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Progress in Physical Geography 2000; 24; 515

DOI: 10.1177/030913330002400403

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Plant functional types: an alternative to taxonomic plant community description in biogeography?

Jennifer C. Duckworth¹, Martin Kent² and Paul M. Ramsay³

¹Plantlife, 21 Elizabeth Street, London SW1W 9RP, UK

²Department of Geographical Sciences, University of Plymouth, Drake Circus, Plymouth, Devon PL4 8AA, UK

³Department of Biological Sciences, University of Plymouth, Drake Circus, Plymouth, Devon PL4 8AA, UK

Abstract: This article critically reviews the concept of plant functional types as an alternative to the traditional taxonomic species-based approach to plant community description in biogeography and ecology. Originally formulated in the last century, there has been an acceleration in interest in the concept over the last decade. Plant functional types are nonphylogenetic groupings of species that show close similarities in their response to environmental and biotic controls. Functional classifications often cut across taxonomic classifications and may be more meaningful in terms of plant response, in addition to overcoming certain problems associated with the traditional taxonomic species-based approach.

Plant functional types are derived from traits based on species morphology, physiology and/or life history, depending on the aims and scale of the research. Whilst some traits can be measured in the field, others require more detailed laboratory measurement and experimentation. A trade-off exists between the time and efficiency gained from using simple traits and those requiring more elaborate analysis, although certain 'key traits' may act as easily measured surrogates for others.

Practical applications of plant functional types in biogeography and ecology are also reviewed. Plant functional types can aid in the understanding of ecological processes, such as the assembly and stability of communities and succession, and facilitate the detection and prediction of response to environmental change at a range of scales. Despite its potential, the plant functional type approach is probably best viewed as a complementary approach to description using traditional taxonomy.

Keywords: classification, disturbance, environmental change, guild, phylogeny, plant community, response, strategy, trait.

I Introduction

One of the current challenges in biogeography and ecology is to move away from the description of individual cases to general principles and general models (Day *et al.*, 1988; Keddy, 1992a; Shugart, 1997). The concept of plant functional types dates back to the last century, but has recently received renewed attention as a possible framework for predicting ecosystem response to human-induced changes such as global warming (Díaz and Cabido, 1997). This increased interest resulted from the realization that a degree of simplification of traditional taxonomic description of species is necessary if responses to human-induced environmental changes and the processes behind them are to be understood and predictions are to be made. For example, the Global Change and Terrestrial Ecosystems (GCTE) project of the International Geosphere Biosphere Programme (IGBP) recognizes the impossibility of developing models for every ecosystem and species contained within it and advocates the use of functional types to reduce the complexity of the models (Woodward and Cramer, 1996; Gitay and Noble, 1997; McIntyre, Díaz *et al.*, 1999).

The traditional approach to vegetation classification is taxonomic in nature and usually performed at the species level. However, taxonomic approaches are often beset with problems, not least in the application of the species concept. Functional classifications cut across the traditional taxonomic classification of plants, with taxonomically closely related species often showing more marked differences in response to environmental factors than taxonomically unrelated species with similar ecological requirements (Box, 1981; Woodward, 1987; Pugnaire and Valladares, 1999; Weiher *et al.*, 1999).

Plant functional types (PFTs) are nonphylogenetic groupings of species that show close similarities in their resource use and response to environmental and biotic controls (Wilson, 1999). They are thus likely to be more useful than taxonomic groupings in the interpretation of plant response and resource use (Duarte, 1999; Westoby, 1999; Wilson, 1999). However, precise definitions of PFTs vary, with some researchers favouring a definition based primarily on resource use and the guild concept (e.g., Boutin and Keddy, 1993; Wilson, 1999), whilst others prefer a definition based on plant response to disturbance (e.g., Gitay and Noble, 1997). Members of a plant functional type share similar morphological, physiological or life-history traits, with the differences between members within one functional type being smaller than those between types (Smith and Huston, 1989). PFTs could also be a potentially unifying concept for equilibrium and nonequilibrium states, acknowledging that plant communities are structured by both competition and response to disturbance and predation, since several studies have delimited PFTs on the basis of traits related to both resource use and response to perturbation (Fernández Alés *et al.*, 1993; Hills *et al.*, 1994; MacGillivray *et al.*, 1995; Grime, Thompson *et al.*, 1997). Functional groups can be formed at any level of organization and for any sort of function (Körner, 1994), and a hierarchy may be developed of PFTs and the traits therein.

This article critically reviews the concept of PFTs as alternatives to taxonomic plant community description and discusses their use and application in biogeography and plant ecology. Having defined PFTs and considered the problems in their delimitation, the review focuses on two specific issues that are of particular relevance:

- 1) The use of PFTs in the understanding of plant community and ecosystem processes.
- 2) How PFTs may provide a pragmatic and sensitive means of detecting, assessing and predicting environmental change.

Attention is also paid to practical issues, particularly with regards to the selection of traits, their ease of use and efficiency as functional descriptors. The relationships between these various components are shown in Figure 1.

