

3. To illustrate this framework we analyse a set of key environmental factors and ecosystem processes. While traits associated with response to nutrient gradients strongly overlapped with those determining net primary production, little direct overlap was found between response to fire and flammability.

4. We hypothesize that these patterns reflect general trends. Responses to resource availability would be determined by traits that are also involved in biogeochemical cycling, because both these responses and effects are driven by the trade-off between acquisition and conservation. On the other hand, regeneration and demographic traits associated with response to disturbance, which are known to have little connection with adult traits involved in plant ecophysiology, would be of little relevance to ecosystem processes.

5. This framework is likely to be broadly applicable, although caution must be exercised to use trait linkages and trade-offs appropriate to the scale, environmental conditions and evolutionary context. It may direct the selection of plant functional types for vegetation models at a range of scales, and help with the design of experimental studies of relationships between plant diversity and ecosystem properties.

Key-words: Biogeochemical cycles, disturbance, effect traits, fire, resource gradient, response traits, scaling-up, trade-offs

Functional Ecology (2002) **16**, 545–556

Introduction

The quest for general rules associating species and environmental conditions and, in particular, the search for associations between abiotic and biotic factors and species characteristics (recurrent patterns of species specialization, Grime 1979; life-history strategies, Southwood 1988) has concerned community ecologists for decades. Recently, the desire to simultaneously predict vegetation responses to global change factors and changes in important terrestrial ecosystem functions (such as biogeochemical cycles, invasion resistance, stability in the face of disturbance) has revived

---

*Author to whom correspondence should be addressed. E-mail: lavorel@cefe.cnrs-mop.fr

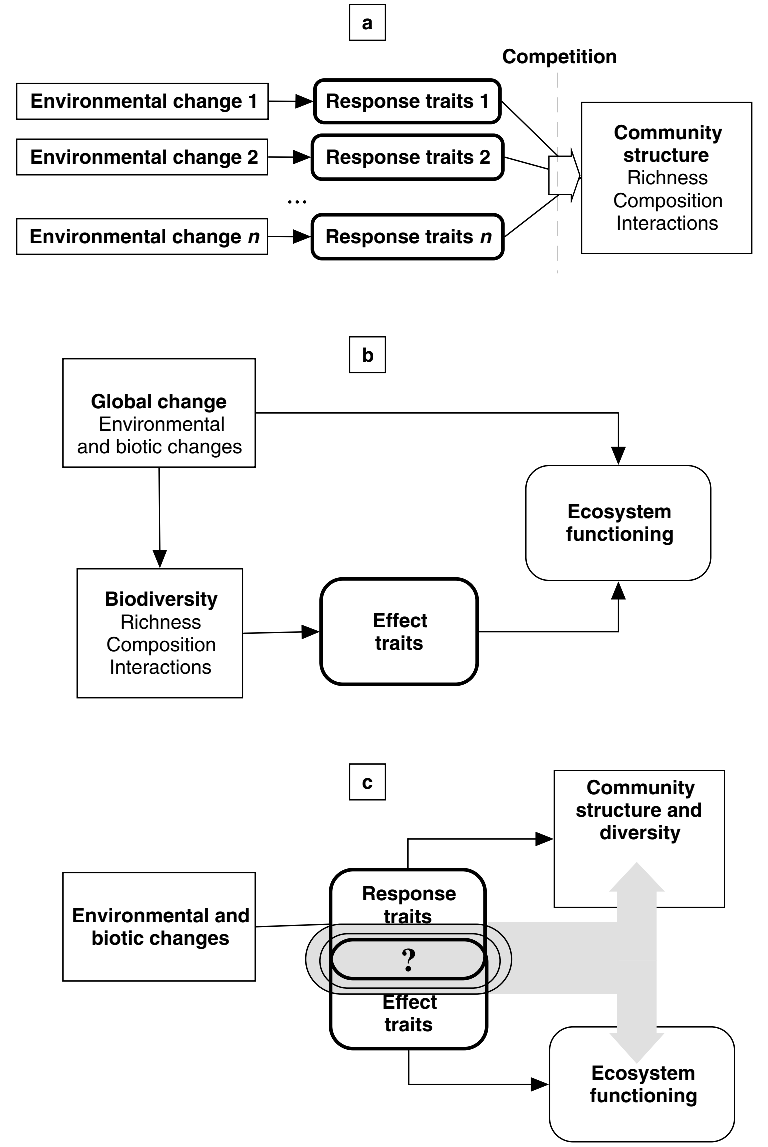

Fig. 1. Conceptual framework for effects of environmental changes on plant community structure (or biodiversity) and ecosystem functioning. (a) Simplification of the filter theory of Keddy (1992) and Woodward & Diament (1991), where response of community structure to environmental conditions is the result of species response traits. (b) Summary of the framework of Chapin *et al.* (2000) predicting the ecosystem consequences of environmental changes via species effect traits. (c) Representation of the proposed conceptual framework that articulates environmental response and ecosystem effects through varying degrees of overlap between relevant traits.

this concept of plant functional classification. A conceptual framework and methods have been developed to predict changes in ecosystem processes such as biogeochemical cycling by considering the role of plant traits in ecosystem structure and processes.

Initial conceptual and large-scale vegetation models (Smith *et al.* 1997; Woodward & Cramer 1996) assumed that grouping plants *a priori*, based on knowledge of their function or on observed correlations among traits, would make it possible to directly predict changes in ecosystem processes from projected changes in plant composition in response to global change. These assumptions, which reflected the belief that *functional effect* groups (species with a similar effect on one or several ecosystem functions, Gitay & Noble 1997; Walker *et al.* 1999) and *functional response* groups (groups of species with a similar response to a particular environmental factor such as resource availability, disturbance or CO_2, Gitay & Noble 1997; Lavorel *et al.* 1997) should coincide, have remained problematic despite sustained efforts on concepts and terminology (Gitay & Noble 1997; Lavorel & Garnier 2001; Lavorel *et al.* 1997).

A priori functional effect groups based on taxonomy (grasses, legumes, non-legume forbs) and/or coarse descriptions of function (N-fixing, phenology, life cycle, photosynthetic pathway) have also been used in experiments documenting the effects of functional diversity on ecosystem functioning (Díaz & Cabido 2001). In contrast, recent tests of functional redundancy and ecosystem resilience (Walker *et al.* 1999) have clearly distinguished between effect and response. These experimental studies examined the hypothesis that response to environmental change should cause species composition turnover but leave biogeochemical cycling unchanged, especially when effect groups are species-rich. Finally, Chapin *et al.* (2000) proposed a conceptual framework where modifications of species composition resulting from environmental change translate into modifications of ecosystem functioning via changes in the representation of species traits (Fig. 1b).

