

A functional classification of wetland plants

Boutin, Céline* & Keddy, Paul A.

¹Department of Biology, University of Ottawa, Ottawa, Ontario, Canada K1N 6N5; *Corresponding author; present address: Centre national de la recherche faunique, Service canadien de la faune, Environnement Canada, 100 boulevard Gamelin, Hull, Québec, Canada K1A 0H3; Tel. +1 819 9976075; Fax +1 819 9536612

Abstract. In this paper we review the search for guilds in plant communities, and provide a summary of the process, emphasizing five steps: (1) defining function, (2) selecting traits which reflect function, (3) screening for those traits, (4) constructing trait matrices, and (5) grouping species according to these traits. We illustrate this process for wetland plant species based upon a matrix of 27 traits and 43 species from across eastern North America. The 43 species were selected to represent the widest range of life history types possible as well as both common species and nationally rare or endangered species. We found three main functional groups: ruderals, matrix and interstitial species, which we subdivide into a total of seven guilds. The growing number of such studies in the literature suggest that this may be an expedient measure for conservation biology and a promising one for predictions.

Keywords: Community ecology; Functional group; Guild; North America; Trait.

Nomenclature: Gleason (1952).

Introduction

“That the plant-species may be classified not only according to their taxonomical relationship into genera, families etc., but also according to their ... types, has been clear to botanists ever since the childhood of botanical science”. Du Rietz (1931).

The concept of classifying species from a community into related assemblages predates Du Rietz (1931). The concept was developed more than a hundred years ago as a way to group plants in relation to environmental adaptation or indicators (van der Maarel 1980). The best known example of classification comes from Raunkiaer (1934) with his life form system, classifying plants into groups adapted to different climates. His system groups terrestrial plants primarily by the vertical position of the vegetative buds in the unfavourable season in relation to the ground surface. Similarly, Iversen (1936) classified plants according to their adaptation to water. Barkman (1973, 1988) based his complicated classification system on observations made all year round. He used eight

types of flowering periodicity and seven types of vegetative periodicity. Out of a theoretical 56 combinations, 29 have been found. The common objective of these systems was to reduce the number of units that led to a descriptive characterization of the plant kingdom.

Many traits considered in early classifications were traits which could be determined upon inspection of the plant form, such as life form, life span, method of vegetative propagation and position of overwintering shoots. However, if we consider the processes which occur in vegetation, such as nutrient uptake, competition, and interaction with agents of disturbance or stress, further traits related to the role the plant plays in a community have to be considered. We could begin by looking for traits that measure performance in these three areas: (1) ability to forage for essential elements in the absence of neighbours, (2) traits associated with interaction with other plants and (3) traits associated with ability to withstand agents such as fire, flooding, grazing, etc.

The term ‘guild’ (Root 1967) is used to describe groups of functionally similar species in a community (Pianka 1983). It relates to species using the same class of resources. This terminology is particularly well-established in the study of bird and mammal communities (e.g. Severinghaus 1981; Pianka 1983; Diamond & Case 1986; Terborgh & Robinson 1986; Simberloff & Dayan 1991). Similarly, the concept of ‘functional feeding groups’ has been successfully applied to aquatic invertebrates (Cummins 1973; Cummins & Klug 1979). This approach is less well-established in the study of plant communities but there has been a recent proliferation of ecological classification schemes (e.g. Grime 1977, 1988; van der Valk 1981; Grubb 1985; Cody 1986; Givnish 1987; Day et al. 1988). With specific reference to wetland plants, Hutchinson (1975) provides a morphological classification of wetland plant life forms. More recently, Menges & Waller (1983) have applied the three functional groups recognized by Grime (1977, 1979) to describe wetland plants growing along an elevational gradient on a flood plain, and Kautsky (1988) has applied a similar functional classification to aquatic macrophytes.

There is one major obstacle to be overcome if we are to succeed in developing guild classifications of plant communities. It is often possible to pick out some obvious subsets of a community and assign them to guilds, but putting all species in a given community into guilds is a problem which is qualitatively and quantitatively more difficult. This problem is compounded by the fact that guild classifications are often built upon groups of organisms which use similar resources, and it has already been observed that it is very difficult to do this with plants since they all use similar resources (Harper 1977; Grubb 1977).

