A generic plant functional attribute set and grammar for dynamic vegetation description and analysis

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Summary

1. Conventional methods of vegetation description rarely convey the behavioural or response-based information needed to describe effectively the world's vegetation for conservation and management purposes. The information required for these purposes may be derived from a generic set of plant functional attributes (PFAs).
2. A grammar provides a syntactic rule base for generating and comparing individuals as functional models or *modi* based on specific PFA combinations.
3. The method facilitates rapid and uniform assessment of plant response to variation in the physical environment at differing spatial scales independently of species. This is illustrated by local, regional and global case studies.

Key-words: Natural resource survey, rapid biodiversity and habitat assessment, semantic rule set, universal descriptors

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Introduction

Traditional methods of vegetation description are designed primarily to convey static, visual rather than behavioural or response-based information; such descriptors cannot be used to construct coherent models of plant behaviour. Yet a knowledge of plant response to environmental change is fundamental to conserving and managing the world's vegation. Inconsistencies between attribute sets used to arbitrarily define vegetation types, such as 'rain forest' and 'savanna', also inhibit the quantitative assessment of vegetational change along physical environmental gradients.

The efficient use of plants as indicators of habitat and habitat modification requires *a priori*, knowledge of features that best reflect plant response to known environmental determinants. In this respect coherent sets of response-based (functional) attributes are preferable to incoherent or unconnected sets of structural, physiognomic or floristic descriptors that are designed to convey essentially visual impressions of vegetation for descriptive purposes. While the latter are of limited value for dynamic investigations they have the advantage of being relatively few and simple (Dansereau 1957; Fosberg 1967; Küchler 1967). On the other hand, the definition and application of existing functional descriptors such as 'life-form' and 'growth form' remain uncertain and complex (Schimper 1894; Warming 1909; Rübel 1930; Raunkiaer 1934; Adamson 1939; Fosberg 1967; Gimingham 1951; Eriksson & Bremer 1992). This paper attempts to remove these uncertainties by framing recently acquired knowledge about plant behaviour within an explicit context of assumed functional relationships.

LIMITATIONS OF METHODS TO DATE

The need for a generic method to record dynamic features of vegetation is highlighted by the limitations of present-day classification systems that are mostly hybrids of visual-descriptive and functional variables (Dansereau 1957; Fosberg 1967; Eiten 1960, 1978; Küchler 1967; Specht, Roe & Boughton 1974). Development of much earlier, 'response-based' classifications (Schimper 1898; Du Rietz 1931; Raunkiaer 1934) has been hindered by the lack of relevant eco-physiological theory and, until relatively recently, appropriate methods for analysing complex data sets across varying environmental and geographic scales (Box 1981a,b; Woodward 1987; Belbin 1992).

The most successful generic vegetation classification method thus far is the life-form system of Raunkiaer (1934) that is based on a single functional criterion — the position of the perennating bud during the most unfavourable season. Unlike other, more complex systems (Rübel 1930; Du Rietz 1931; Cain 1950) Raunkiaer's elegantly simple life forms correlate moderately well with climate (Raunkiaer 1934; Adamson 1939; Woodward 1987). Raunkiaer compensated for insensitivities in his system by adding growth-form qualifiers, such as epiphyte and liane (cf. Fekete & Szujkó-Lacza 1972). Subsequent extensions

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to Raunkiaer's system have been widely used in western Europe and the Middle East (Braun-Blanquet 1932; Ellenberg & Mueller-Dombois 1967; Mueller-Dombois & Ellenberg 1974; Orshan 1983), but they are impractical in complex tropical vegetation, either because of uncertain functional implications or unwieldy attribute combinations. While other, generic functional approaches based on life-history strategies (Grime 1979; Noble & Slatyer 1980) offer more comprehensive and more specific models of plant behaviour, these are limited to applications where life histories are already known or where operational definitions of functional phenomena, e.g. 'stress' (Grime 1979), are unambiguous.

Recent applications of the term 'functional' are most commonly applied to ecological and evolutionary processes including gene flow, disturbance, nutrient cycling and photosynthesis (Franklin 1988; Körner *et al.* 1989; Martinez 1996). To a lesser degree 'function' is applied to plant adaptive features that tend to be merged with structure or physiognomy although many are associated with periodic, seasonal influences on leaves and on the position of perennating organs (Raunkiaer 1934; Dansereau 1957; Fosberg 1967; Küchler 1967; Orshan 1983). While functional phenomena apply to a 'gene–species–ecosystem' hierarchy, there is increasing debate about the role of species diversity in maintaining ecosystem function and whether or not species designations best distinguish functional groupings (Johnson *et al.* 1996). In this sense the perception of species 'guilds' as functional assemblages (Schimper 1894; Johnson 1981) may need re-examination.

