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Journal of Vegetation Science, Vol. 7, No. 3. (Jun., 1996), pp. 309-320.

Stable URL:

http://links.jstor.org/sici?sici=1100-9233%28199606%297%3A3%3C309%3APFTACA%3E2.0.CO%3B2-F

Journal of Vegetation Science is currently published by Opulus Press.

Plant functional types and climate at the global scale

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Abstract. Globally applicable sets of terrestrial plant functional types (PFTs) have been identified as a major need in the development of dynamic global vegetation models for use with global atmospheric models. Global sets of PFTs should represent the world's most important plant types; characterize them through their functional behavior; and provide complete, geographically representative coverage of the world's land areas. Three main schools of thought on PFTs have emerged: (1) a physiological focus on internal function, especially at the level of basic metabolism; (2) an ecological focus on function in relation to plant form and environmental conditions; and (3) a geophysical focus on how plant functions affect the adjacent atmosphere. A structural approach based on pheno-physiognomy permits ready identification of relatively familiar, recognizable plant types. Many of the criteria cited by other approaches also are intimately related to structure and its seasonal changes. An earlier global system of structural-functional PFTs and their climatic relations has been improved, including addition of less well-known plant types, and is briefly described. A more strictly 'functional' approach is proposed, in which major aspects of plant function, initially metabolism and water balance, are used to classify functional types and suggest how these are constrained by climate. Such functional considerations, however, are closely linked to structural manifestations - but also require other functional criteria for more completely functional classifications. A recent global model of potential natural vegetation types suggested ca. 15 major plant types as necessary to cover the world's main terrestrial vegetation patterns. These essential types correspond well with a first-cut set of structural types implied by metabolic considerations.

Keywords: Cold-tolerance type; Form-function relationship; Leaf functional type; Geometabolic type; Minimal PFT set; Pheno-physiognomy; Photosynthetic surface type.

Introduction

Plant functional types (PFTs) are functionally similar plant types which can be used in global ecological modeling. A need for global sets of such PFTs was recognized recently by the International Geosphere-Biosphere Program, especially its core program on Global Change and Terrestrial Ecosystems, in order to make possible the construction of Dynamic Global Vegetation Models (DGVMs) for use with global atmospheric mod-els (e.g. Steffen et al. 1992; Walker 1992; Anon. 1992; cf. Solomon & Shugart 1993; Neilson & Marks 1994; Henderson-Sellers & McDuffie 1995). Function, however, is very difficult to define or classify. Plants change with environmental conditions, along gradients but perhaps also evolutionarily, first through modification of functions such as water economy, metabolism, allocation, and reproductive rate. Some of these functional modifications involve consequent modifications of form, e.g. reduced leaf size in order to control water loss. Other functional patterns and changes, however, are not readily apparent through general structural features, perhaps especially reproductive mechanisms, basic photosynthetic pathways, and response to ambient CO_2 concentrations.

The easiest approach to classification of PFTs may be a structural-functional one, since it permits the use of visible structural attributes as surrogates for functional patterns. Relationships between form and function, in both plants and animals, have been recognized since the time of Alexander von Humboldt. Other approaches, however, include a physiological emphasis, focusing on internal function at the level of basic metabolism, and a geophysical emphasis on how plant functions affect the adjacent atmosphere, interacting with the boundary layer and affecting local and broader-scale water and energy balances. Although criteria for identifying PFTs based on these approaches have generally not been explicitly stated, an attempt was made (Box 1995c) to summarize what appear to be some of the main functional aspects to be considered by each of these approaches.

Some practical criteria for world sets of PFTs, needed for global ecological modeling, can also be suggested:
1. The PFTs should represent the world's most important terrestrial plant types, i.e. major elements in natural (and perhaps some secondary) vegetation and ecosystems.
2. Such plant types must be characterized through their functional behavior and attributes.
3. The set of PFTs should, as a whole, provide complete, geographically representative coverage of the main vegetation types of the world's land areas.

It will also be necessary to quantify the climatic relations of PFTs, since this may greatly facilitate global-scale modeling involving responses to climate change

(cf. Cramer & Leemans 1993). Some global sets of plant/vegetation types have been developed, with quantified climatic relationships (e.g. the 'life zones' of Holdridge 1947, the 'ecophysiognomic' growth forms of Box 1981, and the global biome models of Prentice et al. 1992 and Box 1995b). These models are empirical, however, and do not permit mechanistic simulation of plant and ecosystem function.

Identification of the need for global sets of PFTs has had the fortuitous result of generating a very useful examination and discussion of just what constitutes 'function' in plants and how it can be classified (apart from its structural manifestations) (e.g. Smith & Huston 1989; Körner 1991; Smith et al. 1993; Grime 1993; cf. Numata 1976; Grime 1979). Although mechanistic models for global classifications of structural-functional PFTs have not yet been developed, such classifications may provide a useful starting point for assessing the diversity of plant types which need to be covered.

Plant structural-functional types and climate

That the form manifestations of evolved functional patterns are closely related to environmental conditions was shown by the ability of simple climatic envelopes to predict the worldwide occurrence patterns of strictly pheno-physiognomically defined plant growth forms (Box 1981). Principles relating form and function in plants have been expressed in various places (e.g. Mooney 1974; Box 1981, 1984; Givnish 1986; Anon. 1991) and represent the basis for what may be called a structural-functional basis for identifying PFTs (cf. Chapin 1993). A structural-functional approach might recognize the following:
(1) physiognomic and phenological features at the first level (reflecting form-function relationships and with aerodynamic consequences);
(2) zonal or other geographic subtypes at the next level (e.g. warm-temperate versus cool-temperate or subtropical/tropical evergreen broad-leaved trees), with ecophysiological and less obvious form differences (but perhaps also with significant aerodynamic effects);
(3) functional attributes without form manifestations at the third level.