The approach used here puts emphasis on traits that have to do with function in plants: nutrient uptake, competitive ability, stress tolerance, dispersal ability, etc., in order to classify species according to their function in ecological communities. Since many of these traits are not obvious upon inspection, we need to apply the process of screening as developed by Grime & Hunt (1975) and Grime et al. (1981). The objective of screening is to develop a simple bioassay for a particular attribute, and then apply it systematically to the entire flora of interest (Fig. 1).

Guilds in wetland plants

The following study illustrates the progress to date in systematically applying the scheme in Fig. 1 to the study of wetland plant communities. We present a classification based upon a matrix of 43 species by 27 traits. The species were selected to represent wetland habitats and functional groups from across eastern North America. Species included rare or endangered taxa from infertile lakeshores (*Coreopsis rosea*, *Panicum longifolium*), annuals typical of mud flats (*Bidens cernua*, *Cyperus aristatus*), large perennials (*Phalaris arundinacea*, *Typha glauca*), reeds from river banks (*Scirpus acutus*, *Eleocharis calva*), and an array of other species which represented other life forms and habitats. Where possible we placed an emphasis upon traits associated with function but owing to the magnitude of the project (coordinating seed collection, ensuring adequate germination of many species of contrasting ecology, growing a sufficient number of replicates) we were not able to include as many functional measures as may ultimately be desirable. However, we used traits such as RGR, which is known to be correlated with rates of resource acquisition (e.g. Grime & Hunt 1975) and seedling stress tolerance (Shiple & Keddy 1988). Similarly we used height of juveniles, height of adults, and rates of shoot extension; height is associated with competitive ability for light (e.g. Givnish 1982; Gaudet & Keddy 1988). Above- and below-ground biomass allocation, as well as photosynthetic area, are believed to be associated with foraging for

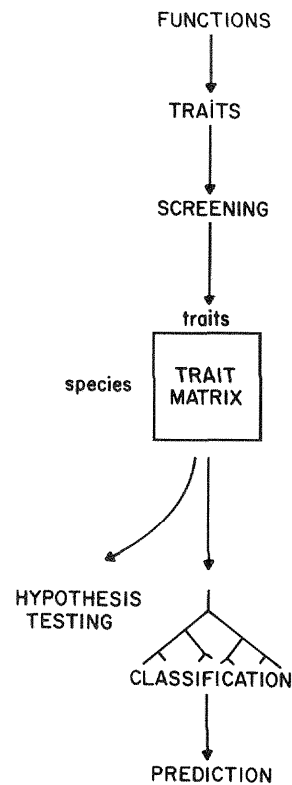


Fig. 1. One possible research strategy for constructing functional groups (guilds) of plants. Essential steps are selecting the traits which are related to different plant functions in communities, screening large numbers of species for these traits, constructing a trait matrix, and building a classification from the trait matrix. The classification of functional groups is then used to make simple predictive ecological models.

different light to nutrient ratios (e.g. Tilman 1982, 1986, 1988). Morphological traits such as shortest and longest distance between aerial shoots measured the way in which different species held space; such traits are important if, as seems to be the case, plant communities are largely under dominance control (Yodzis 1986). The experiment presented here is a first step toward constructing guilds; further studies are underway to determine the minimum number of easily-measured functional traits that can be used for a more rapid classification of wetland plants into functional groups.

Material and Methods

Plants were germinated and grown from May to September 1988 in an outdoor compound at Carleton University, Ottawa, Canada. Each plant was grown individually in a 11.4 L pot containing 10 litres of a