We argue certain attributes, such as leaf size class (commonly used for visual-descriptive purposes), may have little functional meaning when used in isolation from other plant morphological variables; singular attributes may have locally useful correlates with the biophysical environment, but these commonly break down under varying spatial, temporal and environmental scale. For example, the relatively linear correlation between leaf size and mean annual air temperature at regional level becomes non-linear with increasing global scale or where there are major shifts in ambient light–water–nutrient ratios. Possibly for this reason, attempts to reconstruct earlier climates based on paleoobotanical records of leaf size alone (Dolph & Dilcher 1979) failed to produce useful interpretations.

While the use of single, morphological descriptors represents an 'atomized' extreme, the over-simplification of very complex, behavioural phenomena into holistic attributes such as 'r' (pioneer) and 'k' (climax) strategists (MacArthur & Wilson 1967) inevitably submerges important, finer scale information. This is particularly evident in complex habits, such as tropical rain forest where many individuals or species (e.g. of the genera *Aleurites*, *Anisoptera*, *Macaranga*, *Mallotus*) can occur as intermediate or facultative pioneer or climax types depending on local conditions. A lack of awareness of such phenomena can lead to a serious misinterpretation of vegetational dyamics. There is, therefore, a need to construct a useful set of attributes that more efficiently describes vegetation dynamics.

Here we assert that a singular attribute, such as leaf size class, assumes a much greater functional significance when combined with leaf-inclination and other morphological (e.g. dorsiventral) and temporal (e.g. deciduous) descriptors of chlorophyll distribution. This is consistent with the concept of a functionally 'coherent' individual (*sensu* Vogel 1991) where the functional modules that together make up the operational organism can be logically regarded as functional elements. Depending on scale of use, such elements may be aggregated to 'attributes'.

While the selection of such attributes for varying groups of organisms remains a concern for life scientists, a more fundamental ecological issue is the lack of an explicit mechanism for combining such attributes into useful, holistic assemblages or functional entities. We present a minimum set of plant functional attributes to illustrate how such a mechanism can be applied using grammar theory. Although the rationale for attribute selection is important from an ecophysiological viewpoint, it is described elsewhere (Gillison 1981, 1988, unpublished data) and is not relevant to this paper.

Materials and methods

A GENERIC SET OF PLANT FUNCTIONAL ATTRIBUTE DESCRIPTORS AND FUNCTIONAL *MODI*

We have modified an earlier plant functional attribute set (Gillison 1981) that described a plant individual as a two-component, functional model (photosynthetic envelope and vascular support system). To the latter we have added another category of life-form modifiers represented by the above-ground rooting system. The photosynthetic envelope is described according to the most repetitive functional 'leaf' unit using four attribute classes (size, inclination, chlorotype and form). Together these define the spatial and temporal distribution of photosynthetic leaf and stem tissue. The vascular support system is described according to a class of pure Raunkiaerean life forms modifiable by the lianoid form and a class of above-ground rooting systems (Table 1). Following the method of Gillison (1981) a functionally integrated or coherent set of these descriptors for an individual is termed a *modus* (Latin SM II—'Manner or mode of behaviour'). A typical *modal* descriptor for *Eucalyptus populnea* might be:

'no-pe-is-ph'

where

'no' is **No**tophyll leaf size class,
'pe' is **Pe**ndulous leaf inclination,

Table 1. Plant functional attributes classes and elements

Attribute	Class	Element	Description	
PHOTOSYNTHETIC ENVELOPE				
Leaf size	LS	nr	No repeating leaf units	
		pi	Picophyll	$<2\,mm^2$
		le	Leptophyll	2–25
		na	Nanophyll	25–225
		mi	Microphyll	225–2025
		no	Notophyll	2025–4500
		me	Mesophyll	4500–18 200
		pl	Platyphyll	18 200–36 400
		ma	Macrophyll	$36\,400–18\times10^4$
		mg	Megaphyll	$>18\times10^4$
Leaf inclination	LI	ve	Vertical	$30°>$ horizontal
		la	Lateral	$30°\pm$ horizontal
		pe	Pendulous	$30°<$ horizontal
		co	Composite	
Chlorotype	CL	do	Dorsiventral	
		is	Isobilateral or isocentric	
		de	Deciduous	
		ct	Cortic	(photosynthetic stem)
		ac	Achlorophyllous	(without chlorophyll)
Leaf type	LT	ro	Rosulate or rosette	
		so	Solid 3-D	
		su	Succulent	
		pv	Parallel-veined (grass-like)	
		fi	Filicoid (fern-like)	
		ca	Carnivorous	(e.g. *Nepenthes*)
SUPPORTING VASCULAR STRUCTURE				
Life form	LF	ph	Phanerophyte	
		ch	Chamaephyte	
		hc	Hemicryptophyte	
		cr	Cryptophyte	
		th	Therophyte	
		li	Liane	
Root type	RT	ad	Adventitious	
		ae	Aerating	(e.g. pneumatophore)
		ep	Epiphytic	
		hy	Hydrophytic	
		pa	Parasitic	