Physiognomic features include such things as general structural type (tree, shrub, etc.) and overall size, while the main relevant phenologic feature is the seasonal foliation/defoliation pattern. This combination of features has been called pheno-physiognomy (e.g. Orshan 1989) and is probably the most common structural basis for plant and vegetation classification. A structural-functional approach to identification of PFTs has the advantages of being intuitive and visible (also to satellites) but has the disadvantage of relegating some important functional differences, such as between C_3 and C_4 metabolic systems, to a lower level of recognition.

An initial model of plant pheno-physiognomic types and their relations to important climatic factors, based on climatic envelopes, was developed and used to predict occurrence/absence and potential dominance of PFTs worldwide (Box 1981, 1987). A climatic envelope expresses, empirically, the climatic space corresponding to the geographic range within which a plant taxon or vegetation type is considered to grow and reproduce under natural conditions. The plant or vegetation type is assumed not to grow wherever the local value of any climatic envelope variable is outside the envelope limits (cf. also the 'life zones' of Holdridge 1947). The original version of this model, called TVS1, provided a global set of pheno-physiognomically defined plant types, their climatic limits, logic for relating them to some aspects of plant and vegetation function (e.g. metabolism, succession), and a computerized method for predicting presence/absence at climatic data-sites. This model also can suggest limiting factor(s) where a plant type is not predicted.

This model has been improved (version TVS1a) by: (1) using a more geographically balanced, globally accurate estimator for potential evapotranspiration and water balance (see Box 1986, 1987); (2) increasing the number of plant types (to 117), with some redefinitions of types and characters, based on field experience, especially in the tropics, East Asia, Australia and New Zealand; (3) improving the description of foliage types; and (4) improving the climatic limiting values, based on improved software for tabulating/cross-checking occurrences and for recognizing/reconsidering near-misses.

In addition, the use of other temperature variables and development of global data-bases to support their use, especially for absolute minimum temperature, has improved the accuracy of two other envelope models, one for biomes at global scale (Box 1995b) and the other for plant species at local scale (Box et al. 1993). These additional variables may also improve both envelope and more mechanistic models involving PTFs.

A sample prediction by this improved model TVS1a is shown in Table 1, from the area around Pemberton, on the edge of the karri (tall eucalypt) forest region in the moist (maritime) but summer-dry climate of southwestern Australia. This was chosen because of the unusual flora and vegetation, which are often problematic in global models but which also illustrate how climatic models must be interpreted. The vegetation is influenced by low nutrient levels and fire history, both of which are not included in the model. In this region there are two distinct biomes under identical local climates but differentiated by fire and soil conditions (J. S. Beard

pers. comm.; cf. Beard 1995). The model predicts plant types of both 'biomes' but, without more information, it can only suggest the structure of the climatic potential biome, which is not much different from the main structure of the actual vegetation (Table 1). The list of plant types predicted is less accurate, showing both familiar and more typically Australian forms, including two deciduous understorey-tree forms which do not occur there, perhaps for reasons of historical biogeography.

This profile in Table 1 suggests some of the diversity in world plant types, some of which are unusual but perhaps distinct functional types. Such types should not be overlooked in global PFT sets just because they currently cover small areas and should be omitted only when the total number of permissible PFTs is limited and the scale, purpose and limits of the PFT set are clearly stated. An incomplete list of less common plant types, many of which were added to create the new model TVS1a, is shown in Table 2.

Experience with climatic-envelope models and in comparing East Asian and eastern North American vegetation at the same latitudes (Box 1988, 1995a) has suggested that minimum temperatures, perhaps even single events (e.g. absolute minimum temperature), may be very important over large areas in controlling vegetation patterns and the occurrence of plant types (cf. Woodward 1987). Absolute minimum temperature was included in a recent global model for pheno-physiognomic types of potential natural vegetation (PNV) and significantly improved prediction results in several regions, especially East Asia, the southeastern USA, and much of the temperate Southern Hemisphere (Box 1995b). Based on this result, five main climate-related constraints on plant/vegetation metabolism and maintenance, in a global-modeling context, appear:

1. *Maximum temperatures*, which may raise respiration loads beyond the point of a positive carbon balance for long enough periods to preclude or hinder necessary plant functions, including reproduction and allocation of sufficient photosynthate to storage reserves.

2. *Growing-season warmth*, of which at least some minimal level is necessary for various functions, including perhaps threshold temperatures for activating certain enzymes. It was thought that the warmth factor may be simply a heat-sum requirement, but the PNV model required both a peak-warmth and a heat-sum variable in order to predict vegetation patterns accurately.

3. *Minimum temperatures*, including short-term events. The limiting mechanism in many cases may be tissue freezing (ice formation inside cells, etc.) rather than low mean temperatures (cf. Levitt 1972). Tissue freezing

Table 1. Plant types and structure of (potential) vegetation predicted by model TVS1a for the area around Pemberton, Western Australia.

	Lim. Fact.	Distance
T:		
Tall eucalyptoid trees (*Eucalyptus diversicolor*)	MIy	0.06
Eucalyptoid sclerophyll trees (*Eucalyptus*)	Tmin	0.23
Sclero-phyllode trees (e.g. *Acacia melanoxylon*)	Tmin	0.20
Evergreen microphyll trees	Tmin	0.13
Laurophyll evergreen trees	MIy	0.06
Tropical BL conifers (e.g. *Podocarpus*)	MIy	0.06
Scale-leaved cupressoid trees	MIy	0.20
Tall-xeric needle trees (e.g. *Casuarina*)	MIy	0.09
ST:		
Laurophyll evergreen small trees	Tmin	0.14
Raingreen small trees	Tmin	0.09
Evergreen malacophyll trees	MIy	0.06
Sclero-phyllode small trees (e.g. mulgoids)	Tmax	0.11
Summergreen notophyll small trees (cf. *Nothofagus*)	Pmtmax	0.08
Scale-leaved small trees	Tmax	0.17
RT: Palmiform tuft-treelets	Tmin	0.00
A: Laurophyll evergreen arborescents	Tmin	0.14
S:		
Laurophyll evergreen shrubs	MIy	0.25
Evergreen malacophyll shrubs	MIy	0.06
Needle-leaved evergreen shrubs	MIy	0.34
Mediterranean evergreen shrubs	Tmax	0.29
Sclero-phyllode shrubs	Tmax	0.45
Mediterranean dwarf-shrubs	MIy	0.13
RS:		
Palmiform mesic rosette-shrubs	Pmtmax	0.08
Xeric rosette-shrubs	MIy	0.13
G:		
Tall cane-grasses	Tmax	0.25
Short bunch-grasses	Tmin	0.78
Short tussock-grasses	MIy	0.20
Short sward-grasses	Pmtmax	0.08
Restioids	Tmax	0.09
F:		
Raingreen forbs	Tmin	0.13
Summergreen forbs	Tmax	0.55
Temperate evergreen forbs	Pmtmax	0.08
Fn: Xeric evergreen ferns (e.g. *Pteridium*)	Pmtmax	0.08
V: Raingreen vines	Tmin	0.00
E: Wintergreen broad-leaved epiphytes	Tmax	0.29
Th:		
Mat-forming thallophytes	MIy	0.25
Xeric thallophytes	Tmax	0.91