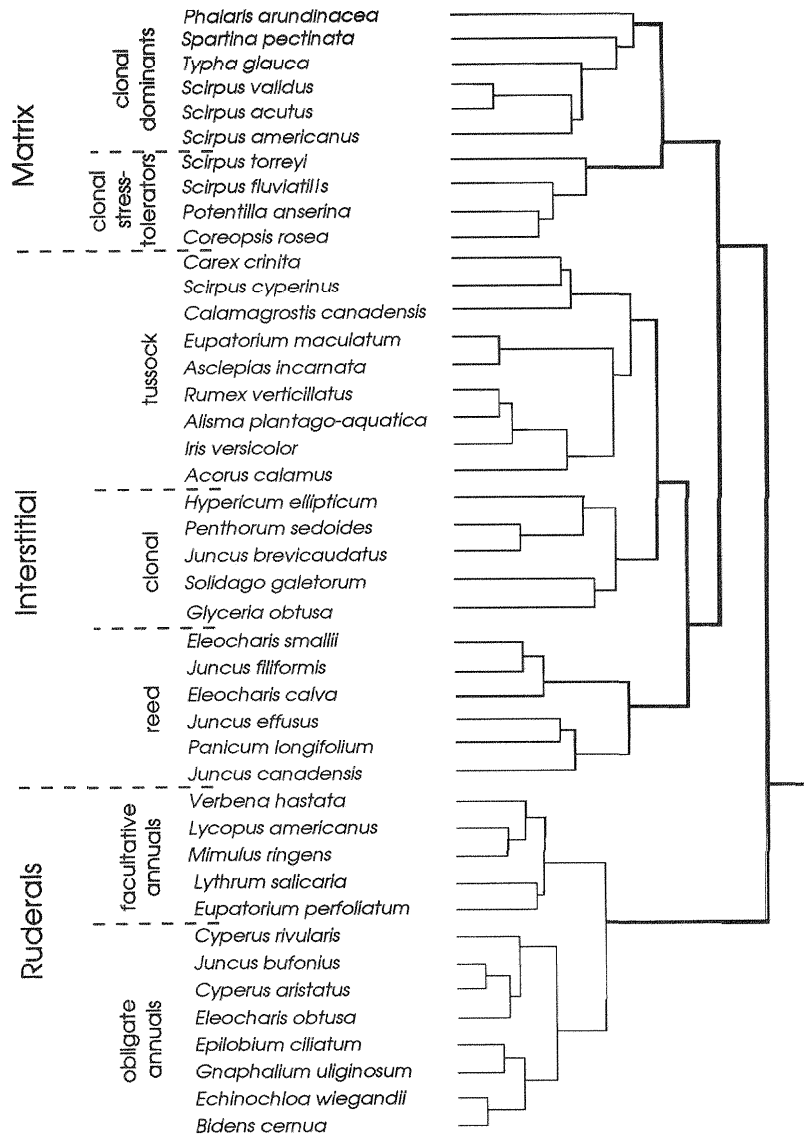


Fig. 2. Dendrogram showing agglomerative clustering of 43 wetland plant species of contrasting ecology. Functional groups are labelled on the left side.

mixture of washed sand (75 %) and commercial potting soil (25 %). From preliminary tests this mixture gives good growth with most wetland species. Two holes (7 mm diameter) were drilled in each pot, 5 cm from the top, to maintain near-flooded conditions in the spring; in mid-June one more hole, 5 cm from bottom, was added to allow the water table to fall. On the 31st of May and 1st of June, seeds were sown on top of the soil and a Petri dish lid was put on top of them to keep the area moist and to prevent the seeds from blowing away. As soon as seedlings were well-established, the dishes were removed. Plants were watered every day and then thinned (or, where necessary, transplanted) to one per pot. Sixty species were at first selected for their different habitats, life forms and life histories; plants of 43 species survived in sufficient numbers. There were 14 replicates

per species for a total of 602 plants.

Standard hydroponic solution fertilizer (7-11-27 + 15-0-0) was added 29 June and 6 July at the rate of 6 g per pot. Slow release fertilizer (10-25-10) was added on 11 July and 1 August at the rate of 3.5 g per pot.

Half the replicates were harvested during the first two weeks of September, the other half being kept for testing predictions from this work. Traits measured in the course of the 1988 growing season and at harvest are shown in Table 1. Traits 20 to 26 were measured on adult plants between mid-August and early October in wetlands near the Ottawa River and some at Wilson Lake, in Nova Scotia, Canada; these are considered as adult traits rather than juvenile traits from the screening experiment. RGR measurements (trait 27) were determined on seedlings between days 10 and 30 grown

Table 1. Traits measured on wetland plant species.**a. Traits measured on 1-yr old plants in the garden**

- 1 Life span:
 - 1 = annuals
 - 2 = facultative annuals (100 % flowering)
 - 3 = partly facultative annuals (>50 < 100 % flowering)
 - 4 = perennials (<50% flowering)
- 2 % flowering first year
- 3 Final height or highest height (cm)
- 4 Rate of shoot extension (cm/day):