The objectives of this paper are to:

1. briefly summarize the rationale, approaches and traits for classifications of plant responses and functional effects;
2. examine commonalities and differences between response traits and effect traits underlying these groupings for an example set of key environmental factors and ecosystem processes;
3. propose a conceptual framework that links traits associated with responses to those that determine effects on ecosystems – the aim of this framework is to integrate analyses of response traits in relation to environmental and/or biotic factors with analyses of functional effects of species, and hence trait composition, in order to analyse the effects of environmental changes on ecosystem processes.

Functional response and functional effect groups

PLANT RESPONSES TO ENVIRONMENTAL CHANGES

We first focus on organism-centred issues, and aim to understand the adaptive significance of traits or combinations of traits in order to predict the responses of organisms to environmental factors. Plant communities can be seen as the result of a hierarchy of abiotic (climatic, 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 (Fig. 1a; Keddy 1992; see review by Díaz *et al.* 1999). Following this model, we should be able to predict the trait pool of plant communities by combining knowledge of the nature and strength of different filters with that of response traits for each of these filters. For each filter, the corresponding principal environmental factor defines response groups and hence species that are retained. The effects of changes in abiotic factors, such as climate, atmospheric CO_2 concentration and disturbance, could then be modelled as changes in the strength of these different filters (Díaz *et al.* 1999; Woodward & Diament 1991).

Recent analyses of the significance of selected traits for plant responses to environmental factors have considered 'soft' traits, which are easy to measure for a large number of species and sites, but are not necessarily explicitly related to a specific functional mechanism; and 'hard' traits, usually less accessible but with a direct functional role (Hodgson *et al.* 1999; Table 1). These commonly include:

1. life form, leaf traits and genome size in response to climate (McGillivray & Grime 1995; Niinemets 2001; Pavón *et al.* 2000);
2. specific leaf area (SLA) and leaf chemical composition for response to soil resource availability (Cunningham, Summerhayes & Westoby 1999; Poorter & de Jong 1999);
3. life cycle, relative growth rate (RGR) and photosynthetic pathway for response to CO_2 (Poorter, Roumet & Campbell 1996);
4. RGR, leaf and root morphology, and seed mass for response to shading (Leishman & Westoby 1994; Reich *et al.* 1998);
5. life cycle, plant height, architecture, resprouting and seed traits for response to disturbance (Bond & Midgley 2001; McIntyre & Lavorel 2001);
6. extensive screenings relating large sets of traits to complex environmental gradients (Díaz & Cabido 1997; Grime *et al.* 1997).

Natural gradients combine variations in climate, resource and disturbance. These underlying simple gradients may be explicit, as for analyses of response to altitude (Pavón *et al.* 2000) or agricultural disturbance (Kleyer 1999). On the other hand, little may be quantified about the nature and amount of environmental variation along complex natural gradients, as in the case of succession (Bazzaz 1996; Prach, Pyšek & Šmilauer 1997). In all cases, the combination of multiple factors and a lack of knowledge about key factors impede the interpretation and prediction of plant distributions, because traits associated with different single gradients can be independent – filters do not match well, as for water vs. nutrient stress (Cunningham, Summerhayes & Westoby 1999); or one filter involves adult and the other regeneration traits (Leishman & Westoby 1992; Shipley *et al.* 1989).

Triangular models, such as Grime's (1979) plant strategy (C-S-R) scheme and Westoby's (1998) leaf-height-seed model, have helped elucidate these issues by explicitly using soil resource availability and disturbance as two orthogonal dimensions for plant classification. These models for responses to combined factors are underpinned by the hypothesis of trade-offs and correlations among plant traits. More generally, the analysis of plant functional types has been guided by the recognition that plants are constrained in their performance for alternative functions, such as resource capture and conservation (Chapin, Autumn & Pugnaire 1993; Grime 1979; Poorter & Garnier 1999); acquisition of different resources such as light and water (Smith & Huston 1989) or light and nutrients (Tilman 1988); or growth and reproduction (Silvertown *et al.* 1993; Solbrig 1993). Growth forms are the ultimate expression of these trade-offs, and of the links between key plant traits and plant response and function (Chapin 1993).

GROUPS, TRAITS AND BIOGEOCHEMICAL CYCLES

We now turn to the issue of how organisms affect the functioning of ecosystems. We restrict our analysis to a snapshot view of ecosystems, where species composition is assumed to be stable and the primary functions considered are fluxes of energy and matter. We concentrate on how species affect components of biogeochemical cycles, taking net primary productivity (NPP) as an example. From an ecosystem perspective, all green plants convert inorganic resources to organic matter and belong to a single functional group: primary producers. The relevant question is therefore how biogeochemical cycles, and NPP in particular, are regulated by particular species groups and/or traits.

To address this issue, many studies have examined differences in NPP among communities of varying composition, without necessarily basing their a *priori* groupings on plant traits. These include the following, in order of increasing refinement of species grouping.

1. Differences in life form (Raunkiaer 1934) or growth form: quantitative assessments of differences in NPP or its components were made across biomes (Lieth & Whittaker 1975; Saugier, Roy & Mooney 2001) or at the community scale, where estimates were related to differences in species composition (herbaceous vs. woody species, Eckardt *et al.* 1977; Hunt *et al.* 1988; grasses vs. forbs, Hooper & Vitousek 1998; Kull & Aan 1997).
2. Differences in life history and/or phenology (Hooper & Vitousek 1998; Jackson *et al.* 2001).
3. Major physiological differences such as direct access to symbiotically fixed atmospheric nitrogen vs. absorbing N from the soil (Hooper & Vitousek 1998; Wardle *et al.* 1999); C_3 vs. C_4 photosynthetic pathway (Sims & Singh 1978; Wardle *et al.* 1999).