Site data for climatic envelope variables (C and mm):

Tmax	Tmin	DTy	Prcp	Pmax	Pmin	Pmtmax	MIy
20.0	10.0	10.0	916	152	19	22	1.06

Symbols: DTy = annual range of monthly mean temperature, MIy = annual moisture index (precipitation/potential evapotranspiration), Pmax = highest average monthly precipitation, Pmin = lowest average monthly precipitation, Pmtmax = average precipitation of the warmest month, Prcp = average annual precipitation, Tmax = mean temperature of the warmest month, Tmin = mean temperature of the coldest month.

The model is based on climatic envelopes involving eight climatic variables. Limiting factor (Lim. fact.) is the closest climatic limit, with standardized distance to that limit (scale: 0 - 1). For explanation of plant types see Box (1981), or Table 2 for newer types. Direct use of taxonomic names in plant-type names is avoided, but some actual taxa are given as examples.

The envelopes identify those plant types which are climatically possible at the site and which would compose the climatic potential natural vegetation, in the absence of frequent disturbances, severe nutrient limitations, etc. The predicted vegetation in this case would be a tall eucalyptoid forest with a perhaps denser understorey of more mesomorphic evergreen trees, etc. (based on proximity to climatic limits, relative shade tolerance of the tree types, etc.). The actual vegetation of the region is tall (to > 50 m) karri forest (*Eucalyptus diversicolor*) with well-developed understorey (but without all of the forms predicted!) (cf. Walter 1968; MacArthur & Clifton 1975; Beard 1979; pers. experience and pers. comm. from J. S. Beard).

Table 2. Pheno-physiognomic plant types not in the original world model TVS1 (Box 1981) but added to model TVS1a.

Relatively well-known types added to model TVS1a:

- Laurophyll trees, arborescents, and shrubs
  (shade-tolerant, hygromorphic evergreens - not coriaceous)
- Tallest, emergent *Eucalyptus* trees
  (which may however be replaced if burning suppressed)
- Bottle trees (both true trees and palms)
- Raingreen poikilohydrous ferns
- Desert geophytes (ephemeroids)

Less common but distinct plant forms added to model TVS1a:

- Tropical evergreen megaphyll trees
- Monopodial, shade-tolerant dicot trees
  (e.g. cool-maritime *Nothofagus* in Tasmania)
- Malaco-evergreen trees, arborescents and shrubs of
  cool-perhumid Southern Hemisphere areas
- Ligno-needle arborescents and shrubs of arid areas
  (mainly Australia)
- Australian arborescents and shrubs with boreal-like
  bunch needles
- Fuller range of stem-succulent forms: columnar, branched-
  arborescent, frutescent, dwarf, microphytic, etc.
- Summergreen conifer krummholz
- Frutescent tropical evergreen forbs
- Tropical-alpine, cool-stenothermal, and other evergreen forbs
- Rattans (climbing palms)
- Stranglers/hemi-epiphytes/pseudo-lianas
- Dwarf bamboos (*Sasa, Sasamorpha*)
- Small epiphytic and ground bromeliads of S. America
- Full range of basic growth forms occurring also as epiphytes
  (stem-succulents, vines, rosettes, dwarf-shrubs, etc.)

The above types were included because they represent pheno-physiognomic forms (i.e. combinations of physiognomy and seasonality) not already in the model. Many are described in the literature but required field experience for complete pheno-physiognomic definition in terms of the characters used in the TVS1 classification.

Table 3. Major functional aspects of plants, with form manifestations. Size = plant size; LA = leaf area; LC = leaf consistency; Wood = Woodiness; Bud = bud protection

Functional aspect	Form manifestation
Resource requirements:	
Water requirement	Size, LC
Energy requirement	Size
Mycorrhizal requirement	
CO_2 requirement/response	
Allocation strategies:	
Leaves/roots vs. storage	Size
Structure vs. growth rate	Wood, lifespan
Reproduction vs. growth	Size
Repair functions	Resprouting forms
Water conservation	LA, LC, Size
Defensive mechanisms (cold, damage)	Bud, Spines, etc.
Cell-sap concentration (cold/drought tolerance)	
Litter lignin/nutrient content	Litter hardness
Growth rates (and capacities):	
Respiration and relative growth rates	Size
Photosynthetic rate	Size, LA
Nutrient absorption rate	
Metabolic specializations:	
- C3 vs C4 photosynthesis	
- Light needs/shade tolerance	Foliage color
- N-fixing/non N-fixing	
- Secondary substances	
Metabolic rhythm:	
Vernalization requirement	
Obligate/facultative defoliation; synchrony	Foliation phenology
Diurnality	Nighttime closure
Dormancy (winter/summer, obligate/facultative)	
Turnover/storage aspects:	
Leaf turnover/longevity	Foliation phenology
Root turnover/longevity	
Tissue N concentration, C:N ratio	
Development:	
Cell size, division rates, differentiation	
Meristem location(s)	Plant architecture
Lifespan (annual, binennial, perennial, etc.)	Size, woodiness
Reproduction and Dispersal:	
Seeds vs. vegetative	Plant architecture
Seed size/number, seed-bank persistence	
Flowering/fruiting phenology	Phenology
Dispersal mode (incl. short/long, fast/slow)	
Light/shade germination	

can be restricted to lower temperatures by cold-hardening but cannot be avoided if temperatures go too low, below ca. – 15 °C for extra-tropical broad-leaved evergreen woody plants (cf. Larcher 1976). Many tropical plants may be damaged without freezing by temperatures up to +5 °C. The critical factor may actually be the return frequency of temperatures below a critical level. For further evidence for the impact of absolute minimum temperatures on plant survival, and its geographical implications, see Woodward (1987).