'is' is **Is**obilateral chlorophyll distribution (as distinct from a bifacial or dorsiventral leaf with chlorophyll mainly on the upper or adaxial surface), and

'ph' is **Ph**anerophyte or woody plant with perennating buds on a vascular support system >1·5 m tall.

We emphasize that a *modus* describes an individual, not a taxon. A species may be represented by multiple *modi* and a *modus* may represent multiple species: i.e. the species–*modus* transformation is a many-to-many mapping. Unlike floristic descriptors, the *modal* system is therefore sensitive to genecotypic variability. It makes no assumptions about guild structures (cf. Schimper 1894; Johnson 1981) or life-history strategies (Grime 1979; Noble & Slatyer 1980) but presents instead, a functional 'snapshot' of an individual via a minimum attribute set that reflects core attributes of growth, physiology and survival. The *modus* provides
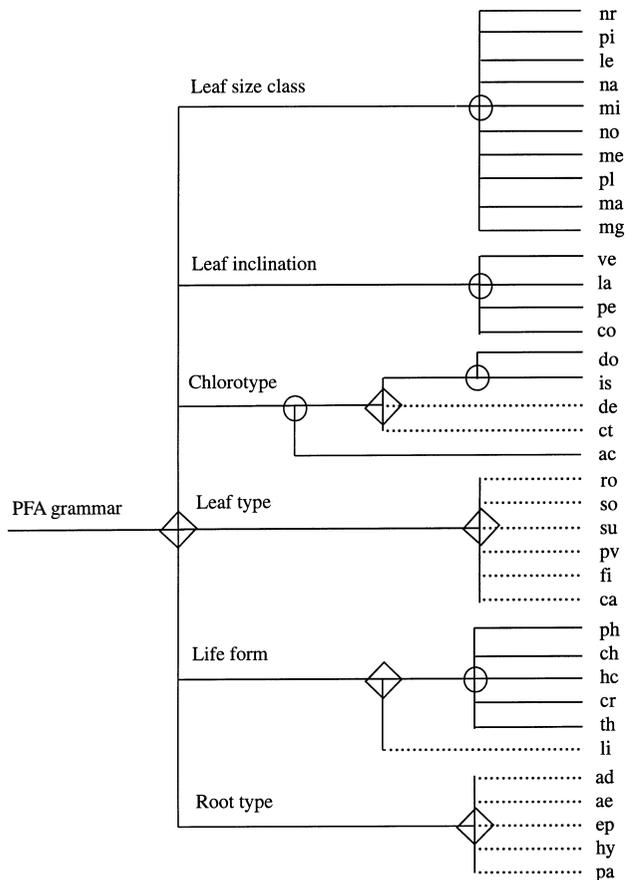
a unique structure for defining functional models as integrated systems based on functional morphology rather than on trophic groups or life-history strategies or size (Grime 1979; Noble & Slatyer 1980; Johnson 1981; Bahr 1982; Vogel 1991).

As presented, the system avoids the pitfalls of using discrete or unconnected, singular variables such as leaf size class and thereby reduces ambiguity in functional interpretation. Survey data acquired to date using this method correspond more closely with physical environment and the distribution of some animal biota than either floristics or broad vegetation structure (Fox & Fox 1981; Nix & Gillison 1985; A. N. Gillison, unpublished data). A pro forma structure and an introductory rationale for the selection of plant functional attributes are available (Gillison 1981, 1988). The plant functional attribute (PFA) set has been iteratively developed over a wide range of global sites and we emphasize it represents a minimum or

core attribute set to which other life-history attributes can be attached where required and where available.