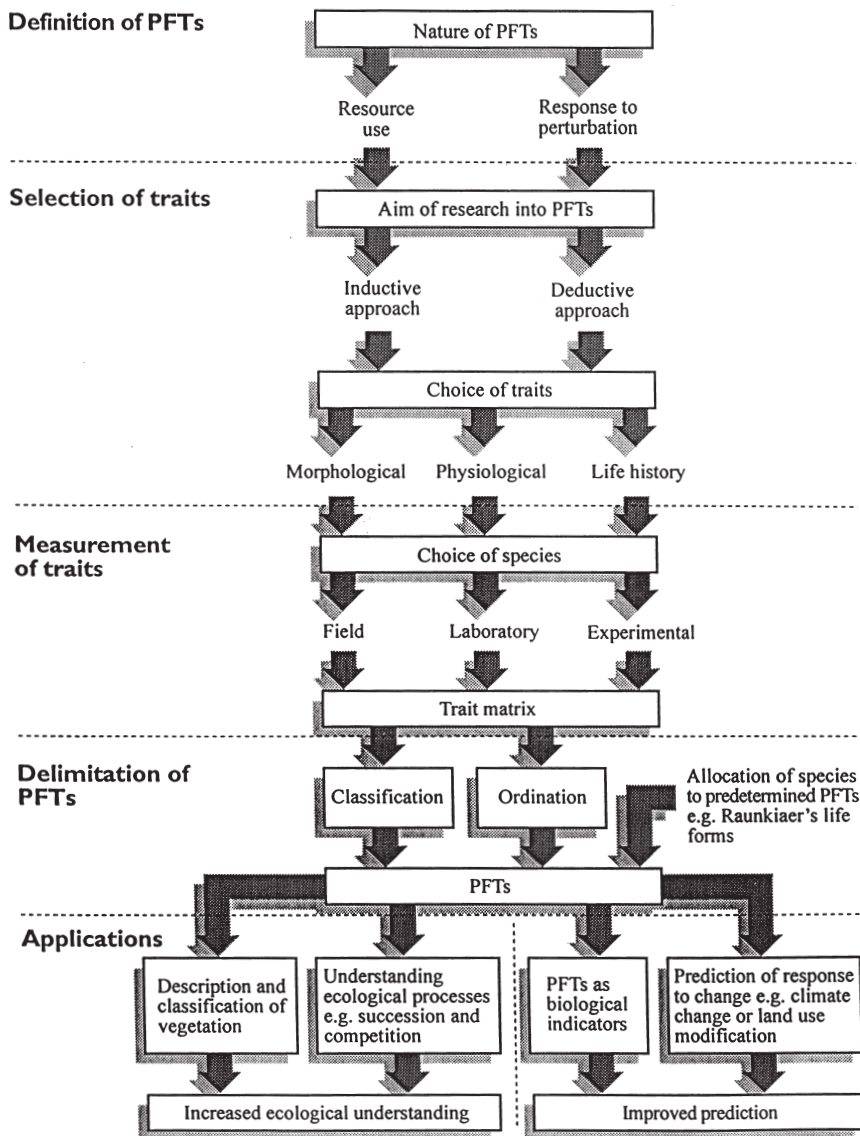


Figure 1 The application of plant functional types (PFTs) in ecology and biogeography

II The concept of plant functional types

1 The history of PFTs

The concept of plant functional types has a long history, which is summarized in Table 1. Von Humboldt (1806) offered the first widely recognized classification of physiognomic plant types following his travels in South America. Grisebach (1872) described 60 vegetative forms and attempted to show their correlation with the climate in which they were found. Later, Warming (1884; 1909) stressed the ecological significance of plant form, noting that ecological similarities crossed traditional taxonomic divisions, and devised a system which grouped plants together according to functional characteristics.

Table 1 A summary of the development of the plant functional type (PFT) concept

Author	Comments
von Humboldt (1806)	First recognized relationship between plant form and function. Developed classification based on growth form
Grisebach (1872)	Classification of 60 vegetative forms correlated with climate
Warming (1884; 1909)	Classification based on simple life history features (e.g., lifespan and vegetative expansion power)
Schimper (1903)	Recognized convergence between plant form and function, despite taxonomic differences, between vegetation types from geographically different, but climatically similar, areas
Raunkiaer (1907; 1934)	Life-forms system
Kearney and Shantz (1912)	Proposed four basic strategies of plants in arid regions in response to drought
Braun-Blanquet (1928)	Added further detail to the life-forms system
Gimingham (1951)	Growth-forms system which also considered branching of stems
Dansereau (1951)	Classification system based on life-form, morphology, deciduousness and cover
Küchler (1967)	Hierarchical classification, with initial division based on whether plant is woody or herbaceous. Lower-order groups are based on life-forms, leaf characteristics and cover
Mooney and Dunn (1970), Mooney (1974)	Investigation of form–environment relationships in the context of convergent evolution
Hallé <i>et al.</i> (1978)	Models of tree architecture based on the underlying ‘blueprint’ for development rather than morphology at any given moment
Box (1981)	Developed global classification based on structural and phenological attributes in relation to climate
Grime (1974; 1979a; 1979b)	Plant strategy theory and C-S-R system of PFTs
Noble and Slatyer (1980)	‘Vital attributes’ classification of plants on basis of life-history factors in relation to response to disturbance

The most important early system of functional classification was the life-forms system of Raunkiaer (1907; 1934), which is still used today (e.g., McIntyre *et al.*, 1995; Pokarzhevskaya, 1995). The Raunkiaer system is based on a simple morphological characteristic, namely, the position of the perennating buds relative to the ground and assumes that species morphology is closely related to climatic controls (Kent and Coker, 1992). The Raunkiaer system was modified for use in the tropics by Ellenberg and Müller-Dombois (1967) to include greater emphasis on the structure and seasonality of crown foliage and the shoot (Ramsay and Oxley, 1997). Box (1981) significantly expanded the geographical scope of Raunkiaer's work and based groups on both structural and phenological attributes, in relation to climatic factors, such as mean temperature of the warmest and coldest months and annual precipitation.

Systems based on factors in addition to life-form continued to be developed by ecologists and biogeographers. Dansereau (1951) devised a classification based on six sets of criteria: life-form; plant size; cover; function (deciduous or evergreen); leaf size and shape; and leaf texture, whilst Küchler (1967) favoured a hierarchical approach, using groups defined on the basis of life-form, leaf characteristics and cover, following an initial division based on whether the plant is woody or herbaceous.

Mooney and Dunn (1970) considered the dominance of evergreen sclerophyll shrubs and its relationship to environmental factors in Mediterranean-type ecosystems, using a variety of features related to water and carbon capture, as well as those involved in mineral conservation, protection from predation and fire. As an explanation for convergence in plant communities, Mooney (1974) proposed that for any given climate–substrate–successional combination, there is an optimum dominant growth form which, through its influence on local environmental characteristics, limits potentially coexisting growth forms. Joffe *et al.* (1999) provide an up-to-date history and summary of the functional types concept in Mediterranean environments.

The limitations of plant form 'snapshots' led Hallé *et al.* (1978) to introduce ideas of plant architecture, whereby plants are classified according to their 'blueprint for growth', using a modular system based on their form and branching system. They produced a set of 23 architectural models and recognized that many trees from unrelated families showed similar organization. They also emphasized the significance of plasticity, for example, by the repetition of all or part of the growth model in response to disturbance (Tomlinson, 1987). Although this approach has been applied mostly to trees, particularly in the tropics (e.g., Hallé *et al.*, 1978; Tomlinson, 1987), work has also been carried out on herb architecture (e.g., Stuefer and Huber, 1998) and plant root architecture (Fitter, 1987). Puigdefábregas and Pugnaire (1999) also demonstrate the relevance of the architecture concept in arid environments, where it is linked to ideas of rainfall/moisture partitioning.

One of the simplest functional classifications is the division of species into those that are 'structural' and those that are 'interstitial' (Huston, 1994). Structural species, such as trees, provide the physical structure of the environment, which is used by the interstitial species and which are invariably smaller, such as epiphytes and understorey herbs. Structural species have a major influence on the diversity of the interstitial species: in most cases the interstitial organisms would not be present in a given area without the structural organisms (Huston, 1994).

Since the 1970s, increasing emphasis has been placed on plant strategies and life-history attributes as functional descriptors, with strategy defined by Grime *et al.* (1988:

3) as 'a grouping of similar or analogous genetic characteristics which re-occurs widely amongst species or populations and causes them to exhibit similar ecology'. Grime (1974; 1979a; 1979b) developed a classification based on plant strategies in dealing with stress and disturbance. This scheme results in three primary strategies: competitor, stress-tolerant and ruderal (often referred to as C-S-R) and several intermediate strategies, which can be displayed in a triangular ordination diagram (Grime, 1974; 1979a; 1979b; Grime, Thompson *et al.*, 1997). Grime's scheme also separates the adult (established) phase from the seedling (regenerative) phase. Although Grime's work has been criticized in that it does not allow for shifts between above and below-ground competition (Tilman, 1988), Grime's ideas remain fundamental to the development of functional classifications and have been used by other workers (Brzeziecki and Kienast, 1994; Hills *et al.*, 1994), in addition to stimulating the development of other strategy-based classifications (Day *et al.*, 1988; Keddy and MacLellan, 1990; Westoby, 1998).