4. *Tissue desiccation*, which may also be of relatively short duration (though perhaps the final result of a cumulative process). For most plants, desiccation and permanent wilting correlate with a soil water suction pressure of around 15 bars (e.g. Brady 1974).

5. *Longer-term moisture balance*, which may result in desiccation but which may also only limit the physiognomy of the plants and vegetation which evolved or colonized a particular region.

Functional approaches

The remainder of this paper is more speculative and attempts to focus on more purely 'functional' approaches to classification of PFTs. Ideally, it would be desirable to identify and classify 'purely functional' aspects of plants and use the corresponding processes and criteria to imply plant functional types with as little reference as possible to form attributes. Alternatively, one may start with 'purely functional' criteria, identify controlling climatic and/or other environmental factors for the functions, and then try to identify the recognizable plant

Table 4. Plant functions directly related to environmental conditions.

Functional aspect	Considerations	Allocation strategy
Metabolism:		
Respiration	Level; rate; amplitude	
Photosynthesis	Seasonality	Evergrowing/seasonal-evergreen/caducous; dormancy; diurnal closure
Tolerance to:		
Drought	Plant size; foliage area	Allocation to leaves versus roots (uptake) versus tissue for water storage
	Leaf structure	Leaf 'hardness', coating, etc.
	Stoma behavior	Metabolic adjustments (incl. C3, C4, CAM, etc.)
Cold/frost	Cell damage	Cell-sap concentration
	Bud protection	Bud covers: none (tropical) / slight (subtropical) / distinct (temperate to polar)
	Leaf protection	Leaf 'hardness', deciduousness
Fire; other tissue loss	Plant repair	Re-sprouting ability
	Foliage repair	Re-foliation ability
Competition	Resources	Maximize resource capture via larger foliage and root systems;
		Minimize resource losses via reduced foliage, biomass, etc.
	Establishment	Maximize growth rate, seed production and dispersal (at expense of lifespan)

Plant environmental adaptations, including resource-allocation strategies, involve adaptations of ongoing metabolism and for tolerance to unfavorable and/or life-threating periods or events. Note that resulting allocation strategies can be: (1) preventive (defensive mechanisms, etc.); (2) adaptive-preventive (e.g. reduced leaf area); (3) Re-active (foliage repair, re-sprouting); or (4) exploitative (e.g. growth rate vs. permanent structure).

forms which might be involved. An initial list of major functional aspects of plants, including plant development, reproduction and dispersal as well as basic metabolism, allocation strategies, and resource requirements, is given in Table 3. Implications of these functional processes for plant form are noted where these seem evident, but there are important plant functions for which no clear form manifestations exist.

Attempts to identify plant types based only on 'functional' criteria, especially those without form manifestations, may be quite instructive. Nevertheless, the start is made here with two central aspects of plant function which do have obvious form relationships: metabolism and interactions of the photosynthetic surface with its immediate environment (gas exchange, light capture, etc.). An attempt is made in Table 4 to list the most important functional aspects which are related directly to climatic conditions, especially temperature and water availability. These include the short-term rates, general levels and ranges of the main metabolic processes (photosynthesis, respiration) during periods of activity; diurnal and seasonal continuity of metabolism; protection of sensitive tissue (buds, leaves, etc.) from damage during unfavorable periods; and the overall water balance of plants and protective adaptations against water loss. These more or less temporally continuous aspects of plant function (i.e. metabolism) and aspects of protection against events which would kill whole plants are central to plant function and suggest initial, more truly function-based approaches to identifying plant types.

Metabolic types of plants

Metabolic rates, ranges and optima may vary with climatic/microclimatic conditions and have been classified by terms such as megathermal (warmth-adapted) or microthermal (characteristic of cool climates, perhaps with winter dormancy). Metabolic activity is also limited, however, by seasonal and/or unusual cold, by plant adaptations to unfavorable periods, and by the damage which cold may cause to plant parts (Levitt 1969, 1972). Such damage is largely to leaves, buds and other structure. To the extent that the resulting collapse of metabolic activity might be regarded by physiologists as function, the resulting metabolic types might be classified as cold-tolerance types, as illustrated in Table 5.

Some truly tropical ('equatorial') plants can be classified as cold-intolerant (see Table 5) and may be damaged by 'cold' temperatures as high as +5 °C (cf. Larcher 1976). Most tropical plants are frost-intolerant, surviving some cold and not being damaged until temperatures fall to ca. −2 °C. For most such plants, major defoliation usually occurs as a result of such temperatures, both for 'evergreens' (in the tropics usually a facultative feature) and for habitually deciduous (rain-green) species. Most temperate-zone broad-leaved evergreen woody plants tolerate short-term frost exposure, to about −15 °C (cf. Larcher 1976; Woodward 1987), some a bit lower (e.g. *Ilex opaca*), and thus may be described as frost-tolerant. These may also occur in cool climates, including cool-maritime climates and

relatively aseasonal tropical mountains, as long as extremes are not lower than ca. – 15 °C.

Most other extra-tropical plants are frost-dormant, in two ways:

1. Cold-sensitive, i.e. deciduous, dropping leaves at temperatures which may be well above freezing (with the plants themselves usually surviving short-term temperatures as low as ca. – 60 °C in extreme cases); and

2. Cold-insensitive, i.e. evergreen boreal conifers, which become dormant while still foliated and may survive (after cold-hardening) to mean temperatures as low as ca. – 30 °C and short-term extremes much lower.