$$\frac{\log_n \text{ height at day 94} - \log_n \text{ height at day 36}}{\text{Day 94} - \text{Day 36}}$$
- 5 Total biomass at harvest (g)
- 6 Above-ground biomass (g)
- 7 Below-ground biomass (g)
- 8 Ratio below-ground / above-ground biomass
- 9 Photosynthetic area (cm²): includes leaves and green stems
- 10 Photosynthetic area/ total biomass (cm²/g)
- 11 Photosynthetic area/ total volume occupied by a plant (cm²/ml) measured by displacement of water in graduate cylinder
- 12 Total biomass/ total volume (g/ml)
- 13 Total number of tillers or shoots
- 14 Crown cover (cm²): $((D_1 + D_2)/4)^2$ where D_1 = 1st measure of crown diameter and D_2 = 2nd measurement at right angle to first
- 15 Stem diameter at ground level (cm)
- 16 Depth to below-ground system (cm)
- 17 Diameter of below-ground system i.e. rhizome or main roots (cm)
- 18,19 Shortest (18) and longest (19) distances between two shoots or tillers (measure of degree of clumping of aerial stems) (cm)

b. Traits measured on plants in natural wetlands (adult traits)

- 20 Total height (cm)
- 21 Total number of tillers or shoots
- 22 Stem diameter at ground level (cm)
- 23,24 Shortest (23) and longest (24) distances between two shoots or tillers (cm)
- 25 Diameter of below-ground system i.e. rhizome or main roots (cm)
- 26 Depth to below-ground system (cm)

c. Trait measured under greenhouse conditions

- 27 Relative Growth Rate (RGR) (g.g/day) between 10 and 30 days (from Shipley & Peters 1990).

under greenhouse conditions (see Shipley & Peters 1990).

Clustering of the matrix of 43 species by 27 traits was carried out using an agglomerative approach. Variables were standardized and Pearson correlation coefficients were used; the clustering was done by average linkage where the admission into a cluster is based on the average of the similarities of that character with members of the cluster (Wilkinson 1984). Discriminant analyses were performed for different groups, using SPSSX, and the pooled within-groups correlations between the variables and the discriminant function(s) were used to explore the traits best distinguishing among functional groups (Norusis 1985).

Results*The guild classification*

Fig. 2 shows the dendrogram resulting from the cluster analysis done with the 43 species that survived to the adult stage. Long-lived clonal perennials are found near the top, whereas small annuals are found near the bottom. There were three main groups, each containing two or three sub-groups, for a total of seven guilds or functional groups (provisional guild names were assigned on the left hand side).

Discriminant analysis

Discriminant analyses were performed to explore further the traits associated with different functional groups. The first one shows that perennials and ruderals do not overlap (Fig. 3a). The variables that best separate the two groups are percentage flowering in the first growing season, and life span. Photosynthetic area was also important.

The second discriminant analysis was done between matrix species and interstitial species (Fig. 3b). Again there was no overlap. The variables that best separate the two groups are relative growth rate, diameter of the below-ground structures and the clumping of shoots. When three groups were considered in the discriminant analysis (ruderals, matrix and interstitial species), a clear separation occurred again (Fig. 3c). The first function which explains 89 % of the variance, is defined with traits of the clumping of shoots, the number of shoots or tillers, and characteristics of the below-ground structures. The second function is mainly defined by the percentage of flowering and life span. The overall discriminant analysis with seven guilds (not illustrated) showed a clear separation between the interstitial, matrix and ruderal species on the basis of clumping, life span, percentage of flowering and size.

Traits of guilds

To assist in providing ecological interpretations of the seven groups, means and 95 % confidence intervals of the 27 traits were calculated for each (Table 2). Mann-Whitney tests were used to detect which traits were significantly different among groups at different levels in the classification tree (Table 3). For example, Table 3 shows that at the first fork in the tree, 18 traits were significantly different between the two groups but some group means overlapped for 11 of these. The remaining 7 traits, marked with asterisks, are critical traits for the first fork in the dendrogram. (Since there were 162 pair-wise tests, caution should be used when