The system of indicator values of Ellenberg (1988) for central Europe, recently calibrated for use elsewhere (e.g., Ertsen *et al.*, 1998), can also be considered a functional type approach. Species are assigned a score for light, moisture, pH, temperature, continentality, salinity and nutrient status and so can be grouped according to their values for each parameter. Although no formal classification has been produced of species according to their Ellenberg values, the grouping of species into broad groups such as 'moisture lovers' or 'calcicoles' is a natural functional classification (e.g., Thompson *et al.*, 1993; Grime, Hodgson *et al.*, 1997).

More recent resource-based approaches have emerged in arid and semi-arid regions. As an example, in the temperate semi-arid region of the Patagonian steppe, Sala *et al.* (1989) demonstrated that two basic PFTs (grasses and shrubs) differed in their water resource use and they used this to generate a biogeographical model of the distribution of arid PFTs (Sala *et al.*, 1997).

An important related concept is that of the guild, defined by Root (1967: 335) as: 'a group of species that exploit the same class of environmental resources in a similar way'. The use of the term has been subject to debate (Hawkins and MacMahon, 1989; Simberloff and Dayan, 1991; Gitay and Noble, 1997) with the term 'guild' in its strictest sense probably more appropriate for animals, since plants only require a few resources, namely, water, light and nutrients (Grubb, 1977; Simberloff and Dayan, 1991). Although some limit the use of the term guild to resource use in plants (e.g., Gitay and Noble, 1997), the term is often used in a looser sense and is considered by many to be synonymous with PFT (Givinish, 1987; Boutin and Keddy, 1993; Huston, 1994; Kindscher and Wells, 1995; Paruelo and Lauenroth, 1996; Wilson, 1999). Wilson (1999) also separates guilds or PFTs into α (alpha) and β (beta) types with beta types based on distribution according to environmental conditions and alpha types based on resource use (named 'Rootian guilds' after Root (1967), as defined above).

A final interesting point in relation to the history of the concept and present-day approaches is that, although many original approaches were both autecological and synecological, interest over the 1990s has focused more on the community-based synecological approach that is the emphasis of this article. Scholes *et al.* (1997) ask the question of whether there are emergent properties at the community level that are more than just the aggregate behaviours of the individual species. In response, they suggest the following examples: 1) biophysical constraints may lead to natural discontinuities in some environmental response axes; 2) plants alter their local environment and by

doing so may maintain other plants; and 3) interactions between taxa may require or preclude coexistence.

2 Definition

Although several attempts have been made formally to define a PFT, no general consensus has been reached. Some favour an emphasis on morphological characteristics, whilst others favour an emphasis on purely 'functional' characteristics (Box, 1995). Some restrict their definition to response to disturbance or resource use, whilst others take a broader view that a functional group consists of organisms which perform the same user-defined function (MacMahon *et al.*, 1981; Friedel *et al.*, 1988). Indeed, function itself is very difficult to classify (Box, 1995). Since species perform many functions simultaneously, a given group of species may be considered part of one group by a physiologist, but placed into several different groups by a population biologist (Solbrig, 1994).

There is therefore no definitive answer to the question of 'what is a plant functional type?' In many studies, PFTs have been based on a wide range of traits embracing morphology, physiology and life history (Leishman and Westoby, 1992; Fernández Alés *et al.*, 1993; Kindscher and Wells, 1995; Díaz and Cabido, 1997; Rösch *et al.*, 1997; Weiher *et al.*, 1999). The type of functional group defined will thus often depend largely on the objectives and context of the classification (Davis and Heywood, 1963; Solbrig, 1994; Noble and Gitay, 1996).

III The value of a plant functional type approach

Research on biodiversity and biological conservation has focused on individual species (autecology) (e.g., Perring and Farrell, 1983; Dinsdale *et al.*, 1997) or plant communities described in terms of taxonomically defined species assemblages (synecology) (e.g., Ellenberg, 1988; Rodwell, 1991–2000). However, there has been considerable debate over what constitutes a species (World Conservation Monitoring Centre, 1992; Bisby, 1995; Duarte *et al.*, 1995). The species concept varies between taxonomists in different places at different times (Bisby, 1995). For example, in *Flora Europaea* (Tutin *et al.*, 1964–80), species described by Russian botanists using one species concept have in a few cases been listed alongside those described by western European botanists, using a different concept. Taxa assigned as separate species by one author may be named by another as subspecies or varieties within a broader species (Bisby, 1995). In addition, the determination of differences between species may require genetic analysis, which is both time-consuming and destructive.

Perfect taxonomic knowledge of an ecosystem is described by Bahr (1982: 213) as 'a quixotic goal, fraught with spatial, temporal and observational problems'. The use of plant functional types does not, in theory, rely on species identification (Orlóci and Orlóci, 1985; Montalvo *et al.*, 1991). This is particularly important in regions where the flora remains largely unknown, such as the tropics. In many ecosystems, some of the most significant organisms from a functional point of view are those that are most difficult to classify because of a lack of taxonomic knowledge (Bahr, 1982). Hence

attention has tended to be concentrated on specific groups of organisms or else poorly known groups of phylogenetically related species have been grouped together, as if they were one species (Bahr, 1982).

Floristic approaches based on taxonomy do not necessarily recognize that communities from distant but ecologically similar sites may be different in floristic composition but very similar in structure. For example, a comparison of the mountain vegetation of Africa and South America would give major differences if based on taxonomy but considerable similarities if based on form and function. In addition, some taxonomically distant species have convergent forms, perhaps with similar ecological roles and structural positions (May, 1976; Cody, 1991; Díaz *et al.*, 1992; Ramsay and Oxley, 1997). This is confirmed by a recent study by Knox and Palmer (1995), based on mountain plants from tropical Africa. Structurally convergent species, which inhabit different mountains at similar altitudes, were found by DNA analysis to be more related to the structurally dissimilar species living at higher or lower altitudes on the same mountain than to their structural analogues on neighbouring mountains.

In recent years, a need for generalization in biogeography and ecology has been identified (Peters, 1991; Keddy, 1992a; Shugart, 1997) in order both to understand processes and to make predictions in the face of environmental change, although some warn this approach is too simplistic (e.g., Grubb, 1985). The number of taxonomically defined plant species in the world is very large, with over 250 000 species of vascular plants alone estimated to exist (World Conservation Monitoring Centre, 1992). Models based on species taxonomy have limited generality because they may not be applicable elsewhere (Keddy, 1992a). In contrast, a classification based on functional types, which is free from phylogeny, should in theory be applicable to other regions of the world with few modifications (Halloy, 1990).