Table 1. Traits relevant to ecosystem response and effects

	Mechanism and corresponding hard traits			
	Environmental response		Ecosystem effect	
Soft trait	Nutrients	Fire	Primary productivity	Flammability
Whole plant				
Growth form	Absorption: rooting depth Decomposition: lignin content	Avoidance: plant/bud height (physical escape), phenology (temporal escape) Regeneration: strategy (resprout vs. seed)	C stock: standing biomass Resource capture: standing biomass Growth: growth rate	Water status: access to deep water
Life span		Tolerance: longevity		
Maturation age		Regeneration		
Period of photosynthetic activity		Avoidance: phenology	Light capture	
Mass of underground reserves		Tolerance: resprouting ability	C stock: carbon sink	
Whole shoot				
Shoot height		Avoidance: physical escape	C stock: standing biomass Light capture	Fire spread Competition: stand structure
Canopy architecture		Avoidance: physical escape	Light capture: leaf area index (LAI) C fixation: whole-plant instantaneous photosynthetic rate Growth: growth rate	Water stress: LAI Fire spread Microclimate in understorey: LAI Allocation: fuel size distribution
Bark thickness		Tolerance: tissue protection		
Leaf				
Specific leaf area (SLA)	Conservation: residence time Decomposition: lignin content Growth: growth rate	Tolerance: resprout RGR Regeneration: seedling RGR	C fixation: leaf instantaneous photosynthetic rate	
Dry matter content	Conservation: residence time Decomposition: lignin content?		Growth: growth rate	Tissue composition: water content Water status: osmotic potential (drought tolerance)
N concentration	Conservation: residence time Decomposition: C : N ratio	Tolerance: resprout RGR Regeneration: seedling RGR	C fixation: leaf instantaneous photosynthetic rate Growth: growth rate Allocation: C : N ratio?	Allocation: fuel size distribution?
Leaf life span	Conservation: residence time	Tolerance: resprout RGR Regeneration: seedling RGR	C fixation: cumulated photosynthesis Growth: growth rate	
Leaf phenology		Avoidance: timing of leaf shedding	C fixation: cumulated photosynthesis	
Photosynthetic pathway			C fixation: leaf instantaneous photosynthetic rate	
Natural ^{15}N abundance	Absorption: root distribution			Water status: access to deep water?
Root				
Rooting depth	Absorption: root distribution, root length	Tolerance: resprouting ability	C stock: root mass	Water status: access to deep water?
Specific root length	Absorption: instantaneous absorption rate		C and nutrient uptake: specific absorption rate Growth: growth rate	
Process of N capture	N capture: N_2 fixation/N absorption		C and nutrient uptake: specific absorption rate Growth: growth rate	

Table 1. *Continued*

Soft trait	**Mechanism and corresponding hard traits**			
	Environmental response		Ecosystem effect	
	Nutrients	Fire	Primary productivity	Flammability
Seed				
Seed mass		Regeneration: fecundity, seedling establishment, dispersal		
Seed shape		Regeneration: seed bank persistence		
Germination phenology		Regeneration: phenology with respect to timing of fire and growing season		
Germination tests		Regeneration: germination cues		

We selected two environmental factors, nutrient gradient (resource) and fire (disturbance), and two ecosystem functions, net primary production (NPP) and flammability. The left-hand column lists soft traits, or substitute measurements when these are not available, that are relevant to these responses or effects. The table presents the specific functions and, when available, the hard trait corresponding to a given soft trait – response or effect association. Our analyses focused on identifying traits that are common to both response and effect, which can be found occupying the same sections of the table. Lists of traits and corresponding processes are compiled from the literature (see Lavorel 2002 for general review).
Response to nutrient gradient: based on Chapin (1980); Grime (1979); Poorter & Garnier (1999); Reich, Walters & Ellsworth (1992).
Response to fire: based on Bond & Midgley (2001); Noble & Slatyer (1980).
Primary productivity: based on Chapin (1993); Monteith (1977); Saugier, Roy & Mooney (2001).
Flammability: based on Bond & Midgley (1995); Schwilk & Ackerly (2001); Whelan (1995).

The impact of species traits on NPP has been studied empirically in a number of cases (Eckardt *et al.* 1977; Herbert *et al.* 1999; see below). Complex, mechanistic models have also been developed which involve detailed calculations of carbon balance components, and explicitly involve traits (mostly hard) (Ågren *et al.* 1991). The general formulation of NPP proposed by Monteith (1977) could theoretically be used to assess the impact of some relevant traits on NPP. However, it is more suited to a whole-stand analysis where the properties of individual species are not taken into account, and it has been widely used for crop production and monospecific stands (reviewed by Sinclair & Muchow 2000; but see Saugier, Roy & Mooney 2001 for applications to natural vegetation). Recently, Chapin (1993); Chapin *et al.* (1996) proposed a different approach to NPP, more suitable for analysis of the effect of functional diversity on biogeochemical cycling in natural, species-rich ecosystems. This formulation explicitly incorporates species traits central to plant functioning in a continuous fashion. Based on these ideas, we develop below an expression of NPP, whose exact form differs from that proposed by Chapin *et al.* (1996). NPP is the sum of the productivity of individual species in the community, and can be written as:

$$NPP = \frac{\sum_{i=1}^{nspecies} N_i \times (Mf_i - Mo_i)}{\Delta T} \qquad \text{eqn 1}$$

where N_i is the number of individuals of species i per unit ground area; Mf and Mo are the final and initial average biomasses of individuals of species i; and ΔT is the period over which NPP is assessed (1 year in many cases). Now Mf_i can be written as:

$$Mf_i = Mo_i \times e^{RGR_i \times (tf-to)_i} \qquad \text{eqn 2}$$

where RGR_i and $(tf-to)_i$ are the average relative growth rate and period of active growth of species i, respectively. Combining equations 1 and 2:

$$NPP = \frac{\sum_{i=1}^{nspecies} N_i \times Mo_i \times (e^{RGR_i \times (tf-to)_i} - 1)}{\Delta T} \qquad \text{eqn 3}$$

According to equation 3, NPP is controlled by the relative initial biomass of each species in the community ($N_i \times Mo_i$; its carbon stock), the integrated functioning of each species (the outcome of carbon assimilation, nutrient uptake, allocation, etc.), and its phenology (duration of active growth period).