There are of course variants. Some 'tropical raingreen' trees, such as *Lagerstroemia indica*, adapt their deciduousness to the temperate-zone winter, essentially becoming summergreen, and tolerate temperatures to around – 15° to – 20 °C in leafless state. There are also the boreal deciduous conifers (*Larix* species) which may tolerate temperatures to as low as around – 80 °C when cold-hardened.

If thermal seasons and metabolic amplitudes/optima are considered more explicitly, as well as wet and dry

Table 5. Plant cold-tolerance types and geographical zones.

Cold-tolerance type	Minimum temperature	Cold requirement	Geographic zone
1. Cold-intolerant	ca. 5 °C	none	Equatorial
2. Frost-intolerant	ca. – 2 °C	?	Tropical/ Subtropical
3. Frost-tolerant	ca. – 15 °C (evergreens)	< 0 °C	Temperate (and montane)
4. Frost-dormant			
a. Cold-sensitive (deciduous)	ca. – 20 °C	< 0 °C	Temperate to Polar
b. Cold-insensitive (evergreen conifer)	ca. – 80 °C	<< 0°C	Boreal/Polar

The concept of cold-tolerance types includes both minimum temperature which can be survived and consideration of low temperatures which may be required, as for vernalization. The minimum temperatures suggested here are for short-term events, which may occur quite infrequently but represent physiological limits. For required cold, << 0 °C may include situations in which temperatures are not far below 0 °C but stay < 0 °C for long periods of time.

Table 6. Plant geometabolic types and thermo-functional characteristics.

Geometabolic type and location	Cold-tolerance	Thermal seasons	Obligate seasonality	Bud protection
1. Warm-Stenothermal (tropical)	Cold/frost-intolerant	W/W	?	None
– Equatorial (aseasonal)	Cold-intolerant (> ca. 5°C)	W	None	None
Cool-Stenothermal (montane) (subalpine/alpine)	Frost-tolerant (Frost-intolerant)	w/w c/c	?	Slight
2. Cold Diurnal-Stenothermal (equatorial alpine)	Frost-tolerant (every night)	c	None	Yes
3. Seasonal: Subtropical	Frost-intolerant (> about -2°C)	W/w	?	Slight
Warm-temperate	Frost-tolerant (EGs: > – 15 °C)	W/c	Vernalization	Yes
– Montane		(c/C)		
– Arid		(W/w dry)		
– Arid coastal		(w/c dry)		
Temperate	Evergreens frost-tolerant Deciduous frost-dormant	W/C	Vernalization	Yes
– Arid		(W/C dry)		
– Cool-temperate		(w/c)		
– Cool-maritime		(c/c)		
– Arid-maritime		(c/c dry)		
– Montane		(c/C)		
4. Cold Eurythermal: Boreal	Frost-dormant (to < – 60 °C if deciduous)	w/C	Vernalization	Yes
Polar	Frost-dormant (to < – 60 °C but snow-insulated)	c/C	Vernalization	Yes

Plant geometabolic types are annual metabolic patterns constrained mainly by cold tolerance (cf. Table 5) and correspond generally to well- recognized climatic zones (sometimes with altitudinal or other geographic variants). Thermal seasons (summer/winter) are defined by the following general levels for mean temperature: W = warm to hot (> 20 °C, perhaps >> 20 °C), w = moderately warm (10 °C - 20 °C), c = cool (0 °C - 10 °C), and C = cold (< 0 °C, perhaps << 0 °C). The concept of geometabolic type includes thermal seasonality (steno-/eury-thermal) and metabolic optimum temperature levels during the growing season, as well as cold-tolerance type. The general growing-season metabolic level associated with each geometabolic type generally corresponds to one of the following general levels of mean temperature: high (> ca. 24 °C for tropical to warm-temperate areas), moderate (ca.12 °C - 24 °C for most other temperate, boreal/austral and montane areas), and low (< ca. 12 °C for polar and alpine areas).

Hardness	Light Requirement (and color)		
	Light-demanding, shade-intolerant (light, often yellowish green)	Intermediate	Shade-tolerant (dark green)
Soft and thin (malacophyllous)	**M A L A C** many ephemerals, ruderals, and deciduous vines	**O P H Y L L** typical deciduous, e.g. *Acer, Betula, Tectona, Macaranga*	L A U *Ligustrum sinense ?*
Thin but reinforced (cf. deciduous *Quercus*)	some deciduous perennial herbs, esp. ruderals (e.g. Compositae)	Deciduous *Quercus* or *Nothofagus*	R O thin-coriaceous rainforest trees/ arborescents
Leathery but pliable (coriaceous)	**C O R I A** e.g. *Pinus, Smilax*	**C E O U S** Many humid-tropical trees/arborescents	P H *Castanopsis, Persea,* L *Laurus, Magnolia virginiana*
Hard and at least somewhat brittle (sclerophyllous)	**S C L E R O** e.g. *Eucalyptus, Olea europaea*	**P H Y L L** *Quercus ilex ?*	L L *Magnolia grandiflora Ilex aquifolium*

Fig. 1. Leaf functional types: hardness and shade tolerance. Independent consideration of leaf 'hardness' (to gas exchange as well as mechanically) and shade-tolerance suggests four basic leaf functional types (foliar strategies). Malacophylls are thin, soft leaves with high photosynthetic and water-loss rates, designed for high productivity in a favorable season, and are usually deciduous (*Lonicera japonica* is an exception: deciduous in Japan but evergreen in the southeastern USA). Coriaceous leaves are usually evergreen and are more resistant to water loss (often with a cuticular coating) but also may have somewhat reduced photosynthetic rates, especially if thicker; these leaves may be thicker (e.g. evergreen *Smilax* spp. as well as many conifers) but may also be quite thin, as in many tropical rainforest trees and arborescents. Sclerophylls are evergreen, more resistant to gas exchange, generally light-demanding, and usually at least a bit hard or even brittle. Laurophylls represent a different dimension, being shade-tolerant and generally hygromorphic, but may range from comparatively soft and/or thin to 'sclero-laurophylls' such as those of *Magnolia grandiflora*, which survives lower temperatures than the usual –15 °C limit for most evergreen broad-leaved tree species.

seasons, one can readily derive a geographic classification of plant 'geometabolic' types, as shown in Table 6, which correspond to well-recognized climatic zones. There are four basic geometabolic types, delimited partly by the cold-tolerance types just described. Warm-stenothermal plants occur in tropical lowlands and are generally cold-intolerant or frost-intolerant. Closely related are cool-stenothermal (tropical montane) plants, which are similarly frost-intolerant despite having cooler temperature levels in general. Diurnal-stenothermal plants represent a special pattern occurring only in the tropical alpine belt, where the plants are frost-tolerant and adapted to frost essentially every night of the year.