A major obstacle in studying patterns and processes in plant communities is the large numbers of species that are present, which generate undue complexity (Wimsatt, 1980). Species data are characterized by both redundancy, which is the duplication of variation in the data, and noise, the minor differences of which are of little real interest to the investigator and which may serve to obscure trends (Kent and Coker, 1992). Several computer programs for vegetation analysis such as the classification package TWINSpan (Hill, 1979) and ordination package CANOCO (ter Braak, 1990) have options to downweight the importance of infrequently occurring species in the analysis or make them passive, acknowledging the inherent noise in species data. A major claim of the PFT approach is the elimination of both noise and redundancy, thus simplifying plant community description.

It is important to recognize that although PFTs are free from the taxonomic rigidity of species concepts, they are not entirely free of phylogenetic constraints. Plant species have often been treated as independent data points in the delimitation of PFTs – that is, an attribute carried by a large number of species in a habitat is inferred to be necessary to the conditions of that habitat (Kelly, 1996). However this trait may be present because it was inherited from a previous ancestor and not because it is a present-day ecological function. One way of dealing with the confounding effects of species-relatedness has been to apply a 'phylogenetic correction' (Westoby *et al.*, 1995; Westoby, 1999), although this has been subject to controversy (e.g., Harvey *et al.*, 1995; Westoby, 1999).

IV Approaches to deriving plant functional types

Approaches to recognition of plant functional types are either deductive or inductive (McIntyre, Lavorel *et al.*, 1999). The deductive approach derives functional types following an a priori statement of the importance of particular processes or properties (Gitay and Noble, 1997), whilst the inductive approach derives functional types from measurement of a wide range of descriptive observations or experimental results (Woodward and Cramer, 1996).

The choice of processes used to derive the classification in the deductive approach is determined by personal experience and knowledge, and is considered well suited to process modelling and dynamics (Woodward and Cramer, 1996). An example is the vital attributes approach (Noble and Slatyer, 1980; Noble and Gitay, 1996), in which the attributes selected were considered fundamental to the underlying model seeking to predict community dynamics following recurrent disturbances. Similarly, Bugmann (1996) used a deductive approach to construct a functional classification of temperate and boreal trees based on their response to climatic factors and their feedbacks to the climate system.

Inductive approaches have been widely used (e.g., Díaz *et al.*, 1992; Leishman and Westoby, 1992; Chapin *et al.*, 1996; Condit *et al.*, 1996; Díaz and Cabido, 1997) to construct a classification from a range of attributes often by quantitative analysis of relatively large data sets (Woodward and Cramer, 1996). A problem lies in choosing which attributes to include, since an element of subjectivity is unavoidable (Gitay and Noble, 1997). Although Leishman and Westoby (1992) stress the need to avoid any pre-conception of which traits are the most important, a more pragmatic approach that has been used is to select traits which can be easily observed in the field or determined with simple laboratory analysis (Díaz, Acosta *et al.*, 1992; Díaz and Cabido, 1997; Díaz, Cabido, Zak *et al.* 1999; Díaz Barradas *et al.*, 1999; Weiher *et al.*, 1999).

Some examples of traits that are commonly measured are listed in Table 2, and Weiher *et al.* (1999) have made an initial attempt at deriving a common core list. Whilst some, such as growth form, can be recorded in the field, others such as tolerance to nutrient stress require detailed experimentation or screening (see below), although some information can be gained from the literature (McIntyre, Lavorel *et al.*, 1999; Weiher *et al.*, 1999). Because several traits may covary simultaneously, with this relationship fixed for several species in different ecosystems (Reich *et al.*, 1992), a limited set of traits can often be measured in the knowledge that they vary in a similar manner to others which then need not themselves be measured (Reich, 1993). For example, specific leaf area, which is simple to measure, may be used in place of relative growth rate, which requires more sophisticated measurement techniques (Díaz and Cabido, 1997; Westoby, 1998; 1999).

The delimitation of plant functional types, particularly by inductive means, is often achieved by the multivariate methods of classification and ordination, since the data for traits are usually multidimensional (e.g., García-Mora *et al.*, 1999). Classification is commonly carried out on species based on their traits using a variety of methods, all of which have a similar aim. For example, Zavala-Hurtado *et al.* (1996) used Ward's (1963) method to classify 107 semi-arid Mexican species into 18 groups on the basis of their morphological characteristics, whilst Díaz and Cabido (1997) used TWINSpan (Hill, 1979) to classify 100 species into eight groups on the basis of 23 traits related to

Table 2 Commonly measured traits used in the definition of plant functional types (PFTs) and their modes of measurement

Trait	Method of measurement	Examples ¹
<i>Structural/morphological</i>		
Growth form	Field	Leishman and Westoby (1992), Ramsay and Oxley (1997)
Life-form	Field	Leishman and Westoby (1992), McIntyre <i>et al.</i> (1995)
Canopy height	Field	Hills <i>et al.</i> (1994), Westoby (1998)
Stem diameter	Field	Brzeziecki and Kienast (1994)
Specific leaf area	Simple laboratory analysis	Díaz <i>et al.</i> (1998), Westoby (1998)
Leaf succulence	Field	Díaz and Cabido (1997)
Leaf hairiness/waxiness	Field	Leishman and Westoby (1992), Díaz and Cabido (1997)
Leaf thorniness	Field	Díaz and Cabido (1997)
Leaf inclination	Field	Díaz <i>et al.</i> (1992)
Number of leaves	Field	Hills <i>et al.</i> (1994)
Root system	Field	Leishman and Westoby (1992)
Presence of root storage organs	Field	Díaz <i>et al.</i> (1998)
<i>Physiological</i>		
Relative growth rate	Experimentation ²	Grime, Thompson <i>et al.</i> (1997)
Root/shoot mass ratio	Simple laboratory analysis	Reader (1993)
Photosynthetic pathway	More complex laboratory analysis	Kindscher and Wells (1995), Díaz and Cabido (1997)
Nitrogen fixation	More complex laboratory analysis	Kindscher and Wells (1995)
Drought sensitivity	Experimentation	Brzeziecki and Kienast (1994), MacGillivray <i>et al.</i> (1995)
Tolerance of specific nutrient stress	Experimentation	MacGillivray <i>et al.</i> (1995)
Leaf nutrient contents	More complex laboratory analysis	Hills <i>et al.</i> (1994), Grime, Thompson <i>et al.</i> (1997)
Mycorrhizal status	More complex laboratory analysis	Reader (1993)
Palatability to herbivores	Literature or experimentation	Leishman and Westoby (1992), Díaz and Cabido (1997)
DNA content	More complex laboratory analysis	Grime, Thompson <i>et al.</i> (1997)

<i>Phenological</i>		
Lifespan	Field	Leishman and Westoby (1992), Díaz <i>et al.</i> (1998)
Deciduousness	Field	Box (1995), Díaz and Cabido (1997)
Timing of flowering	Field	Leishman and Westoby (1992)
Shoot phenology	Field	Leishman and Westoby (1992)
<i>Reproductive</i>		
Seed size	Simple laboratory	Díaz <i>et al.</i> (1998)
Seed mass	Simple laboratory	Fernández Alés <i>et al.</i> (1993), Westoby (1998)
Seed number	Field	Díaz and Cabido (1997)
Pollination mode	Field	Kindscher and Wells (1995), Díaz and Cabido (1997)
Dispersal mode	Field	McIntyre <i>et al.</i> (1995), Díaz <i>et al.</i> (1998)
Vegetative reproduction	Field	McIntyre <i>et al.</i> (1995), Díaz and Cabido (1997)

Notes:

¹This list is not exhaustive.