On a broad scale, when different biomes or vegetation types are compared, differences in NPP are strongly correlated to the first factor in equation 3, standing biomass or height of the dominant species (Chapin *et al.* 1996; Saugier *et al.* 2001) – two closely related variables at this scale of comparison (Niklas &

Table 2. Nitrogen mineralization rate, above-ground net primary productivity (ANPP) and leaf characteristics of dominant species taken from various vegetation types in Central Europe

Vegetation type/ dominant species	Net N mineralization (kg N ha^{-1} year^{-1})	Minimum above-ground biomass (g m^{-2})	ANPP (g m^{-2} year^{-1})	Mean SLA (m^2 kg^{-1})	Mean leaf N concentration (mg g^{-1})	Estimated $A_{\max}$ (nmol g^{-1} s^{-1})
Ellenberg/Poorter						
Sand dunes	12–19	≈0	90	9·9	13·5	67·2
Heath	11–30	≈700*	210	18·7	16·7	124
Chalk grasslands	20–30	≈0	330	21·3	15·7	130
Fertilized meadows	130–160	≈0	1080	31·8	36·1	328
Aerts and co-workers						
Wet heathland:						
Erica tetralix	4·4	600	376	8·0†	12·6	54·8
Molinia caerulea	7·8	117	867	21·3†	19·3	152
Dry heathland:						
Calluna vulgaris	6·2	710	540	8·0†	na	na
Molinia caerulea	10·9	56	614	22·7†	14·0	125

In the first case (Ellenberg/Poorter), mineralization rates were taken from Ellenberg (1977), and vegetation characteristics from Poorter & de Jong (1999) for ecosystems of similar characteristics (only ecosystems for which a clear equivalence could be made between the two studies were included). In the second case (Aerts and co-workers), mineralization rates were taken from van Vuuren *et al.* (1992), data for the wet heathland from Aerts & Berendse (1989), and for dry heathland from Aerts (1989). Estimated instantaneous photosynthetic rate ($A_{\max}$) was calculated using multiple regression on SLA and leaf N concentration as given by Reich, Walters & Ellsworth (1997).
*Estimated from Aerts (1989); Aerts & Berendse (1989).
†Taken from Poorter & de Jong (1999).

Enquist 2001). The similarity of broad relationships involving organisms as different as unicellular algae and terrestrial macrophytes have led Niklas & Enquist (2001) to argue that NPP depended mostly on community standing biomass, not on species composition. However, when biomes of similar physiognomy found under different climates are compared, substantial differences in NPP can still be observed (as also seen in the data of Niklas & Enquist 2001), and are a likely consequence of differences in metabolic activity and length of growing season (second and third factors in equation 3). At a more local scale, the influence of biomass weakens and the physiology of the species predominates (Table 2). The role of phenology in NPP has not been thoroughly assessed, but some examples show that increasing the growing season either of individual plants (Jackson *et al.* 2001) or at the community level (for example in mixtures of C_3 and C_4 species, Epstein *et al.* 1999) could significantly increase NPP.

This approach could probably be extended to other processes, such as the rate of litter decomposition, provided that a model linking the decomposition constant of litter and traits of either the litter itself (its chemical composition, Heal *et al.* 1997) or living leaves (Cornelissen *et al.* 1999) can be developed.

From community response to ecosystem functioning: a framework and some case studies

A FRAMEWORK TO LINK RESPONSE AND EFFECT GROUPS

As outlined in the two previous sections, the two types of functional classifications – response groups and effect groups – correspond to different approaches and, to some extent, traits measured. Physiological, harder traits at the individual level are more commonly used for effect groups (Chapin 1993; Herbert *et al.* 1999), whereas response groups are identified through community-level studies of changes in soft, morphological or behavioural traits in response to abiotic or biotic factors. The frequent use of lists of traits that do not overlap makes it difficult to reconcile the two types of classifications (Weiher *et al.* 1999; but see Hodgson *et al.* 1999), which is needed to build a more comprehensive framework of response–effect linkages onto the ideas of Chapin *et al.* (2000).

To achieve this, we need to match attribute lists for responses with the known effects of some of these attributes (or their correlates) on ecosystem processes. From a global perspective, the primary environmental factors determining plant community structure are resources and disturbances. Although a wider range of axes should be considered for a comprehensive study, for illustration we restricted our comparative analysis of response and effect traits to one type of resource (soil nutrients) and one important disturbance (fire). Similarly, we chose two main ecosystem effects (primary productivity and flammability). Traits were selected based on the literature and on expert opinion synthesized during a workshop (Building a Global Key of Plant Functional Types; http://gcte.org/focus2/). We favoured traits that are continuous (SLA, shoot height) rather than categorical, although some traits, such as life form or photosynthetic pathway, are by definition categorical. Where possible we preferred soft traits, but in some instances where this knowledge is not yet available, harder traits or phenomenological surrogates had to be chosen. In an attempt to examine the mechanisms responsible for differing degrees of overlap between responses and effects, we also listed specific functions associated with each trait. For instance, disturbance response is classically split into three processes: avoidance, tolerance and regeneration, and the specific relevance of these for different fire-response traits was listed. Similarly, for traits associated with primary productivity we noted which of the three components of equation 3 they were relevant to. Having done this, we were able to construct a table listing relevant functions (in terms of responses and effects) for each trait (Table 1). Our comparison then examined which traits were associated with at least one response process and at least one effect process.

A first examination of Table 1 reveals that the resource axis shows maximum overlap between response and effect traits, whereas overlaps for the disturbance axis are more limited. To address the causes of differing degrees of trait overlap between response and effects, we must analyse the specific functions for the traits involved. Analyses are presented in the following section, first for the relationship between resource gradients and productivity, then for the apparently tenuous relationship between fire tolerance and flammability. We then expand our investigation to consider general causes of independence between disturbance response and ecosystem effects, and finally discuss the extent to which overlaps between response and function can be inferred from trait linkages.

HOW DO SPECIES TRAITS AND ECOSYSTEM PRIMARY PRODUCTIVITY COVARY ALONG GRADIENTS OF SOIL NUTRIENT AVAILABILITY?

Early syntheses on changes in species traits along nutrient gradients (Chapin 1980; Grime 1979) recognized that species from nutrient-rich habitats tend to be inherently fast-growing, with rapid resource capture and fast turnover of organs leading to poor internal conservation of resources, while the reverse is true for species from nutrient-poor habitats (Table 1). More recently, a series of quantitative traits has been associated with this fundamental trade-off in plant function (Grime *et al.* 1997; Poorter & Garnier 1999; Reich *et al.* 1992). Fast-growing species from nutrient-rich habitats usually have a combination of high SLA; high tissue nutrient concentration (in particular, N); low tissue density and cell wall content; high rates of carbon and nutrient uptake; and short-lived leaves. Opposite traits characterize species from nutrient-poor habitats in which the mean residence time of nutrients tends to be maximized through longer organ longevity (in particular, leaf) and/or higher resorption of nutrients from senescing organs (Aerts & Chapin 2000; Garnier & Aronson 1998).