Seasonal plants may occur over a continuum of less distinct patterns from subtropical to temperate. These are united, however, by being generally frost-tolerant if evergreen or cold-sensitive (frost-dormant) if deciduous. (Deciduousness is thus generally obligatory in the temperate zones, as opposed to apparent facultative deciduousness in the tropics.) Finally, cold-eurythermal plants are frost-dormant, whether evergreen or deciduous (although some boreal evergreen trees may break dormancy periodically). The variety of montane, arid, and other subtypes shown for the temperate zone reflect variations in thermal seasonality and/or moisture balance but with essentially the same cold-tolerance limitations.

Types of plant photosynthetic surfaces

The classification of photosynthetic surface types in TVS1 (Box 1981, 1987) did not adequately describe light-based successional dynamics and is replaced by a two-dimensional concept which separates the 'hardness' of the photosynthetic surface (to gas exchange) from its light requirements, as illustrated in Fig. 1. The gas-exchange properties of leaves and other photosynthetic surfaces are almost impossible to separate from their form (or 'consistency'), being intimately linked to internal structure, production 'cost' and lifespan (as well as seasonality), and external morphology (thickness, cuticle, color, etc.) (cf. Körner 1991). In addition to gas exchange, light absorption and related light requirements for photosynthesis and positive carbon gain are also involved. Malacophyllous, coriaceous and sclerophyllous leaves represent a gradient of adaptations to dryness, as well as nutrient availability and herbivory. Dark green, shade-tolerant, mesomorphic 'laurophylls', on the other hand, occur across several hardness classes, are often synusial dominants, and represent a second dimension (cf. Fig. 1). This does not necessarily contradict the 'trade-off model' of Smith & Huston (1989) but does suggest that light requirements may not always be directly related to leaf consistency. Inclusion of shade-tolerant laurophyll types in the model of world PNV (biome) types greatly improved the accuracy of its succession module.

Table 7. Photosynthetic functional forms of plants. 1 = Photosynthetic organ; 2 = Duration; 3 = Photosynthetic functional form; 4 = Examples.

1	2	3	4
Broad leaves[1]	E	LAUROPHYLL (shade-tolerant)	*Camellia*
		CORIACEOUS (leathery)	
		SCLEROPHYLL (hard)	*Eucalyptus*
		SARCOPHYLL (succulent)	
		Duri-malacophyll	
		Duri-pubescent	
	D	MALACOPHYLL (soft)	*Acer, Betula, Tectona*
		PUBESCENT	*Artemisia*
		Caduci-laurophyll	
		Caduci-coriaceous	
Needle-leaves	E	Lauro-acicular	*Picea, Araucaria*
		Corio-acicular	*Pinus, Podocarpus*
		Sclero-acicular	*Pinus rigida, Juniperus*
		Minilauro-acicular	*Sequoia, Prumnopytis*
	D	Caduci-acicular	*Larix*
		Caduci-compound acicular	*Taxodium, Metasequoia*
Phyllodes[2]	E	LIGNOPHYLL	
Photosynthetic stems	E	STEM-SUCCULENT	*Carnegia, Ferrocactus*
		LIGNEOUS[3]	

[1]including microphyll/leptophyll variants; [2](with or without green stems); [3]with or without auxilliary/primary photosynthesis by leaves (usually microphyll or smaller, evergreen or deciduous, hard to soft).

Photosynthetic functional forms represent combinations of the basic photosynthetic strategies (see framework in Fig. 1) and a particular type of photosynthetic organ (including non-leaves). The functional forms in capital letters represent the prototypes, while the others are secondary types, sometimes perhaps 'hybrid' types. Malacophylls and laurophylls generally have the highest potential photosynthetic (and water-loss) rates, while pubescent, coriaceous, sclerophyll, lignophyll, and sarcophyll/stem-succulent photosynthetic surfaces have lower rates, in roughly that order. Microphylls/leptophylls without green stems can be considered variants of the broad-leaved types; those with green stems essentially represent the ligneous type but with additional photosynthetic possibilities.

The different gas-exchange (cf. aerodynamic), light-requirement, and seasonality properties among leaf types and of leaves versus photosynthetic stems, phyllodes, etc., require that the type of photosynthetic organ be basic to a classification of photosynthetic functional types. Using the framework in Fig. 1, an attempt is made in Table 7 to classify basic photosynthetic functional forms, based on light requirements/shade tolerance and resistance to water loss. 'Harder' leaves (e.g. sclerophylls) and other photosynthetic surfaces (phyllodes, succulent stems, woody stems) resist water loss but also generally have lower CO_2 uptake potentials and lower photosynthesis rates/total productivity (cf. Larcher 1976). This classification combines form and function of the photosynthetic organ and supports the basic concept

(Smith & Huston 1989) of functional trade-offs among light needs, resistance to water loss, and potential photosynthetic rates. Leaves are not whole plants, and useful PFTs must reflect functional potentials at the level of whole plants (e.g. productivity) as well as the leaf level (e.g. carbon gain/loss per unit leaf area per second/minute/hour). Nevertheless, since gas-exchange surfaces represent integrations of such fundamental functional processes and potentials, photosynthetic functional forms may offer a useful basis for more complete concepts of functional types of whole plants.