²Specific leaf area can be used as a surrogate for RGR (e.g., Díaz and Cabido, 1997).

morphology, physiology and life history. Although ordination methods are usually used to relate variation in species composition or plant traits to environmental gradients (e.g., Díaz, Acosta *et al.*, 1992; Díaz and Cabido, 1997; Díaz, Cabido, Zak *et al.*, 1999; García-Mora *et al.*, 1999), or to simplify data for several covarying traits to trait complexes (e.g., MacGillivray *et al.*, 1995), they are sometimes used as a means of delimiting PFTs (Fernández Alés *et al.*, 1993; Kindscher and Wells, 1995; Skarpe, 1996; Díaz Barradas *et al.*, 1999).

One approach which has received considerable attention is the Integrated Screening Programme (ISP) – a programme of research relating to herbaceous plants based in northern England, which attempts a formal search for functional types using a series of standardized tests and procedures (Grime *et al.*, 1988; Grime, Hodgson *et al.*, 1997; Grime, Thompson *et al.*, 1997; Grime, Thompson and MacGillivray, 1997). Some tests examine basic features of morphology, physiology and biochemistry at different stages of development, from the seed to the established plant, whilst others measure responses to factors such as nutrient stress tolerance (MacGillivray *et al.*, 1995). A total of 67 traits were measured for 43 species over the period 1987–95 (Grime, Thompson *et al.*, 1997). The species were then classified and ordinated in terms of the measured traits and interpreted in terms of C-S-R strategy theory, with separate analyses carried out for the established and regenerative phases.

The majority of procedures were conducted over a relatively short period of time, under standard conditions, on material of known and consistent genetic origin. This could be criticized, in that the results may not necessarily be translatable into field

situations, although results from the ISP have additionally been interpreted in the context of information derived from field experimentation (Díaz *et al.*, 1994; Thompson *et al.*, 1996). Furthermore, the results are based on a local flora and may not necessarily be applicable elsewhere. A more important problem is the amount of time and effort that was needed to generate results for what is essentially a rather limited number of species. Such a programme, despite being a 'visionary initiative' (Rutherford *et al.*, 1995), could never be carried out for all species.

V The question of scale

The concept of PFTs can be applied at a range of spatial scales, from the plant community, through the ecosystem and landscape, to global scales, with the types of attributes that are important dependent on the scale in question. Although functional classifications based largely on growth form have been found to reflect environmental gradients at the global scale, different sets of traits that explore the interactions between the plant and its biotic and abiotic environments may be required at the landscape and community scale (Thompson *et al.*, 1996; Hobbs, 1997; Lavorel *et al.*, 1997) and may add to understanding at the global scale.

An important question is whether knowledge of PFTs can be successfully extrapolated from a detailed to a broader spatial scale – the concept of 'scaling up' (Grace *et al.*, 1997). Broad-scale comparisons are more likely to reveal important patterns because they capture more functional variance and are likely to be applicable to a wider range of habitats and ecosystems (Duarte *et al.*, 1995). Some attempts to scale up from physiological models to predicting the performance of plants in the field have tended to fail in the past because plants respond to environmental factors in a common fashion at broader scales and because other factors such as life-history traits emerge as important (Duarte *et al.*, 1995). However, results from the ISP (Grime *et al.*, 1988; Grime, Hodgson *et al.*, 1997; Grime, Thompson *et al.*, 1997; Grime, Thompson and MacGillivray, 1997) demonstrate the potential for scaling up. The perspective emerging from the ISP is that, despite the considerable global variety in plant design, evolutionary and ecological specialization in plants is tightly constrained with respect to certain key attributes such as seed size (Hodgson and Mackey, 1986; Grime, Thompson and MacGillivray, 1997). The application of C-S-R plant strategy theory can be scaled up from individual plant to community and regional floras both in Britain and in other parts of western Europe (Hodgson, 1991; Hills *et al.*, 1994; Grime, Thompson and MacGillivray, 1997), although the potential for extrapolation to other areas is less certain. However, Westoby (1998; 1999) doubts the applicability of the theory for other regions and proposes a new strategy system based on the more readily measured traits of leaf area, plant height and seed mass (LHS), which could potentially be applicable worldwide. Weiher *et al.* (1999) lend support to Westoby's ideas in their list of common-core plant traits.

Recognition of a continuous hierarchy or nesting of functional types (Smith *et al.*, 1993; Grime, Hodgson *et al.*, 1997) is important, particularly if responses to environmental change are to be considered. Such a hierarchical classification of PFTs has been proposed by Chapin *et al.* (1996) for arctic tundra species, with higher-order divisions allowing the prediction of vegetation distribution in relation to climate, whilst lower-order subdivisions gave a greater insight into the transient dynamics of vegetation.

Ecosystem functional types are a broader grouping, based on the manner in which plants modify their environment and hence the ecosystems in which they are found, by changing the temporal or spatial nature of the system response (Shugart, 1997). The relationship between plant and ecosystem functional types is not always simple. Species that are quite different at the PFT level might alter ecosystem response in similar ways and can thus be considered similar ecosystem functional types. Vegetation functional types are those areas of the land surface that have similar ecological attributes such as composition in terms of PFTs, phenology or productivity (Scholes *et al.*, 1997). This concept corresponds closely to that of the biome. The life zone model of Holdridge (1947) can be considered a vegetation functional type model, as can the BIOME model of Prentice *et al.* (1992).

VI Plant functional types and biodiversity

In recent years, considerable attention has been paid to the threats to biodiversity resulting from human activity (e.g., Solbrig, 1991; Lamont, 1992; Walker, 1992; Huston, 1994; Mooney, 1997). Most concern has been focused at the species level, because the loss of species is well documented, frequent and irrevocable (Solbrig, 1991). An intimate knowledge of the autecology of all species is theoretically necessary in order to assess the effects of species loss, but is clearly an unachievable goal. One solution is to consider species on a functional basis rather than solely as taxonomic entities (Main, 1992; Walker, 1992; Mooney *et al.*, 1997). Functional approaches to the understanding of biodiversity may be particularly valuable, since they address the sustainability of the ecosystem via interactions between the components and provide a basis for predicting changes when components are modified or lost (Lamont, 1992).

If the key traits of an organism are known, it may be possible to predict the impacts of species invasions and losses on ecosystems (Pyšek *et al.*, 1995; Chapin *et al.*, 1997). The impact of the addition or deletion of a species in an ecosystem also depends on its degree of functional similarity to other species in the community. A functionally similar species will have less effect than if the species has traits that uniquely affect community or ecosystem processes (Mooney *et al.*, 1997).