At the ecosystem level, limitation of primary production by nutrient availability – particularly N, on which we concentrate here – is widespread (Aerts & Chapin 2000; Vitousek & Howarth 1991). Net mineralization rates of N vary tremendously among ecosystems, from 0 to 0·5 kg N m^{-2} $year^{-1}$ in arctic tundra or bogs, to 300 kg N m^{-2} $year^{-1}$ in ruderal vegetation (Ellenberg 1977; Larcher 1995). These rates correlate positively with above-ground net primary productivity (ANPP) in several ecosystems (Hunt *et al.* 1988; Reich *et al.* 1997). Table 2 shows two examples for different types of vegetation in northern Central Europe: in the first, a tenfold variation in mineralization rates from sand dunes to fertilized meadows (Ellenberg 1977) was associated with a 12-fold increase in ANPP (Poorter & de Jong 1999); in the second, increases in mineralization rates associated with a shift in dominants from *Erica tetralix* and *Calluna vulgaris* to the perennial grass *Molinia caerulea* (van Vuuren *et al.* 1992) paralleled the increase in ANPP (Aerts 1989; Aerts & Berendse 1989).

Is there a relationship between these changes in NPP along gradients of N availability and the shifts in plant traits highlighted above? We are not aware of any study in natural vegetation in which the variation in NPP along gradients of N availability was analysed according to equation 3. Indirect assessments of the different factors can be deduced for the two sets of experiments presented in Table 2. The impact of length of growing season on NPP is likely to be low in these cases, as all data were collected from communities with a similar length of growing season (Aerts 1989; Aerts & Berendse 1989). Contrary to the prediction of Niklas & Enquist (2001), standing biomass had no consistent effect on ANPP in either case. In the study by Aerts and co-workers, the vegetation with the highest initial standing biomass (dominated by Ericaceae) showed the lowest ANPP. By contrast, consistent differences in leaf structure and function were found among species. In nutrient-rich habitats, species tend to have leaves with high SLA, N concentration and photosynthetic rates per unit dry mass (Table 2). These traits and process are positively related to whole-plant RGR (Poorter & Garnier 1999; Reich *et al.* 1992), the physiological factor in equation 3. We therefore conclude that, in this case, differences in ANPP would mainly result from differences in physiology of the dominant species at the different sites.

We cannot rule out the possibility that length of growing season and standing biomass may play a role in other instances. However, the evidence presented here suggests that the species traits involved in changes in primary productivity of ecosystems along a nutrient gradient (effect traits) strongly overlap with those involved in the response of species to the same gradient (response traits). These traits include primary traits such as SLA, as well as some of their correlates (leaf dry matter content, leaf longevity), or other (physiological) traits which represent a scaling mechanism from environmental factor to function (photosynthetic rate, C : N ratio).

ARE FIRE-TOLERANT ECOSYSTEMS MORE FLAMMABLE?

In contrast to the case of nutrients and productivity, traits determining ecosystem flammability showed little direct overlap with traits associated with response to fire (Table 1).

Fire tolerance is related to alternative sets of traits that allow plants to avoid fire entirely (height taller than flames, annuals with dormant seeds during the fire season); or to tolerate fire by surviving and regrowing vigorously (thick bark, resprouting ability resulting from investment in underground reserves) or regenerating from seeds (canopy or soil seed banks, fast growth rate, fast maturation). The relative importance of the two tolerance mechanisms, seeding or sprouting, has been related to fire frequency and intensity (Bellingham & Sparrow 2000; but see Pausas 2001), and to resource availability (Bond & Midgley 2001).

Ecosystem flammability is a complex emergent property which involves two successive processes and traits linked with each (Whelan 1995). First, fire must ignite plant material, then it must propagate through the canopy and/or understorey. Traits relating to the ignition phase (flammability) are those determining tissue moisture, such as water content and traits conferring drought resistance; and, to a debated extent, chemical composition – volatiles, waxes and resins increase flammability while high lignin and mineral content decrease it. Fire spread relates to two characteristics: the energy produced by the initial burning, which depends largely on the same traits as flammability; and the spatial distribution of fuel, which is a consequence of total biomass accumulation and its spatial arrangement. Traits promoting biomass accumulation through rapid growth and slow decomposition therefore increase flammability. Architecture and structural traits then determine the spatial distribution of this biomass. A high surface area-to-volume ratio of organs (fine foliage, thin branches), low stature, wide lateral spread, low canopy density and retention of dead branches are attributes that increase fire propagation. Two additional effects of individual plant traits on communities must finally be considered for a complete picture of flammability: the effects of species on soil moisture and temperature in the understorey; and their effects on stand vertical structure and density.

This list of traits relevant to ecosystem flammability shows little of the overlap with traits relating to fire response that would be expected from evolutionary arguments about the co-occurrence of flammability and fire tolerance (Bond & Midgley 1995). Phylogenetically independent contrasts among pine species have shown associations between flammability-enhancing traits and fire tolerance (Schwilk & Ackerly 2001). Models have demonstrated that these can be sustainable if flammability-promoting traits warrant additional fitness benefits such as secondary compounds with antiherbivore benefits, increased growth rate associated with early and prolific branching, or enhanced carbon gains for resprouters (Bond & Midgley 1995). Alternatively, the occurrence of flammability-enhancing traits in a species could merely reflect response to factors other than fire, such as herbivory and drought.

Consequently, if functional linkages exist between traits promoting fire tolerance and those involved in ecosystem flammability, they would have to be mostly indirect, through character associations or trade-offs. For instance, a high growth rate is required to increase the success of seed regeneration after fire, and is also associated with canopy architectures with many thin stems and high surface : volume ratios. The association between sprouting and drought tolerance (which allows low water potential and hence increases flammability), both of which result from investment in large underground structures, is another example. However, inferring such response–effects associations from a series of correlations of varying strengths needs to be done with caution. 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.

From community response to ecosystem functioning: some generalizations

INDEPENDENCE BETWEEN DISTURBANCE RESPONSE AND ECOSYSTEM PROCESSES: A GENERAL RULE?

The limited degree of convergence between disturbance response traits and ecosystem effect traits – seen in Table 1 for response to fire and flammability or primary productivity – is not surprising, for several reasons. As hypothesized within plant strategy schemes (Grime 1979; Westoby 1998), the disturbance and resource axes are mostly independent and therefore relate to distinct trait sets. Indeed, disturbance response relates to a great extent to regeneration traits whose lack of correlation with adult traits, more relevant to response to environmental resource factors, is notorious (Leishman & Westoby 1992; Shipley *et al.* 1989). Seed mass has been used as the single soft trait that simultaneously captures aspects of regeneration (dispersal, seed persistence, recruitment success, Thompson, Band & Hodgson 1993; Westoby, Jurado & Leishman 1992) and seedling response to environmental stress (drought, Jurado & Westoby 1992; shading, Walters & Reich 2000). Disturbance response also involves demographic rather than physiological traits. Although Silvertown *et al.* (1993) proposed to match Grime's plant strategies with demographic strategies described by allocation to survival (stress-tolerant), fecundity (ruderal) and growth (competitor), their scheme was only a first step from which more general relationships between demographic and physiological traits or their soft proxies remain to be established.