A SYNTACTIC, RULE-BASED GRAMMAR

Until now, our inability to utilize the combinatorial information contained within a *modus* has restricted the labelling of data either to unconnected *modal* elements or, as with taxa, to a unique numeric identifier for each *modus*. We are now able to access combinatorial information via a grammar (Chomsky 1956) that defines precisely how plant functional attributes and elements may be coupled. Using the grammar, we also describe a quantitative method for analysing differences between *modi*. These differences are conveyed via multidimensional scaling (Belbin 1992) and minimum spanning trees (MSTs, Prim 1957). Case sudies at three biogeographic scales illustrate how an MST can be used to display *modal* similarities within and between sites.

The PFA grammar (Fig. 1) represented graphically and in Backus-Naur form (Wirth 1977) provides an unambiguous definition of attribute combinations that constitute valid *modi*. The use of a grammar allows us to develop syntactic rules that enforce constructs such as mutual exclusivity between attributes. We have compiled a table of transformations weighted subjectively (Table 2) according to generalized levels of derived and primitive characteristics (cf. Davis & Heywood 1963) and our own intuitive approximation of functional 'distance'. The Table prescribes subjectively weighted values to attribute transformations based on the relative difference between *modal* states (analogous to character-weighting of operational taxonomic units or OTUs in numerical taxonomy). This facilitates quantitative comparison between *modi*. Rules exist to substitute one attribute for another, to create and to extinguish attributes. For example, while we allocate a transformation value of '1' between adjacent leaf size classes, creation or extinction of adventitious rooting has a value of '3'. Transition rules for some classes, such as *leaf size*, require multiple substitutions to transit to non-adjacent forms. For example a translation from nano to noto involves a nano → micro substitution followed by a micro → noto substitution. A set of 46 rules provides sufficient richness to transform any *modus* into any other *modus* using a series of transformations. The distance between two *modi*, A and B, is thus defined as the minimum cumulative value required to 'transform' A into B. This method defines a Levenshtein distance metric (Sankoff & Kruskal 1983) over the set of all possible *modi*. The transformation table contains no zero-weight transformations, no asymmetrically weighted transformations, and consequently the distances satisfy the formal properties of a metric, that is:

(a) positive definitiveness: $d(a,b)$ is a positive real number for $a \neq b$ and is zero for $a = b$
(b) symmetry: $d(a,b) = d(b,a)$
(c) triangle inequality: $d(a,c)$ $d(a,b) + d(b,c)$.

Because our primary concern is to develop a metric, we assume equi-directional transformation values between all *modal* elements (i.e. we define all transformation rules symmetrically, such that: $A \rightarrow B = B \rightarrow A$). For asymmetric transformations ($A \rightarrow B \neq B \rightarrow A$) the inter-*modal* distances cease to be a metric as they violate the symmetry property and thus require different analytical methods.

Applications at varying scales

Figure 2 shows a minimum spanning tree generated from the distance matrix for a sub-set of *modi* from within a single 40×5 m plot in a north Queensland rain forest. The distance between *modus* 'A' (no-pe-do-ph-li) and *modus* 'K' (no-ve-do-de-ct-ph-ad) is calculated by summing the weighted values of the

X   = LS LI CL LT LF RT
LS = nr |pi |le |na |mi |no |me |pl |ma |mg
LI = ve |la |pe |co
CL = ((do |is) [de] [ct]) |ac
LT = [ro] [so] [su] [pv] [fi] [ca]
LF = (ph |ch |hc |cr |th) |li
RT = [ad] [ae] [ep] [hy] [pa]

◇ AND: follow all paths
○ Or: follow exactly one path
...... OPT: subpath is optional

Fig. 1. Grammar structure for 36 plant functional elements contained within six attribute classes (Table 1). The Backus–Naur notation (Wirth 1977) is displayed at lower left.

required transformations:

no-pe-do-ph-li	pe → la	:2
no-la-do-ph-li	la → ve	:2
no-ve-do-ph-li	→ de	:3
no-ve-do-de-ph-li	→ ct	:3
no-ve-do-de-ct-ph-li	li →	:3
no-ve-do-de-ct-ph-ad	→ ad	:3
	Total	16

The availability of an inter-*modal* distance metric permits analysis of vegetation assemblages using standard quantitative analysis methods. A multidimensional generalization of the Wald–Wolfowitz two-sample test (Friedman & Rafsky 1979) in conjunction with multidimensional scaling, has proven useful for comparing and visualizing vegetation assemblages. The Wald–Wolfowitz test is used to estimate the probability that two samples originate from the same population. A complete inter-site association matrix of variance values can be compiled for a given set of PFA-sampled sites. Figures 2 and 3 give examples of two such sets at differing geographic scales.

