

Plant functional types: are we getting any closer to the Holy Grail ?

Sandra Lavorel¹, Sandra Díaz², J. Hans C. Cornelissen³, Eric Garnier⁴, Sandy P. Harrison⁵, Sue McIntyre⁶, Juli G. Pausas⁷, Natalia Pérez-Harguindeguy², Catherine Roumet⁴, Carlos Urcelay²

¹ Laboratoire d'Ecologie Alpine, CNRS UMR 5553, Université Joseph Fourier, BP 53X, 38041 Grenoble Cedex 9, France. sandra.lavorel@ujf-grenoble.fr

² Instituto Multidisciplinario de Biología Vegetal (CONICET – UNC) and FCECFyN, Universidad Nacional de Córdoba, Argentina

³ Department of System Ecology, Institute of Ecological Science, Vrije Universiteit, De Boelelaan 1085, 1081 HV Amsterdam, The Netherlands

⁴ Centre d'Ecologie Fonctionnelle et Evolutive, CNRS UMR 5175, 1919 route de Mende, 34293 Montpellier Cedex 5, France

⁵ School of Geographical Sciences, University of Bristol, University Road, Bristol BS8 1SS, UK

⁶ CSIRO Sustainable Ecosystems, GPO Box 284, Canberra ACT 2601, Australia

⁷ Centro de Estudios Ambientales del Mediterraneo (CEAM), C/ Charles R. Darwin 14, Parc Tecnologic, 46980 Paterna, Valencia, Spain

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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 & 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 & 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 & 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 CO₂; Gitay & 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 & Noble 1997, Lavorel *et al.* 1997, Lavorel & 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 modelling and mapping of the biosphere.

A large amount of research has been initiated on plant functional 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 section 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 though, has been quite successful in detecting significant associations between particular plant traits and environmental factors (reviewed in section 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 section 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, indirectly, or not at all with the traits that determine ecosystem functions such as biogeochemical cycling or flammability (Lavorel & Garnier 2002; reviewed in section 5). Finally, we return to asking how these results have helped modellers working at larger scales, and what key challenges remain.

2. Individual plant structure and function

Among all possible traits measurable on an individual plant, those of interest to global syntheses and modelling must fill four conditions: (i) bear some relationship to plant function; (ii) be relatively easy to observe and quick 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 & 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 (Figure 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 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 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. 2003b¹).

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 specialisation', 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 & Garnier 1999), acquisition of several different resources (light and water, Smith & 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 specialisation 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 versus large leaves remain to be formalised. Still, identifying an axis relevant to temperature variation, and especially response to extremes, stands as a challenge to ecophysiologicals and ecologists.

However, the previous syntheses focussed on aboveground traits, which are easily accessible. Recent studies have endeavoured to provide the same kind of information belowground, focussing on the functions of root traits, trade-offs among them, and how they

¹ <http://www.publish.csiro.au/nid/65/paper/BT02124.htm>

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 & 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 & 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 *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 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 & Lee 2003, Craine *et al.* 2005).

As recognised by early work (Theophrastus ca. 300 B.C., 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 effects 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 productiveness (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 (Westby *et al.* 1990).

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 modelling. 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 & 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 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 & Grime 1995, Díaz & Cabido 1997, Pavón et al. 2000, Niinemets 2001, Schenk & 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 & de Jong 1999) as do specific root length, tissue density and diameter (Reich *et al.* 2003, Robinson & Rorison 1988). Responses to CO₂ depend on life cycle, relative growth rate (RGR), photosynthetic pathway, and stoichiometric relationships (Poorter et al. 1996). Response to water availability is associated with variation in SRL, root diameter and root architecture (Fitter 1991, Wright & Westoby 1999, Nicotra *et al.* 2002). RGR, leaf and root morphology, and seed mass determine response to shading (Leishman & Westoby 1994, Reich et al. 1998b). Response to disturbance is associated with variation in life cycle, plant height, architecture, resprouting and seed traits (McIntyre & Lavorel 2001, Bond & Migdley 2001, Pausas et al. 2004, Díaz et al. submitted). Following, we summarise recent progress in the identification of plant traits associated with response to those simple factors that vary most significantly across communities within a landscape: resource availability and disturbances.

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 1, 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 &

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 & Aronson 1998, Boot 1989, Aerts & Chapin 2000, Westoby et al. 2002).

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 & Cramer 1999, Pausas et al. 2003), a theoretical framework comparable to that developed for resource economy remains elusive. Moving beyond the well-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 (Marañón & 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 & 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 et al. 1999 c). 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, 1999b).

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. (submitted) 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 favour 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 relatively 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 & 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, fertilisation 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 which structuring 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 further structure woodlands and forests (McIntyre & Martin 2002, 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 & 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: Individual-persistence capacity, Propagule-persistence capacity (persistence at the population level), Competitive capacity (persistence at the community level) and Dispersal 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.