The relative independence of traits relevant to disturbance response and those involved in ecosystem effects supports the redundancy and insurance hypotheses (Lawton & Brown 1993; Walker 1992). If disturbance selects species according to traits that are unconnected with functional effects, then biogeochemical cycles will be maintained. In Australian semiarid rangelands, the distribution of effects traits (plant height, SLA, longevity, total biomass, leaf litter quality) was unchanged in heavily compared to lightly grazed communities (Walker *et al.* 1999). Larger numbers of quantitative comparisons of effect traits before and after disturbance are needed to establish the range of applicability of this hypothesis in terms of disturbance characteristics, initial diversity and abiotic conditions.

TRAIT CORRELATIONS AND TRADE-OFFS: USEFULNESS AND LIMITATIONS

In the previous discussion we pointed out potential linkages between response and effect traits, either directly through shared traits or through trait correlation. Plant strategy schemes and other proposed functional trait lists have emphasized the usefulness of correlation among traits, either to infer process from easily measured structure (Hodgson *et al.* 1999), or to capture several response or effect processes with few traits (Weiher *et al.* 1999; Westoby 1998). However, many correlations that hold true over entire floras or across steep environmental gradients may no longer be relevant to less contrasted ranges of conditions, or within species assemblages that present little variation in those key traits (such as assemblages with a single life form, McIntyre *et al.* 1999). In addition to the weakening of correlations when trait ranges are narrow, the use of surrogate correlated traits can lead to a loss of information unique to particular traits. This is particularly true for loose correlations, such as those involving seed mass to infer persistence in the seed bank or dispersal ability (Weiher *et al.* 1999).

Growth forms provide the most interesting and extreme example of the usefulness and limitations of trait correlation patterns (Chapin 1993). Many analyses of trait correlations within floras have highlighted that growth form captures patterns of variation in several important functional traits, and is one of the best correlates of plant regional distributions (Chapin *et al.* 1996a; Díaz & Cabido 1997; Leishman & Westoby 1992; Raunkiaer 1934). Growth form can then be a surrogate for other traits in vegetation containing sufficiently wide variations in growth form. This observation has been applied for models of vegetation response to global climate that use classifications based on subdivisions of growth forms, assuming that key traits for biogeochemical cycling are constant within them (Foley *et al.* 1996; Steffen *et al.* 1996). However, we know little about the mechanisms by which response and effect traits are represented by growth form, other than the resource capture–conservation trade-off. Raunkiaer's (1934) life-form classification was initially designed with a well defined function in mind – response to cold winters – related to a well identified trait – the position of dormant meristems over this unfavourable period. Nevertheless, it is also relevant to other environmental responses (Table 1), but relationships between dormant meristem position and traits relevant to these responses need to be clarified. Life form has some relationships with stem height, leaf characteristics (Garnier *et al.* 2001) and, to some extent, phenology, and hence with primary productivity. It is also a robust predictor of responses to disturbance (McIntyre *et al.* 1999) as it reflects strategies and associated traits for avoidance (phenology and position of vulnerable meristems), tolerance (resprouting capacity), and regeneration through seeds or underground organs.

Conclusion

We present a conceptual framework aiming to unify a series of ideas drawn from community (Keddy 1992); ecosystem (Chapin, Autumn & Pugnaire 1993; Eckardt *et al.* 1977); and evolutionary (Solbrig 1993) ecology. Although precursors of this framework have been presented previously (Chapin *et al.* 2000; Díaz *et al.* 1999; Grime 2001), we have now linked disconnected conceptual elements and a suite of empirical data. Our framework is built on three key tenets (Fig. 1), as follows.

1. The keystone hypothesis is that traits can simultaneously explain individual plant responses to biotic and abiotic factors, and ecosystem effects such as biogeochemical cycling and propensity to disturbance.
2. Ecosystem functioning is the end result of the operation of multiple filters at a hierarchy of scales which, by assembling individuals with appropriate responses, result in communities with varying trait composition (Woodward & Diament 1991; Keddy 1992). Ecosystem functioning is predictable from composition if those traits involved in the response to environmental filters can be used to estimate ecosystem processes. Rather than discontinuous classifications into functional types, the use of continuous traits representing changes in the intensity of processes is likely to make this linking more operational.
3. Functional linkages and trade-offs among traits that each relate to one or several processes determine whether filtering by different factors matches or not, and whether ecosystem effects can be deduced easily from knowledge of the filters. However, linkages and trade-offs must be used with caution, depending on the scale, environmental conditions and evolutionary context.

Although the detailed examples presented here focus on two well documented linkages between response and effects, similar analyses should be developed for other environmental factors and ecosystem processes, including nutrient or water gradients and cycling, and grazing and palatability. We predict that overlap between traits determining response and those determining effects will be most common for biogeochemistry, where ecosystem fluxes may be calculated by scaling-up from individual physiological traits (Schimel *et al*. 1995) because the traits concerned relate to fundamental resource capture–conservation trade-offs. On the other hand, we expect little convergence between traits and processes associated with disturbance response and those relating to ecosystem functioning. Cases of overlap (leaf area and leaf toughness) correspond with traits that are involved in the acquisition–conservation trade-off, the exact primary function of which has been debated.

Our framework offers potential for developing a better understanding both of the role of biodiversity in ecosystem functioning, and of their coupled vulnerabilities to local and global environmental changes. It should assist researchers in selecting traits covering a broad range of processes which could be used to design observations, experiments and models. Finally, although the framework is presented here at ecosystem level, its applicability to the landscape and larger scales needs to be considered.

Acknowledgements

This work resulted from the GCTE workshops ‘Plant Functional Types: Concepts and Applications’ and ‘Building a Global Key of Plant Functional Types’, sponsored by the French Ecophysiological Society and the Dutch Global Change Committee, respectively. Sandra Díaz and Karl Grigulis helped substantially with successive drafts of the manuscript.

References

Aerts, R. (1989) Aboveground biomass and nutrient dynamics of *Calluna vulgaris* and *Molinia caerulea* in a dry heathland. *Oikos* **56**, 31–38.

Aerts, R. & Berendse, F. (1989) Above-ground nutrient turnover and net primary production of an evergreen and a deciduous species in a heathland ecosystem. *Journal of Ecology* **77**, 343–356.