A good review of the functional role of species diversity in ecosystems is provided by Johnson *et al.* (1996). Of particular relevance is the concept of redundancy – some species may substitute for each other in terms of ecosystem function (Walker, 1992). Because species exhibit unique responses to environmental change (e.g., Huntley, 1991), any change severe enough to cause extinction of one species is unlikely to eliminate all members from a functional group (Walker, 1992). If one species goes extinct, another from the same functional group can take its place and the loss of one species will have less effect if others from the functional group are retained (Lawton and Brown, 1993). Thus, the more species there are in a functional group, the more stable the system is and the less serious the consequences of extinction are likely to be (Walker, 1992; Huston, 1994; Chapin *et al.*, 1997).

VII Plant functional types as a key to understanding plant community processes and vegetation dynamics

Plant functional types, guilds and their traits are useful concepts to aid the understanding of the ecological processes of competition and succession, both of which are fundamental to the nature and structure of plant communities and ecosystems. Variation in relative competitive ability has been proposed to control the species composition of plant communities (Gaudet and Keddy, 1988; Wilson and Tilman, 1995). Plant traits are important in determining and predicting an individual's competitive ability (e.g., Grime, 1979b; Gaudet and Keddy, 1988; Tilman, 1988). Although it has not been ascertained which traits confer competitive advantage on to a species (Rösch *et al.*, 1997), one of the key traits correlated with competitive ability is maximum growth rate (Grime, 1979b; Grace, 1991).

1 Community structure and assembly rules

Assembly rules provide a means of being able to predict the future state of communities (Keddy, 1992b; Belyea and Lancaster, 1999). An understanding of assembly rules enables the prediction of which subset of a region's species pool, given its traits, will occur in a particular habitat (Diamond, 1975; Drake, 1990; Keddy, 1992b; Belyea and Lancaster, 1999). Because the approach is based on traits and environments, answers should be applicable to systems with very different taxonomic composition (Keddy, 1992b). A related concept is that of response rules, which specify how species composition will respond when an environmental factor is changed, for example, in response to fire or grazing (Keddy, 1992b).

Taxonomic approaches operating at the species level are not necessarily the best starting point for assembly and response rules (Keddy, 1992b). Prediction of which functional groups will be present will be easier than which species will be present within a functional group (Keddy, 1992b). If prediction is carried out at the 'coarser' scale of functional groups, it may then be possible to refine this for fine-scale prediction within the functional groups themselves (Keddy, 1992b). Studies using the functional group approach (usually referred to as 'guild' in this case) are therefore increasingly used in this predictive aspect of plant community ecology (Cody, 1986; Givinish, 1987; Day *et al.*, 1988; Wilson and Watkins, 1994; Weiher and Keddy, 1995a; Wilson and Whittaker, 1995). A fundamental tenet is that competition will be stronger within the guilds than between guilds (Hawkins and MacMahon, 1989; Simberloff and Dayan, 1991; Wilson and Roxburgh, 1994).

The environment can be considered to act as a filter, in preventing the establishment of species lacking a specific combination of traits. The species which comprise the community are those which survive the filter (Keddy, 1992b). Assembly rules specify which particular subset of traits and therefore species possessing the traits will be filtered out. Such filters operate at a range of scales. Woodward and Diament (1991) consider climate, disturbance and productivity as successive filters on a global scale, whilst Box (1981) used information about the environmental conditions tolerated by different growth forms as a preliminary filter. The members of the remaining subset were then ranked according to their relative competitive abilities, which left a second,

smaller subset of potential dominant PFTs (Box, 1995). On a regional scale, Díaz *et al.* (1998) investigated the relationship between plant functional traits and filters, whilst the work of Van der Valk (1981), who predicted species composition after a specified change in water level, used filters at a more local scale.

Although Wilson and Watkins (1994: 598) state that 'Because of the limited mobility of plants, it seems likely that assembly rules for plants will operate mainly at a very local spatial scale, . . . and be generally inoperative, or at least not discernible, at greater spatial scales', evidence exists to suggest they also operate at greater spatial scales (e.g., Drake, 1990; Smith *et al.*, 1993; Díaz *et al.*, 1998; Weiher *et al.*, 1998; Belyea and Lancaster, 1999).

The concepts of assembly and response rules have not been free of controversy. The questions of how they operate (Wilson and Roxburgh, 1994; Wilson and Watkins, 1994; Weiher and Keddy, 1995b; Belyea and Lancaster, 1999) and whether they even exist at all (Drake, 1990; Wilson, 1994; Weiher and Keddy, 1995b) have been the subject of intense debate, centred on whether communities can be proven to be structured by more than chance (Drake, 1990; Smith *et al.*, 1994). Whether they 'exist' or not, assembly rules certainly provide a useful conceptual framework for the understanding of community structure and processes, which can operate at several scales and, being based on traits, can be applied at both the species or functional group level.

2 Plant community succession

Succession, the sequential temporal changes in the relative abundances of the dominant species in a community (Huston and Smith, 1987), is related to the process of community assembly. A review of the main theories of succession is provided by McCook (1994). Competition between individual plants can explain species replacements during succession, involving shifts in the relative competitive ability of different types of plants along environmental gradients (Huston and Smith, 1987). The life history and autecology of species involved in succession are generally accepted to change during the process (Noble and Slatyer, 1980; Huston and Smith, 1987; Prach *et al.*, 1997). The assertion that correlations in life-history traits can explain successional patterns has been acknowledged for a considerable time (e.g., Grime, 1974; Noble and Slatyer, 1980; Huston and Smith, 1987), although there have been virtually no tests of the assertion itself (McCook, 1994). Life-history traits adaptive to different conditions are likely to be inversely correlated (McCook, 1994). Thus, those that are important in early succession are less likely to be important in late succession and *vice versa*.

These correlations have been used by Smith and Huston (1989) to develop a functional classification of plant types, on the basis of plant strategies for light and water use. They interpreted succession in terms of the shifting ecological roles of functional types, which could change as resource conditions changed. For example, functional types that dominate in late succession under xeric conditions may also appear in high light conditions under mesic conditions, where shade tolerance is not critical. However, as light is reduced by increased leaf area during mesic succession, shade tolerance becomes more important. Thus the functional type that was able to dominate in late succession under xeric conditions, because it was the most shade-

tolerant type under those conditions, will be replaced by more shade-tolerant mesophytic types under mesic conditions (Smith and Huston, 1989).

VIII Plant functional types and climate change

GCTE has initiated a research programme to investigate and predict the nature of vegetation responses to future global change (Steffen *et al.*, 1992; McIntyre, Díaz *et al.*, 1999). Plant communities consist of species, each of which will respond individualistically to changes in the environment (Huntley, 1991). Thus research into the impacts of future climate change is usually considered best carried out at the individual species level (e.g., Huntley *et al.*, 1995; Sætersdal and Birks, 1997). However, since it will not be possible to develop models and make predictions for every species, the approach adopted by GCTE has been to use PFTs (Woodward and Cramer, 1996). The PFT approach has therefore been used to assess sensitivity and predict responses to several aspects of climate change, including elevated CO₂ (Díaz, 1995), increased temperature (Díaz and Cabido, 1997), precipitation changes (Condit *et al.*, 1996) and changes in the frequency of extreme events such as drought and frosts (MacGillivray *et al.*, 1995). In addition, a PFT approach allows an easier interface between the different scales of study involved (Hobbs, 1997) and between present and predicted circumstances (Thompson *et al.*, 1996).