Although the language defined by the grammar contains all syntactically or logically valid *modi*, not all such models are realizable in practice, owing to physiological and architectural constraints. For example, the syntactically valid *modus* mega-vertic-solido-epi-hydro-cham is mechanically non-feasible. This is analogous to other combinatorial models such as those for shell spirals (Raup 1966) where only a small subset of geometrically possible models has been

observed. A supplementary semantic rule-set under development will help generate a more realistic 'periodic table' of observed and potential *modi* (cf. Thomas & Reif 1993). While it is important for ecological applications to understand the functional limitations of potential *modi*, for most computing purposes the potential number of combinations is largely irrelevant.

Implications for studies of vegetation dynamics and conservation management

The relevance of the method to studies of vegetation dynamics is illustrated in Fig. 3 where the MST corresponds closely with both a readily identifiable vegetational sequence and a rainfall seasonality gradient. As portrayed in Figs 3 and 4, comparisons can be made between geographically variable and taxonomically different *modal* assemblages to measure congruence among functional attribute sets. Such measures are potentially useful in refining broad-scale, spatial models of on-ground performance of species or genotypes that have been derived by matching known performance profiles with regional homoclimes (Box 1981a; Booth 1990). Congruence of this kind may be useful for evaluating vicariant patterns of functional characeristics between sets of individuals or taxa within and between continents.

The rule-set contained in our grammar, together with the subjective weightings between transition states, are clearly approximative and greatly simplified. Nonetheless they provide for the first time, a sufficiently robust mechanism for generating a finite framework for analysing plant performance in terms of integrated sets of readily observable and arguably functional variables. The method allows questions about plant adaptation to the physical environment to be formulated in a way that avoids sole reliance on discrete variables (e.g. leaf size). A better understanding of the adaptive role of PFAs may thus be achieved by seeking reasons for the occurrence or non-occurrence of certain attribute combinations in nature.

The system has a number of advantages for field operations. First, the PFA set has been used in Australia, by observers with minimal training, to obtain highly repeatable observations. [Preliminary trials in Indonesia and Latin America by observers for whom English is not a first language have proved encouraging. More formal testing is underway.] Second, while floristic coding of *modal* assemblages is ultimately desirable, there is no need *a priori* for species identification in order to conduct an analysis of functional components. Third, it is argued elsewhere (Gillison 1988) that PFAs represent key adaptive features that can be used for general purposes and this reduces the need for detailed knowledge of life-history attributes. Fourth, because the system is generic, PFAs can be applied to any assemblage of vascular plants (although the set described is intended

Table 2. Subjectively weighted transformation values between *modal* elements listed in Table 1

Non-repeating leaf unit		Leaf size class		Leaf inclination		Chlorotype	
nr ↔ pi	:4	pi ↔ le	:1	ve ↔ la	:2	ac ↔ do	:6
nr ↔ le	:4	le ↔ na	:1	la ↔ pe	:2	ac ↔ is	:6
nr ↔ na	:4	na ↔ mi	:1	co ↔ ve	:2		
nr ↔ mi	:4	mi ↔ no	:1	co ↔ la	:2	do ↔ is	:3
nr ↔ no	:4	no ↔ me	:1	co ↔ pe	:2	de ↔ {}	:3
nr ↔ me	:4	me ↔ pl	:1			ct ↔ {}	:3
nr ↔ pl	:4	pl ↔ ma	:1				
nr ↔ ma	:4	ma ↔ mg	:1				
nr ↔ mg	:4						

Leaf type		Raunkiaer life form		Root type	
ro ↔ {}	:3	ph ↔ ch	:1	ad ↔ {}	:3
so ↔ {}	:3	ch ↔ hc	:1	ae ↔ {}	:4
su ↔ {}	:3	hc ↔ cr	:1	ep ↔ {}	:3
pv ↔ {}	:3	hy ↔ {}	:1	pa ↔ {}	:6
fi ↔ {}	:3	th ↔ ph	:1		
ca ↔ {}	:5	th ↔ ch	:1		
		th ↔ hc	:1		
		th ↔ cr	:1		
		li ↔ {}	:3		

{} Denotes no PFA symbol.