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 & Smith 1989) along which traits are studied has not been quantified or formalised. For instance, this is the case of successional gradients (Bazzaz 1996, Prach et al. 1997, Garnier et al. 2004, Richardson et al. 2005) or along 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 & 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 & 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 Section 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 & Williams 2004), as will novel combinations of atmospheric CO₂ concentration, climate and disturbance regimes. Our ability to apply plant functional responses to generate future vegetation projections must therefore rely on more experimental and modelling work. One remaining challenge for modelling, however, lies in the construction of PFTs from analyses of continuous plant traits. This methodological challenge can be solved with statistical approaches (Pillar & Sosinsky 2003, Nygaard & Erjnaes 2004), but is also a more fundamental issue because of the assumption that future responses to multiple factors will be stable within groups.

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 & 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 & Williams 2004). Effects of changes in climate or land use might be modelled as changes in the strength of different abiotic (climatic, atmospheric CO₂ 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 & Wright 2003; see also Díaz *et al.* 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 & 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 monopolisation 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 & 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 & 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, Cebrian 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 section 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 defence, litter decomposition, or allelopathy (Pellissier & Souto 1999) can also be affected by microclimate and resource availability (Herms & Mattson 1992, Hartley & 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 & 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 among plants with mycorrhizal association strategies. This results in slow carbon cycling in ericoid and ectomycorrhizal plant species from temperate ecosystems with low pH, versus 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 & 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 & 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 immobilisation (Michelsen et al. 1995, Hättenschwiler & Vitousek 2000); while also facilitating subordinates by herbivore protection. The converse would be expected in nutrient-rich environments.

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 & Chapin 2003; see also Díaz et al. this volume; see Tables 1 & 2 and Table 1 *in* Lavorel & 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 & Garnier 2002; see Table 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, Cebrián et al 1998, Wardle 2002). Association with N₂ 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 & Corbin 2002). 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 & Garnier 2002, Eviner & 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 & Chapin 1993). Such formulations have been proposed for aboveground primary productivity (Chapin 1993 and further modifications by Lavorel & 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:

$$SANPP = \frac{\log_e \left[\sum_{i=1}^{n_{species}} p_i x e^{RGR_i x (t_f - t_o)_i} \right]}{\Delta T}$$

where p_i is the relative contribution of species i to the biomass of the community, RGR_i and $(t_f - t_o)_i$ 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) 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 & 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 & Chapin 2003, Díaz et al. 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 & 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 & Midgley 1995), even once phylogeny has been accounted for (Schwilk & 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).

6. So, are we getting closer to the Holy Grail? Scaling beyond ecosystems

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 & 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. 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 sophistication by addition of new processes. Examples include applications to Australian wet sclerophyllous forest (Noble & Gitay 1996), Mediterranean shrublands (Pausas 2003) and of coniferous-dominated forests of northwestern America (Roberts & Betz 1997).

More complex versions of VA, such as the FATE model (Moore & Noble 1990) have been adapted to model landscape-fire interactions (LAMOS Grigulis et al. 2005; FATELAND, Pausas & 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 & Stafford Smith 2003).

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 & 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 behaviour is, in turn, determined by basic physiological constraints. DGVMs can be used with some confidence to predict the broad-scale behaviour 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. this volume). Plant functional classification is central to all current approaches to modelling 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 modelling of the response to both disturbance and of migration. The IPCD approach (see Section 3) could provide a generic framework for modelling 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 & Higgins, 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 behaviour 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. 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 Section 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 modelling 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 & 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 & Roderick (2002a, 2002b) 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 CO₂. 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 modelling the carbon cycle at continental scales (Berry & 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. this volume).

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 & Foley 1995; Grassl 2000;

Joussaume & 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 & Webb 1998; Kohfeld & 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 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.

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 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 modelling 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 recognise 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. this volume), biodiversity experiments (Hooper et al. 2005, Naeem et al. this volume) 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 emphasise the importance of classifying plants according to well-defined, readily observable and usually continuous plant traits with known responses to particular environmental factors (CO₂ 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 modelling.

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Table 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 'defence' against herbivores and pathogens (i.e. 'biological filters'), and (3) plant effects on biogeochemical cycles and disturbance regimes

See also Chapin *et al.* (1993a), 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 CO₂ 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
<u>Whole-plant traits</u>								
Growth form	*	*	*	*	*	*	*	*
Life form	*	*	*	*	*		*	*
Plant height	*	*	*	*	*	*	*	*
Clonality	*	?	*	*	*			?
Spinescence	*	?			*	*		?
Flammability		?			*	?	*	*
<u>Leaf traits</u>								
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	*				*	*		
<u>Stem and below-ground traits</u>								
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	*	*	*	*	*		*	
<u>Regenerative traits</u>								
Dispersal mode				*				
Dispersule shape and size				*				
Seed mass			*	*	*	*		
Resprouting capacity		*	*	*			*	

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

Figure 1 – Examples of soft traits and associated functions

See separate JPEG file