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

Ågren, G.I., McMurthrie, R.E., Parton, W.J., Pastor, J. & Shugart, H.H. (1991) State-of-the-art of models of production–decomposition linkages in conifer and grassland ecosystems. *Ecological Applications* **1**, 118–138.

Bazzaz, F.A. (1996) *Plants in Changing Environments – Linking Physiological, Population and Community Ecology*. Cambridge University Press, Cambridge, UK.

Bellingham, P.J. & Sparrow, A.D. (2000) Resprouting as a life history strategy in woody plant communities. *Oikos* **89**, 409–416.

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

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

Chapin, F.S. III (1980) The mineral nutrition of wild plants. *Annual Review of Ecology and Systematics* **11**, 233–260.

Chapin, F.S. III (1993) Functional role of growth forms in ecosystem and global processes. *Scaling Physiological Processes: Leaf to Globe* (eds J.R. Ehleringer & C.B. Field), pp. 287–312. Academic Press, San Diego, CA.

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

Chapin, F.S. III, Reynolds, H.L., D'Antonio, C.M. & Eckhart, V.M. (1996) The functional role of species in terrestrial ecosystems. *Global Change and Terrestrial Ecosystems* (eds B. Walker & W. Steffen), pp. 403–428. Cambridge University Press, Cambridge, UK.

Chapin, F.S. III, Zavaleta, E.S., Eviner, V.T. *et al.* (2000) Consequences of changing biotic diversity. *Nature* **405**, 234–242.

Cornelissen, J.H.C., Pérez-Harguindeguy, N., Díaz, S. *et al.* (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.

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

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. (2001) *Vive la différence*: Plant functional diversity matters to ecosystem processes. *Trends in Ecology and Evolution* **16**, 646–655.

Díaz, S., Cabido, M. & Casanoves, F. (1999) Functional implications of trait–environment linkages in plant communities. *Ecological Assembly Rules – Perspectives, Advances, Retreats* (eds E. Weiher & P. Keddy), pp. 338–362. Cambridge University Press, Cambridge, UK.

Eckardt, F.E., Berger, A., Méthy, M., Heim, G. & Sauvezon, R. (1977) Interception de l'énergie rayonnante, échanges de CO_2, régime hydrique et production chez différents types de végétation sous climat méditerranéen. *Les Processus de la Production Végétale Primaire* (ed. A. Moyse), pp. 1–75. Bordas, Paris.

Ellenberg, H. (1977) Stickstoff als Standortsfaktor, insbesondere für mitteleuropäische Pflanzengesellschaften. *Oecologia Plantarum* **12**, 1–22.

Epstein, H.E., Burke, I.C. & Lauenroth, W.K. (1999) Response of the shortgrass steppe to changes in rainfall seasonality. *Ecosystems* **2**, 139–150.

Foley, J.A., Prentice, I.C., Ramankutty, S. *et al.* (1996) An integrated biosphere model of land surface processes, terrestrial carbon balance and vegetation dynamics. *Global Biogeochemical Cycles* **10**, 603–628.

Garnier, E. & Aronson, J. (1998) Nitrogen-use efficiency from leaf to stand level: clarifying the concept. *Inherent Variation in Plant Growth. Physiological Mechanisms and Ecological Consequence* (eds H. Lambers, H. Poorter & M.M.I. Van Vuuren), pp. 515–538. Backhuys, Leiden, the Netherlands.

Garnier, E., Laurent, G., Bellmann, A. *et al.* (2001) Consistency of species ranking based on functional leaf traits. *New Phytologist* **152**, 69–83.

Gitay, H. & Noble, I.R. (1997) What are functional types and how should we seek them? *Plant Functional Types: Their Relevance to Ecosystem Properties and Global Change* (eds T.M. Smith, H.H. Shugart & F.I. Woodward), pp. 3–19. Cambridge University Press, Cambridge, UK.

Grime, J.P. (1979) *Plant Strategies and Vegetation Processes*. John Wiley & Sons, Chichester, UK.

Grime, J.P. (2001) *Plant Strategies, Vegetation Processes and Ecosystem Properties*, 2nd edn. John Wiley & Sons, Chichester, UK.

Grime, J.P., Thompson, K., Hunt, R. *et al.* (1997) Integrated screening validates primary axis of specialisation in plants. *Oikos* **79**, 259–281.

Heal, O.W., Anderson, J.M. & Swift, M.J. (1997) Plant litter quality and decomposition: a historical overview. *Driven by Nature: Plant Litter Quality and Decomposition* (eds G. Cadisch & K.E. Giller), pp. 3–30. CAB International, Wallingford, UK.

Herbert, D.A., Rastetter, E.B., Shaver, G.R. & Ågren, G.I. (1999) Effects of plant growth characteristics on biogeochemistry and community composition in a changing climate. *Ecosystems* **2**, 367–382.

Hodgson, J.G., Wilson, P.J., Hunt, R., Grime, J.P. & Thompson, K. (1999) Allocating C-S-R plant functional types: a soft approach to a hard problem. *Oikos* **85**, 282–294.

Hooper, D.U. & Vitousek, P.M. (1998) Effects of plant composition and diversity on nutrient cycling. *Ecological Monographs* **68**, 121–149.

Hunt, H.W., Ingham, E.R., Coleman, D.C., Elliott, E.T. & Reid, C.P.P. (1988) Nitrogen limitation of production and decomposition in prairie, mountain meadow, and pine forest. *Ecology* **69**, 1009–1016.

Jackson, R.B., Lechowicz, M.J., Li, X. & Mooney, H.A. (2001) Phenology, growth, and allocation in global terrestrial productivity. *Terrestrial Global Productivity* (eds J. Roy, B. Saugier & H.A. Mooney), pp. 61–82. Academic Press, San Diego, CA.

Jurado, E. & Westoby, M. (1992) Seedling growth in relation to seed size among species of arid Australia. *Journal of Ecology* **80**, 407–416.

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

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.

Kull, O. & Aan, A. (1997) The relative share of graminoid and forb life-forms in a natural gradient of herb layer productivity. *Ecography* **20**, 146–154.

Larcher, W. (1995) *Physiological Plant Ecology*, 3rd edn. Springer-Verlag, Berlin.

Lavorel, S. (2002) Plant functional types. *The Earth System: Biological and Ecological Dimensions of Global Environmental Change* (eds H.A. Mooney & J. Canadell), Vol. 2, pp. 481–489. John Wiley & Sons, Chichester.

Lavorel, S. & Garnier, E. (2001) Aardvarck to *Zyzyxia* – functional groups across kingdoms. *New Phytologist* **149**, 360–363.

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.