mostly for land-based plants). While the method can be used to illustrate and compare successional dynamics within and between geographically remote sites, we emphasize our primary aim here is to illustrate the potential use of the method for comparing organism response to environmental change. Provided basic functional attribute sets are available, the system could be applied equally to birds or bacteria. A number of other advantages arise specifically from the use of the grammar. For example, distance matrices are well suited to exploratory data analyses (Raup 1966; Belbin 1992) and illegal PFA combinations can be detected during the compilation of data. For studies of vegetation dynamics, the grammar can be used to
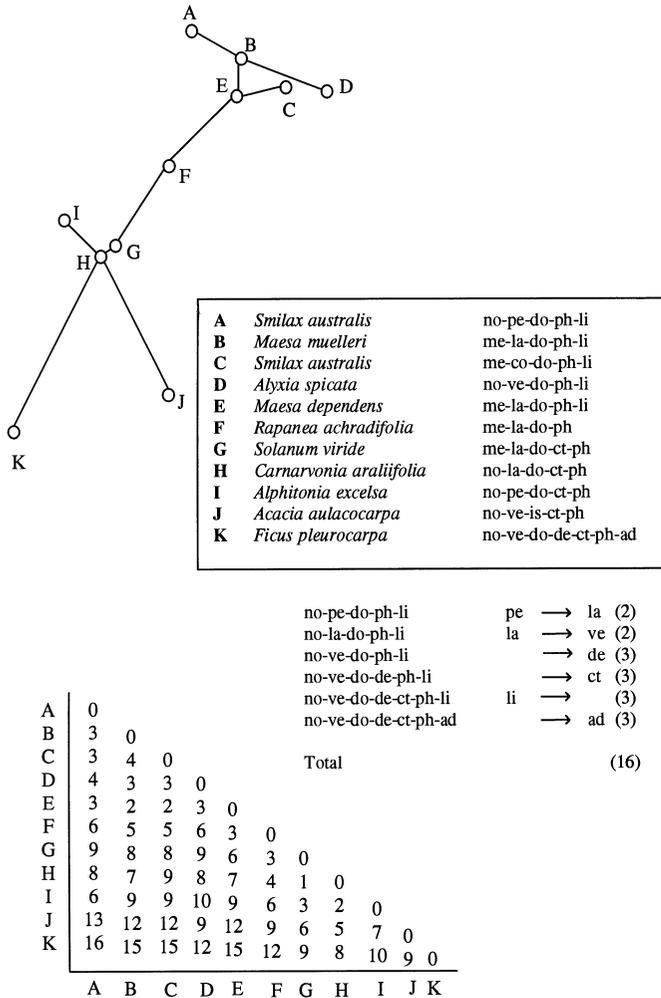

Fig. 3. Minimum spanning tree of vegetated sites along rainfall seasonality and disturbance gradients in the Lamb Range (North Queensland, Australia) (Table 3). (a) A Kauri pine (*Agathis atropurpurea*) dominated, cool-moist rain forest links with (b) a warmer site without *A. atropurpurea*; (c) a cool-moist, sclerophyll, eucalypt-dominated forest; (d) a disturbed wet sclerophyll forest with eucalypts and successional rain-forest elements; (e) a highly-disturbed, early successional rain forest; (f) a tall open forest dominated by eucalypts, subject to frequent wildfire. The overlap of plant functional *modi* along the tree indicates a graded response to both seasonality and fire history. Distances are computed using a multidimensional generalization of the Wald–Wolfowitz (Friedman & Rafsky 1979) two-sample test. Node positions are determined as for Fig. 2.

Fig. 2. Minimum spanning tree (Prim 1957) generated from the distance matrix for all plant functional *modi* within one rain-forested locality in the Lamb Range, far north Queensland, Australia. The figure shows infra-specific variability in functional elements within *Smilax australis* and indicates how a liane cluster (li) is distinguished from non-lianoid woody plants with and without photosynthetic stem tissue (ct) and adventitious rooting (ad). Inter-*modal* distances are computed from the cumulative, values of transformations required to translate between *modi* using a table of weighted transformation values (Table 2). MST node positions were determined using a simulated annealing optimization method (Kirkpatrick, Gelatt & Vecchi 1983) which attempts to minimize stress between the distance matrix and the 2-d node distances. The minimum spanning tree (Prim 1957) links shown were given twice the priority of the other links for optimization.
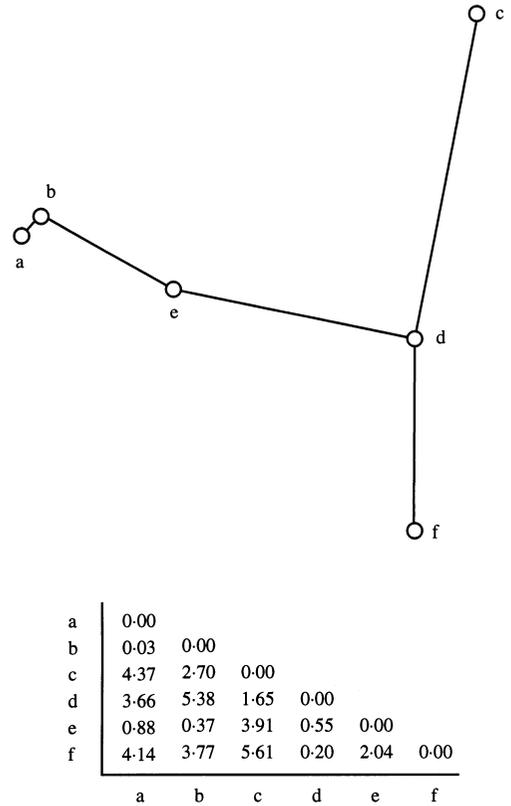
explore functional differences along successional pathways and to monitor, and thus help predict vegetation response to environmental impact.