There is a recognized relationship between PFTs and climate, particularly at the global or biome scale (e.g., Woodward, 1987; Prentice *et al.*, 1992; Box, 1981; 1996). PFT-based models can be used to simulate vegetation response under different environmental conditions and are therefore appropriate to use in relation to climate change modelling. Several global or biome-scale models have been produced (Prentice *et al.*, 1992; Haxeltine and Prentice, 1996; Steffen *et al.*, 1996; Cramer, 1997; Leemans, 1997).

The application of remote sensing in ecological research is an important recent development (e.g., Matson and Ustin, 1991; Roughgarden *et al.*, 1991; White, 1994; Gamon and Qiu, 1999). Most description of vegetation using remote sensing is based on physiognomic and structural characters rather than floristic composition (Armitage *et al.*, 2000). PFTs thus represent a natural extension of this approach. In the future, remote sensing has the potential to obtain information on vegetation composition at a fine spatial scale and the type of stress that vegetation is experiencing (Wickland, 1991), which will provide valuable information for the prediction of environmental change. An alternative approach for the monitoring of global vegetation is one where the vegetation is classified into broad classes based on canopy structure and dynamics that can be observed by remote sensing (Nemani and Running, 1996). Additional biome variability is then represented through a remote sensing-derived leaf area index map, and direct climate data sets driving an ecosystem model to map net primary production and evapotranspiration. The classification can then be expanded on the basis of climate zones. The resulting vegetation classes correspond to many of the existing global vegetation schemes, but retain the measure of actual vegetation in that the original broad classes were defined by remote sensing (Nemani and Running, 1996).

GIS approaches are becoming increasingly important in ecological research (Johnson, 1990; Rutherford *et al.*, 1995; Van Gardingen *et al.*, 1997; Johnston, 1998; Wadsworth and Treweek, 1999), and may be employed in the investigation of environmental change.

Plant ecological databases such as the ACKDAT database for South Africa (Rutherford *et al.*, 1995), provide a potentially powerful tool for grouping and regrouping species according to different functional frameworks at a regional level, including the derivation of types sensitive to climate change (Rutherford *et al.*, 1995).

Models predicting vegetation change over the coming decades to centuries should consider factors and traits governing rapid responses to climate change (Chapin *et al.*, 1996). For PFTs to be useful in predicting such responses, at least one member of each functional type must be capable of migrating rapidly enough to keep pace with climate change (Chapin *et al.*, 1996). Correlative evidence between sets of traits suggests that traits influencing migratory capacities such as dispersal and seed dormancy are not tightly linked to the traits defining functional types (Chapin *et al.*, 1996; Díaz and Cabido, 1997; Grime, Thompson *et al.*, 1997). Thus it is unlikely that a given PFT will fail to be represented in vegetation following climate change simply because it cannot migrate rapidly enough. The consideration of regenerative strategies allows further refinement of predictions of vegetation response to climate change, although it will vary regionally and be strongly influenced by patterns of land use (Grime, 1993; Díaz and Cabido, 1997).

Palaeoecological records of past vegetation changes provide a valuable resource for the prediction of future changes, with large-scale projects such as the BIOME 6000 project of IGBP (e.g., Prentice and Webb, 1998; Yu *et al.*, 1998) aiming to reconstruct palaeovegetation records for 6000 BP in a global synthesis. This was not possible in the past, due to the problems involved in combining data from regions with taxonomically different floras, but has been now addressed using PFTs (Prentice and Webb, 1998). In addition, the use of PFTs has provided an ecological basis for the treatment of plants from different regions in a compatible way whilst reducing the number of entities involved (Prentice and Webb, 1998).

PFTs therefore seem a promising tool for predicting the direction and rate of changes in vegetation in the face of climate change, with GIS and remote-sensing applications providing additional assistance. However, some problems are apparent. There is still very limited knowledge about how different plant traits and different combinations of environmental factors will interact in determining whole-plant responses and thus responses to climate change at a higher scale of organization (Díaz and Cabido, 1997). In addition, there exists uncertainty about the feedbacks which are likely to arise at the community and ecosystem level such as the mineralization:immobilization balance (Díaz, 1995).

IX Plant functional types as indicators of response to disturbance

A functional classification of plants for predicting the dynamics of plant communities in landscapes subject to regular disturbances needs to be applied to current issues in land management, such as fire and grazing management (Noble and Gitay, 1996; McIntyre, Díaz *et al.*, 1999). Knowledge of traits related to life history, seed biology, phenology and vegetative ecology is important for models of vegetation dynamics (Leishman and Westoby, 1992), both in relation to climate change, as mentioned above, and in relation to disturbance. Disturbance is classified by Grime (1979b: 39) as 'the total or partial destruction of plant biomass that arises from the activities of herbivores,

pathogens or man and from phenomena such as wind damage, frosting, drought, soil erosion and fire', with those species with short life-cycles and high potential growth rates producing many small seeds being favoured under these conditions.

One of the traits most frequently used to classify species according to their response to disturbance is growth form (Noy-Meir *et al.*, 1989; McIntyre *et al.*, 1995). Other approaches for classification according to species' responses to disturbance are the vital attributes model (Noble and Slatyer, 1980; Noble and Gitay, 1996) and the regeneration niche concept of Grubb (1977). McIntyre *et al.* (1995) considered life-form to be the most useful type of trait in characterizing community response to disturbance. They found traits related to regeneration to be relevant only to particular forms of disturbance (in their case, soil disturbance) and to be difficult to interpret ecologically and to be correlated with other attributes. Different disturbances may therefore require different functional classifications (Belsky, 1992; McIntyre, Lavorel *et al.*, 1995; McIntyre, Díaz *et al.*, 1999).

Grazing can be considered a less intense but more continuous form of disturbance (Fernández Alés *et al.*, 1993; Landsberg *et al.*, 1999; Lavorel *et al.*, 1999). Díaz *et al.* (1992) investigated the responses of grassland vegetation to disturbance resulting from grazing, using a classification based on morphological attributes of the species and their modes of response. Photosynthetic structures became progressively smaller and biomass became concentrated towards the ground as disturbance intensity increased. Plant species were found either to have adaptations to evade herbivory, or had high morphological variability in morphs growing under different grazing intensities. Other studies have investigated responses to grazing in terms of changes in the representation of different life-form groups (McIntyre, Lavorel *et al.*, 1995; Pettit *et al.*, 1995; Hadar *et al.*, 1999; Landsberg *et al.*, 1999; Lavorel *et al.*, 1999; McIntyre, Lavorel *et al.*, 1999).