Minimal global sets of plant functional types

A next step is to look at the implications of such approaches for global but perhaps minimal sets of PFTs. Doing this in detail is beyond the scope of this paper, but three simple results can be described, one based on biogeographic considerations, one on plant resource acquisition and allocation patterns, and a third on the photosynthetic surface types described above.

1. Biogeographical approach: How many types are needed?

Based on major climatic factors and world vegetation geography, a model of world potential dominant vegetation types was developed in order to address the question of how many vegetation types might be needed in order to cover the main features of world terrestrial vegetation (Box 1995b). The resulting roughly 50 types were grouped into 15 more general pheno-physiognomic vegetation classes, essentially at the biome level. From this list, an attempt is made in Table 8 to characterize these vegetation classes in terms of dominant plant types and important functional characteristics, including biomass architecture (woody vs herbaceous, determinate vs indeterminate growth), seasonal activity, and some other characteristics such as light requirements and cold tolerance. This procedure yielded 15 major plant types, but some could be subdivided into more distinct types. Such a list could serve as an initial, fairly minimal set of global PFTs for modeling and would not differ greatly, for example, from the set of types suggested by Prentice et al. (1992) in their global biome model (or, for that matter, by Rübel 1930).

2. Resources and growth form

Basic functional processes of plants, in addition to metabolism, include resource acquisition, internal transport, and allocation to structures for greater permanence and/or competitive ability. However, as shown in

Table 8. Dominant plant types suggested by pheno-physiognomic biome types with structural and functional characteristics.

Dominant plant type	Biome type(s)	Structure	Habit	Other
1. Tropical evergreen broad-leaved trees	Tropical rainforests	Tall woody determinate	Evergrowing	Mesomorphic
2. Tropical deciduous broad-leaved trees / arborescents	Raingreen forests, woodlands, scrub	Woody determinate	Deciduous (facultative?)	
3. Extra-tropical evergreen broad-leaved trees (mainly laurophyll)	Evergreen broad-leaved forests, Temperate rainforests	Woody determinate	Evergreen (seasonal)	Mesomorphic, shade-tolerant
4. Temperate deciduous broad-leaved trees	Summergreen broad-leaved forests and woodlands	Woody determinate	Deciduous (obligate)	Winter-dormant
5. Temperate/boreal needle-leaved evergreen trees	Needle-leaved evergreen forests/open woodlands	Woody monopodial	Evergreen (seasonal)	Winter-dormant (cold-tolerant)
6. Boreal/cool-temperate deciduous needle-leaved trees	Deciduous boreal needle-leaved forests/open woods	Woody monopodial	Deciduous (obligate)	Winter-dormant (cold-tolerant)
7. Sclerophyll trees/ arborescents	Subhumid woodlands/scrub	Short woody determinate	Evergreen/ semi-evergreen	Xeromorphic, light-demanding
8. Sclerophyll/coriaceous shrubs/dwarf-shrubs	Shrublands, krummholz, semi-deserts	Basally determinate	Evergreen/ semi-evergreen	Xeromorphic light-demanding
9. Deciduous shrubs/ dwarf-shrubs	Shrublands, krummholz, semi-deserts	Basally determinate	Deciduous	Rapid growth, seasonally dormant
10. Short-season broad-leaved dwarf-shrubs	Tundra: dwarf-shrub, graminoid, etc.	Basally ramifying	Evergreen/ deciduous	Winter-dormant (cold-tolerant)
11. Diurnally active tuft-arborescents/ frutescents/forbs	Tropical alpine scrub	Monopodial rosettes	Evergreen (diurnal)	Tolerant to diurnal frost, high UV, etc.
12. Grasses and related graminoids	Grasslands and savannas	Herbaceous (marcescent)	Opportunistic	Rapid growth, spreading
13. Stress-tolerant succulents	Semi-desert scrub	Stem/leaf/ root-succulents	Evergreen	Slow growth, water storage in tissue
14. Ephemeral herbs	Semi-desert scrub	Annual/ perennial	Ephemeral	Short life cycle/ growing season
15. Stress-tolerant lower plants, especially mosses, lichens	Tundra, cold-desert	Non-vascular cryptogams (small)	Seasonal/ stable	Winter-dormant; very slow growth; cold-tolerant

The plant types in the left column are (co)dominants or other important constituents of the pheno-physiognomic biome types in the second column and thus represent potentially the most important plant types in world vegetation, in a geographic as well as ecological sense. These plant types could then constitute an initial minimal global set of PFTs able to represent the main global vegetation types. Important functional characteristics are shown at the right and include, in particular: (1) permanence and potential height growth, as indicated by woodiness vs. herbaceousness, and by multiple branching (determinate) vs. monopodial (indeterminate) development of above-ground structure; (2) seasonal or other temporal activity pattern (evergreen vs deciduous, etc.); and (3) other characteristics such as stress-tolerance, dormancy, light/shade relationships, etc. The biome types resulted from a global model of potential dominant vegetation types needed to cover the physiognomic, seasonal, and geographic variation in global terrestrial vegetation (Box 1995b).

Table 9, the basic physiognomic types of plants (growth forms: trees, shrubs, epiphytes, etc.) follow fairly directly from resource-acquisition and allocation patterns. Some architectural results are less distinct functionally, such as trees versus less determinate arborescents. Nevertheless, the direct implication of structure by such functional 'decisions' suggests that a truly function-based classification of plant types, involving all main plant functions (not only selected ones), might not be radically different from more familiar structural-functional classifications.

3. Photosynthetic surface types and PFTs

Alternatively, one might relax some structural distinctions, such as trees versus shrubs or arborescents, and take the functional trade-offs of the main photosynthetic surface (cf. Table 7) as a basis for classifying PFTs. It may be necessary to keep some unavoidable structural distinctions, such as woody versus non-woody, and some upper parts of Table 9. Nevertheless, with such an approach one could get about 18 woody photosynthetic forms, plus about 10 broad-leaved non-woody

Table 9. Plant functional strategies and resulting growth forms.