Although the grammar deals with phenetic rather than phylogenetic variables, some cladistic algorithms may be applied to *modal* data for exploratory purposes. More direct cladistic analysis may be appropriate where there is evidence for canalization and evolutionary direction of specific attribute sets (Farris 1972; Swofford 1992). When coupled via the grammar as *modi*, PFAs may indicate genecotypic variability among plant assemblages that is otherwise undetectable by functional elements alone, or by floristics or by vegetation structure or physiognomy. Recent use of minimum spanning path distances to estimate phylogenetic diversity via the feature diversity of subsets of taxa (Faith 1992,1996) also suggests an analogous use of the PFA grammar for estimating functional richness as a partial measure of plant-based

biological diversity. The addition or subtraction of plant assemblages as functional *modi* to or from a known MST structure may be used to assess representativeness of target areas for conservation management purposes. Recent and as yet unpublished data by A. N. Gillison from tropical forests in Indomalesia and the Western Amazon basin indicate the method can be used to detect vegetation response to different logging prescriptions.

For surveys involving potentially large species data sets, the use of PFAs provides a greatly reduced data matrix. This in turn has implications for generating and manipulating data for global comparisons and for research stations where computing services for data storage and analysis may be very limited. The ecological information latent in increasingly large national and international species-based data sets [e.g. Environmental Resources Information Network (ERIN, Australia); World Conservation Monitoring Centre (WCMC, Cambridge, UK); FISHBASE (International Center for Living Aquatic Resources Management, Manila, Philippines)] is severely limited owing to the sole reliance on taxonomic nomenclature. The generation of minimum functional attribute sets provides a basis for cross-referencing species assemblages that can then be subjected to comparative analysis via an appropriate grammar. Low-cost, high-return methods of this kind have the potential to improve greatly the scientific, management and conservation value of data that are otherwise constrained by reliance on species names. Where geographic co-location of data permit, a grammar-based approach makes possible computer-based simulations of interactions between biological, physical environmental and socio-economic data. The need to be able to extrapolate taxonomic and ecological data from surveys is predicated by both the nature and quality of the data and the particular mapping algorithm (cf. Collins & Benning 1996). The spatial mapping software package DOMAIN (Carpenter, Gillison & Winter 1993) has been used recently to generate maps of both target groups of animal and plant species, species richness classes and plant functional groups from an intensive baseline survey in Central Sumatra (Gillison, Liswanti & Arief-Rachman 1996). Such methodology is becoming increasingly relevant in an age that demands a facility to forecast the impact of climate change on the distribution and behaviour of specific groups of organisms.

Acknowledgements

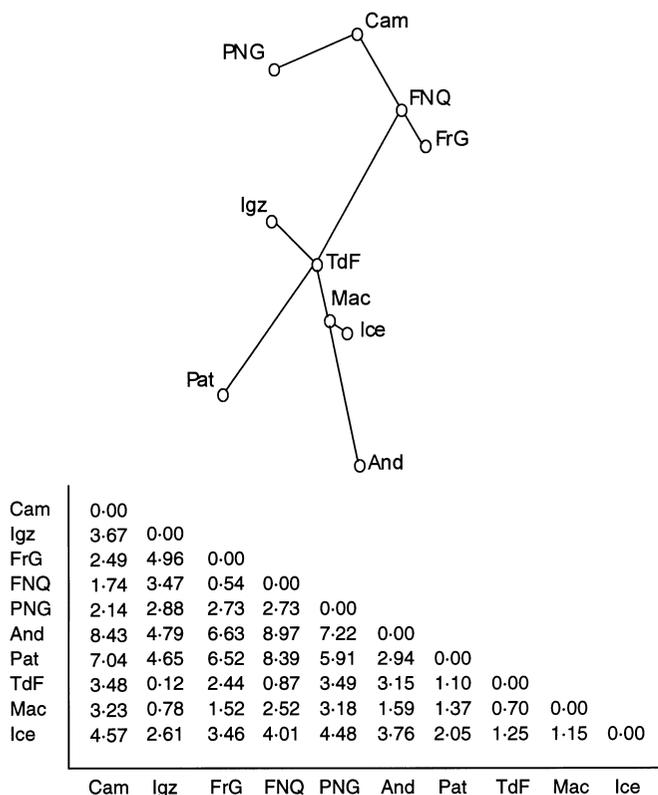| Cam | 0·00 | | | | | | | | | |
Igz	3·67	0·00								
FrG	2·49	4·96	0·00							
FNQ	1·74	3·47	0·54	0·00						
PNG	2·14	2·88	2·73	2·73	0·00					
And	8·43	4·79	6·63	8·97	7·22	0·00				
Pat	7·04	4·65	6·52	8·39	5·91	2·94	0·00			
TdF	3·48	0·12	2·44	0·87	3·49	3·15	1·10	0·00		
Mac	3·23	0·78	1·52	2·52	3·18	1·59	1·37	0·70	0·00	
Ice	4·57	2·61	3·46	4·01	4·48	3·76	2·05	1·25	1·15	0·00
	Cam	Igz	FrG	FNQ	PNG	And	Pat	TdF	Mac	Ice