In some ways fire can be viewed as analagous to a herbivore that consumes fuel through grazing, but those traits which reduce herbivory often promote fires via increased flammability (Bond and van Wilgen, 1996; Pausas, 1999). A number of traits contribute to fire survival, such as thick bark, crown architecture and bud protection (e.g., Starker, 1934), and many species characteristic of fire-prone vegetation have the ability to resprout vegetatively from protected buds. However, this ability appears to exact an energetic cost (Pate *et al.*, 1990) and burned areas are often dominated by species lacking this trait (Bond and van Wilgen, 1996). Fire mortality is offset by higher reproduction and faster growth in these species and they have their own characteristic sets of traits related to competition for open space. The relative abundance of species belonging to these broad functional groups ('sprouters' and 'nonsprouters') has been related to fire regime (Keeley and Zedler, 1978; Specht, 1981). This has been further refined by adding emphasis to the nature and location of the regenerating tissues (Gill, 1981) or whether plants are fire recruiters, with reproduction stimulated by fire, or not (Bond and van Wilgen, 1996). Modelling also has a role to play. Pausas (1999) used four functional types based on regeneration and growth attributes to derive two simulation models to predict fire response in Mediterranean shrublands.

PFTs have been used to predict vegetation response to fire using 'vital attributes' according to fire interval (e.g., Nobel and Slatyer, 1980), fire intensity and season (e.g., Bond and van Wilgen, 1996; Bond, 1997). Fire-prone vegetation has so far received most attention in terms of these vital attributes, owing to its evident nonequilibrium

disturbance regime, but there is an opportunity to develop these models further by incorporating competitive species interactions between fire events. Since fire-prone vegetation responds to the fire regime, which is related to broad-scale climate patterns, PFTs may represent a unifying concept linking fire ecology with climate change.

X Plant functional types and ecotoxicology

Ecotoxicology is concerned with the effects of pollutants on ecosystems (Brouwer *et al.*, 1990; Moriarty, 1993; Romble and Moltmann, 1995; Newman, 1998). Although a single species approach to monitoring the effects of pollutants has been advocated by some (e.g., Moriarty, 1993), it may not be possible to find a single specific indicator for each known or unexpected polluting agent (Kovács, 1992). In addition, different ecotypes of a species may have evolved which have differing degrees of tolerance to pollutants (e.g., Bradshaw and McNeilly, 1981). Biomonitoring of pollutants may therefore be better carried out at the community level, where a multispecies response will be exhibited (Attrill and Depledge, 1997). However, taxonomic investigations at the community level may be unduly complex and require the identification of difficult taxa. An approach based on PFTs simplifies the system and enables the consideration of the effects and interactions between species at different levels of organization. If toxic substances concentrate in a resource that is shared by a functional unit, the entire group may come under stress, affecting the ecosystem processes being performed (Levin *et al.*, 1984). In addition, the effects will transfer to consumers; for example, if a toxin concentrates in the sap, it will affect sap-feeding herbivores. A classic example of the application of PFTs in ecotoxicology is the use of epiphytic and epilithic lichens, which are sensitive to pollutants such as SO_2 , in the monitoring of air pollution (e.g., Hawksworth and Rose, 1970). Functional groups of lichens have been recognized and their distribution mapped in zones for England and Wales, so that the presence of a member of a given functional group can be interpreted in terms of levels of pollutants (Hawksworth and Rose, 1970).

XI Conclusions

This article has introduced the concept of PFTs and reviewed their application at a range of scales. The potential relevance and application of PFTs to biogeographic research are considerable. However, biogeographers have been slow to become involved in the new directions of research into PFTs that have developed in the 1990s and should give greater consideration to the concept and its application.

A summary of the uses of PFTs and the procedures involved in their delimitation is given in Figure 1. Future applications of PFTs and directions of research into them are potentially wide ranging and include:

- 1) The use of PFTs in the prediction of vegetation response to environmental change involving more explicit links to remote sensing and GIS.
- 2) The use of PFTs in the detailed study of transition zones, within which response to change may first manifest itself.

- 3) The identification of a minimum set of plant functional traits that retain discriminatory power whilst optimizing efficiency in terms of time and resources.

As technologies develop and remote-sensing outputs become available at a finer scale of resolution, it may be possible explicitly to link actual vegetation with functional classifications at narrower scales than is currently possible. This could provide a basis for the dynamic modelling of vegetation change in response to environmental change, and for the linkage of models at different scales. Another approach to the prediction and identification of change is the use of changes in space as a proxy for changes in time (the ergodic hypothesis of Chorley and Kennedy, 1971, and Bennett and Chorley, 1978), particularly along steep environmental gradients (Díaz and Cabido, 1997; Díaz *et al.*, 1998). Community and ecosystem boundaries, as reviewed by Kent *et al.* (1997), are likely to be particularly sensitive to environmental change. Changes in PFTs rather than taxonomically defined species across such boundaries may provide a valuable insight into the underlying processes occurring and a framework for the prediction and monitoring of future change.

An important point to reiterate is that, although conventional taxonomic approaches are fraught with difficulties, PFTs also come with their own particular limitations. In addition to problems associated with the definition of the concept, there are those involved in determining which traits to measure and how to measure them. Some involve considerable time and effort, whilst Friedel *et al.* (1988) warn that data should not be collected at the functional group level until the autecology of a species is well known. In theory, there could be more functional groups than there are species, since each species has a number of different traits (Mooney, 1997), which defeats the objective of simplification. Another problem is how to delimit the groups. In many cases, there will be no clear breaks between different functional types; discrimination between them may be subjective and arbitrary and subject to as many problems and differences of opinion as classification of organisms into species (Huston, 1994). In reality, PFTs form a continuum, with different degrees of generality along this continuum appropriate for answering different ecological questions (Day *et al.*, 1988).

A goal for future research is to identify a minimum set of traits that can usefully describe functional variation and retain maximum discriminatory power, whilst minimizing the time and effort required. The LHS scheme of Westoby (1998; 1999) has already gone some way towards achieving this, although it has yet to be tested on different species in different regions, whilst Hodgson *et al.* (1999) propose a regression model for the allocation of species to C-S-R functional types on the basis of a few, simple predictor variables. One question is whether a useful, universal classification into PFTs can ever be achieved (Noble and Gitay, 1996; Weiher *et al.*, 1999). This is certainly a worthwhile goal, but is unlikely to be achieved in the near future. Although research into PFTs has sometimes been carried out in an integrated, co-ordinated manner, such as that under the GCTE in relation to climate change (e.g., Woodward *et al.*, 1997), most has been carried out on individual, independent basis. Such studies should not be discounted and yield valuable information in themselves, particularly since it may be possible to use results at a later stage to 'scale up' (Duarte *et al.*, 1995).

In conclusion, plant functional types provide a valuable tool for the understanding of ecological and biogeographical processes and the prediction of change. Although they avoid several of the problems associated with taxonomic approaches to vegetation

description, they are not without problems themselves. Heal and Grime (1991) state that taxonomic classifications will have to give way to functional classifications, but this is unlikely to happen in the near future, nor is it necessarily desirable. Perhaps it is more realistic to view PFTs as complementary to species-based approaches to description in plant ecology and biogeography.

Acknowledgements

The authors would like to thank the University of Plymouth for the postdoctoral funding for JCD upon which the research for this article was based. They also wish to thank Jamie Quinn for kindly drawing the figure.

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