Functional strategy ('decisions')	Yes	Resulting growth form(s) No
Water and nutrients taken from a relatively stable source?	Plant growing on the ground, rooted in soil	EPIPHYTES
Able to transport water significantly upward?	Vascular plants	THALLOPHYTES
Living more than one growing season (as opposed to emphasis on seed dispersal)?	Perennial plants	ANNUALS
Allocation to a permanent energy-acquisition apparatus above ground (e.g. stem, foliage, etc.)?	Woody and other highly lignified perennials, incl. STEM-SUCCULENTS and smaller evergreen FORBS, FERNS, GRAMINOIDS	Seasonal FORBS, FERNS, GRAMINOIDS, SEMI-SHRUBS
Allocation to competitive, upward-growing structure for greater resource capture?	Tall-growing, esp. woody, plants	FORBS, FERNS, GRAMINOIDS (excl. bamboos, tall tree ferns, etc.)
(a) Self-supporting structure (as opposed to cheap, very rapid growth)?	(non-vines)	VINES / LIANAS
(b) Essentially monopodial indeterminate growth?	TREES (esp. needle-leaved conifers); TUFT-TREES, plus tall bamboos	(broad-leaved woody plants)
(c) Determinate growth but with elevated branching?	TREES (broad-leaved); some ARBORESCENTS	SHRUBS and ROSETTE-SHRUBS; some ARBORESCENTS

The functional strategies in the left column result in the attributes (lower-case letters) and more specific growth forms (capital letters) shown in the two columns to the right. This illustrates the intimate relationship between plant form and major ecological plant functions.

forms (both from Table 7), plus a few other, general types such as graminoids, epiphytes and vines. This would give a total of about 30 PFTs based on photosynthetic trade-offs and basic allocation patterns.

Conclusion

A major world classification of structural-functional plant functional types already exists, in a hierarchical form which can be adapted easily for smaller PFT sets. This PFT set has been improved, both functionally (e.g. characteristics of photosynthetic surface) and geographically (increased number of plant types). The climatic relationships of these plant types are known empirically with some accuracy, which at least provides a basis for comparison.

Empirical models are quickly disparaged when they are employed without a theoretical foundation. In the case of structural-functional PFTs and envelope models, the theoretical basis is provided by the ecophysiological evidence linking leaf function (water loss, CO_2 gain, light needs, etc.) to leaf structure (e.g. leaf size, specific leaf weight); accepted form-function relationships (e.g. big plants have higher respiration totals, other things being equal); and the use of climatic variables which represent accepted major limiting factors for plant growth and maintenance (cf. summary Table 2 in Box 1995c). With this as a basis, there is no substitute for 'empirical' field experience to identify the plant

types which represent the links between form and function. There is also probably no substitute, initially, for empirical climatic and similar relationships in the calibration of more satisfying and instructive mechanistic models.

Purely 'functional' approaches to classification of PFTs should include a focus on metabolism, water balance and disturbance as major functional aspects of plants. Unavoidable relationships between form and function, however, bring such a functional approach quickly back to a recognition of form manifestations and structural types (including seasonal disturbance). Some important aspects of plant function do not have obvious (if any) external form manifestations, as shown in Table 10 (condensed from Table 3). Satisfying world classifications of PFTs must have a basis involving at least some of these non-structural aspects – and may indeed focus on items such as response to ambient CO_2 concentrations, but always with a basis in basic metabolism.

The question remains how structural classifications of PFTs, however well-developed the form-function relationships may be, may help in projecting the impacts of future environmental change. Only climatic change is addressed here. It has become fairly clear that increased CO_2 levels lead to understandable and somewhat predictable changes in stomatal behavior and initial metabolic rates, with compensatory (and less easily predicted) changes in plant allocation patterns, water and nutrient-use efficiency, and biomass distribution. The degree to which a given plant structural-functional type

Table 10. Aspects of plant function without or with only very indirect structural manifestations.

Resource requirements	
- MYCORRHIZAL REQUIREMENT	
- CO_2 REQUIREMENT/RESPONSE	
Allocation strategies:	
- CELL-SAP CONCENTRATION	
- Repair functions	(cf. resprouting)
- Defensive mechanisms	(cf. bud protection, spines)
- Litter lignin/nutrient content	(cf. leaf structure)
Growth rates (and capacities):	
- NUTRIENT ABSORPTION RATE	
- Respiration/relative growth rates	(cf. plant size)
- Photosynthetic rate	(cf. plant size, leaf area)
Metabolic specializations:	
- C_3 VS C_4 PHOTOSYNTHESIS	
- N-FIXING/NON N-FIXING	
- Light needs/shade tolerance	(cf. foliage color)
Metabolic rhythm:	
- VERNALIZATION REQUIREMENT	
- Obligate defoliation	(cf. foliation phenology)
- Diurnality	(cf. day/night closure)
- Dormancy	(cf. foliation)
Turnover/storage aspects:	
- ROOT TURNOVER/LONGEVITY	
- TISSUE N-CONTENT, C: N RATIO	
- leaf turnover/longevity	(cf. foliation phenology)
Development:	
- CELL SIZE, DIVISION RATES,	
DIFFERENTIATION	
- meristem location(s)	(cf. plant architecture)
Reproduction and Dispersal:	
- SEED SIZE/NUMBER, SEED-BANK	
PERSISTENCE	
- DISPERSAL MODE	
(incl. short/long, fast/slow)	
- LIGHT/SHADE GERMINATION	
- seeds vs. vegetative reproduction	(cf. plant architecture)

The main functional aspects without form manifestations are shown in capital letters, those with perhaps some indirect form manifestations in lower-case letters. The most important non-form aspects of function appear to involve reproduction, dispersal and establishment, development rates, nutrient dynamics, mycorrhizal relationships, and primary responses to CO_2 enrichment.

responds to especially the first of these, may depend largely on aspects of water and energy budgets which are related to pheno-morphological characters such as leaf consistency, foliar seasonality, and even plant size. It is beyond the scope of this paper to try to trace such changes through the various plant forms, but a major effort in this direction would perhaps be very useful.

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