Fig. 4. Minimum spanning tree of widely differing sites at global scale (Table 4). Linkage cluster PNG-Cam-FNQ-FrG groups similar plant functional *modi* in tropical, maritime, megatherm, lowland sites; linkage FNQ-TdF-Igz shows a gradation of *modi* from moist-megatherm FNQ (far north Queensland) to moist-microtherm TdF (Tierra del Fuego) to disturbed inland continental, moist mesotherm rain forest Igz (Iguazú); TdF-Pat grades to dry-mesotherm, Patagonian steppe; TdF-Mac-Ice illustrates a gradation from microtherm Fuegian beech forest to more extreme microtherm maritime steppe in closely related environments at sub-polar extremes (Macquarie Island, Sub-Antarctic and Iceland); the last being connected to tropic-alpine Andean steppe in Venezuela. Distances are computed as for Fig. 3. The pattern illustrates functional congruence at global environmental extremes.

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Table 3. Description of sites along a regional climate gradient in far north Queensland

Site no.	Rainfall* seasonality	Minimum air temp (°C)	Vegetation description
(a)	69	8·1	Rain forest dominated by Kauri pine (*Agathis atropurpureum*)
(b)	71	8·4	Rain forest without Kauri pine, numerous lianes, epiphytes
(c)	68	7·8	Recently-regenerating rain forest on disturbed site
(d)	77	8·9	Mixed rain forest and wet sclerophyll (*Eucalyptus grandis*, *E. resinifera*) emergents on disturbed sites
(e)	77	8·9	Drier aspect of wet sclerophyll forest with graminoid understorey and *E. grandis*, *E. resinifera* dominants; infrequent wildfire
(f)	99	10·3	Tall, open forest with graminoid understorey, dominated by *E. citriodora*, *E. crebra*; fired semi-annually

* Coefficient of variation per cent of monthly rainfall.

Table 4. Description of global sites for modal analyses

Site code	Locality	Lat./Long.	Elevn. (m a.s.l.)	Vegetation*
Cam	Campo, Cameroon	02°25'N 10°00'E	20	Megatherm maritime, rain forest
Igz	Iguazú, Argentina	25°39'S 54°35'W	300	Meso-megatherm, rain forest
FrG	Petit Saut, French Guyana	05°04'N 53°03'W	100	Megatherm 'Terra firme' rain forest
FNG	Cairns, N. Queensland, Australia	17°00'S 145°44'E	50	Megatherm, maritime rain forest
PNG	Lihir Island, Papua New Guinea	03°35'S 153°40'E	50	Megatherm, maritime rain forest
And	Cordillera do Merida, Venezuela	08°24'N 71°08'W	3500	Microtherm moist Andean steppe
Pat	Pilcaniyeu, Argentina	41°04'S 70°40'W	1200	Mesotherm dry Patagonian steppe
TdF	Ushuaia NP, Tierra del Fuego (Arg.)	54°48'S 68°20'W	40	Microtherm moist beech forest
MaC	Macquarie Island, Sub-Antarctic	54°30'S 158°56'E	20	Microtherm maritime tundra
Ice	Reykjanes Peninsula, Iceland	63°50'N 22°42'W	10	Microtherm maritime tundra

* All vegetation variously disturbed by logging or grazing or fire. Thermal zones after Schimper (1894).

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