Lawton, J.H. & Brown, V.K. (1993) Redundancy in ecosystems. *Biodiversity and Ecosystem Function* (eds E.D. Schulze & H.A. Mooney), pp. 255–270. Springer-Verlag, Berlin.

Leishman, M.R. & 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, M.R. & Westoby, M. (1994) The role of large seed size in shaded conditions – experimental evidence. *Functional Ecology* **8**, 205–214.

Lieth, H. & Whittaker, R.H. (1975) *Primary Productivity of the Biosphere*. Springer-Verlag, New-York.

McGillivray, C.W. & Grime, J.P. (1995) Genome size predicts frost resistance in British herbaceous plants: implication for rates of vegetation response to global warming. *Functional Ecology* **9**, 320–325.

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

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

Monteith, J.L. (1977) Climate and the efficiency of crop production in Britain. *Philosophical Transactions of the Royal Society of London, Series B* **281**, 277–294.

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

Niklas, K.J. & Enquist, B.J. (2001) Invariant scaling relationships for interspecific plant biomass production rates and body size. *Proceedings of the National Academy of Sciences, USA* **98**, 2922–2997.

Noble, I.R. & Slatyer, R.O. (1980) The use of vital attributes to predict successional changes in plant communities subject to recurrent disturbances. *Vegetatio* **43**, 5–21.

Pausas, J.G. (2001) Resprouting vs. seeding – a Mediterranean perspective. *Oikos* **94**, 193–194.

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.

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

Poorter, H. & de Jong, R. (1999) A comparison of specific leaf area, chemical composition and leaf construction costs of field plants from 15 habitats differing in productivity. *New Phytologist* **143**, 163–176.

Poorter, H., Roumet, C. & Campbell, B.D. (1996) Interspecific variation in the growth response of plants to elevated CO_2: a search for functional types. *Carbon Dioxide, Populations, and Communities* (eds C. Körner & F.A. Bazzaz), pp. 375–412. Academic Press, San Diego, CA.

Prach, K., Pyšek, P. & Šmilauer, P. (1997) Changes in species traits during succession: a search for pattern. *Oikos* **79**, 201–205.

Raunkiaer, C. (1934) *The Life Forms of Plants and Statistical Plant Geography*. Oxford University Press, Oxford, UK.

Reich, P.B., Walters, M.B. & Ellsworth, D.S. (1992) Leaf lifespan in relation to leaf, plant and stand characteristics among diverse ecosystems. *Ecological Monographs* **62**, 356–392.

Reich, P.B., Walters, M.B. & Ellsworth, D.S. (1997) From tropics to tundra: global convergence in plant functioning. *Proceedings of the National Academy of Sciences U.S.A.* **94**, 13730–13734.

Reich, P.B., Grigal, D.F., Aber, J.D. & Gower, S.T. (1997) Nitrogen mineralization and productivity in 50 hardwood and conifer stands on diverse soils. *Ecology* **78**, 335–347.

Reich, P.B., Tjoelker, M.G., Walters, M.B., Vanderklein, D.W. & Buschena, C. (1998) 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.

Saugier, B., Roy, J. & Mooney, H.A. (2001) Estimations of global terrestrial productivity: converging towards a single number? *Terrestrial Global Productivity* (eds J. Roy, B. Saugier & H.A. Mooney), pp. 543–557. Academic Press, San Diego, CA.

Schimel, D.S., Brown, V.B., Hibbard, K.A., Lund, C.P. & Archer, S. (1995) Aggregation of species properties for biochemical modeling: empirical results. *Linking Species and Ecosystems* (eds C.J. Jones & J.H. Lawton), pp. 209–214. Chapman & Hall, New York.

Schwilk, D.W. & Ackerly, D.D. (2001) Flammability and serotiny as strategies: correlated evolution in pines. *Oikos* **94**, 326–336.

Shipley, B., Keddy, P.A., Moore, D.R.J. & 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.

Sims, P.L. & Singh, J.S. (1978) The structure and function of ten western North American grasslands. III. Net primary production, turnover and efficiencies of energy capture and water use. *Journal of Ecology* **66**, 573–597.

Sinclair, T.R. & Muchow, R.C. (2000) Radiation use efficiency. *Advances in Agronomy* **65**, 215–265.

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

Smith, T.M., Shugart, H.H. & Woodward, F.I., eds (1997) *Plant Functional Types, Their Relevance to Ecosystem Properties and Global Change*. Cambridge University Press, Cambridge, UK.

Solbrig, O.T. (1993) Plant traits and adaptive strategies: their role in ecosystem function. *Biodiversity and Ecosystem Function* (eds E.D. Schulze & H.A. Mooney), pp. 97–116. Springer-Verlag, Berlin.

Southwood, T.R.E. (1988) Tactics, strategies and templets. *Oikos* **52**, 3–18.

Steffen, W.L., Cramer, W., Plöchl, M. & Bugmann, H. (1996) Global vegetation models: incorporating transient changes to structure and composition. *Journal of Vegetation Science* **7**, 321–328.

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

Tilman, D. (1988) *Plant Strategies and the Dynamics and Structure of Plant Communities*. Princeton University Press, Princeton, NJ.

Vitousek, P.M. & Howarth, R.W. (1991) Nitrogen limitation on land and in the sea: how can it occur? *Biogeochemistry* **13**, 87–115.

van Vuuren, M.M.I., Aerts, R., Berendse, F. & de Visser, W. (1992) Nitrogen mineralization in heathland ecosystems dominated by different plant species. *Biogeochemistry* **16**, 151–166.

Walker, B.H. (1992) Biodiversity and ecological redundancy. *Conservation Biology* **6**, 18–23.

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.

Walters, M.B. & Reich, P.B. (2000) Seed size, nitrogen supply, and growth rate affect tree seedling survival in deep shade. *Ecology* **81**, 1887–1901.

Wardle, D.A., Bonner, K.I., Barker, G.M. *et al.* (1999) Plant removals in perennial grassland: vegetation dynamics, decomposers, soil biodiversity and ecosystem properties. *Ecological Monographs* **69**, 535–568.

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., Jurado, E. & Leishman, M. (1992) Comparative evolutionary ecology of seed size. *Trends in Ecology and Evolution* **7**, 368–372.

Whelan, R.J. (1995) *The Ecology of Fire*. Cambridge University Press, Cambridge, UK.

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

Woodward, F.I. & Diament, A.D. (1991) Functional approaches to predicting the ecological effects of global change. *Functional Ecology* **5**, 202–212.

Received 13 October 2001; revised 27 March 2002; accepted 17 May 2002