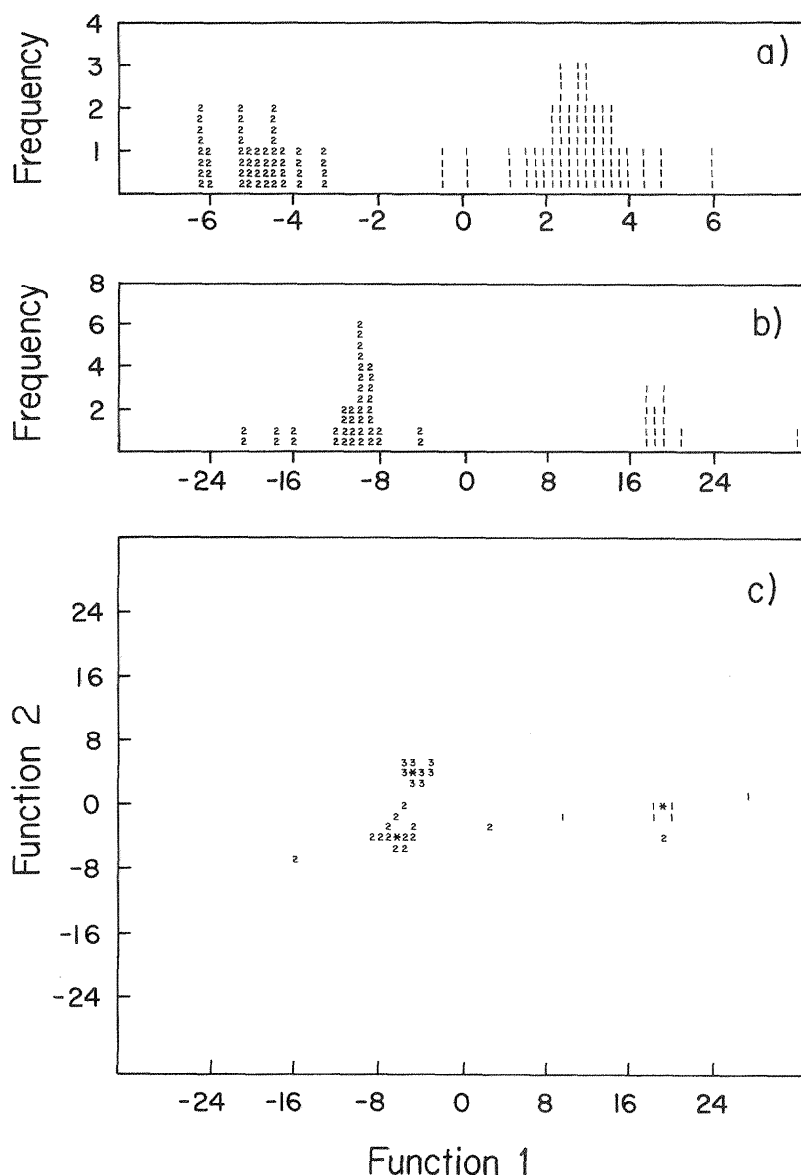


Fig. 3. Results of discriminant analyses at different stages in the classification. Figures show discriminant plots; the factors with the heaviest contribution to separation of groups as measured by pooled within-group correlations between discriminant variables and canonical discriminant functions are given in parentheses:

a. Perennial and ruderal; (key traits: % flowering, -0.55; Life span, 0.52, Photosynthetic area, -0.28);

b. Matrix and interstitial; (key traits: Relative growth rate, -0.29; Below-ground diameter in the field, 0.27; Shortest distance between shoots in the field, 0.26);

c. Matrix, interstitial and ruderal species; (key traits on axis 1: Longest distance between shoots in the field, 0.13; Longest distance between shoots in the garden, 0.12, Shortest distance between shoots in the garden 0.10. Key traits on axis 2: Percent flowering 0.53, Life span -0.51, Photosynthetic area 0.29).

interpreting p -values, particularly those greater than $p=0.01$.) The same process was followed for forks two and three. For forks four, five and six all the traits with significant differences were considered; the results are given in Fig. 4, which combines a summary of the dendrogram with key traits indicated.

Summary of guilds

Of the two main groups, one subgroup of 13 species had a high percentage of individuals and species flowering in their first growing season, and no lateral spreading of their vegetative growth (Fig. 4). They put emphasis on photosynthetic tissues with a high photosynthetic area and a low below-ground to above-ground biomass

ratio. In contrast the other group of 30 species did not flower much in their first year of growth but they expanded the vegetative parts, especially the below-ground system. These two groups apparently reflect the distinction between 'ruderal' (sensu Grime 1979) and 'perennial' strategies.

The 'ruderals' consisted of two further groups. While plants in both groups flowered in the first year, one subgroup died at the end of the growing season ('obligate annuals') whereas the other was perennial ('facultative annuals'). 'Obligate annuals' (e.g. *Bidens cernua*) also had numerous short stems, a large crown area and a tendency to direct more growth towards the above-ground structures relative to facultative annuals; they died at the end of the growing season. The 'facultative

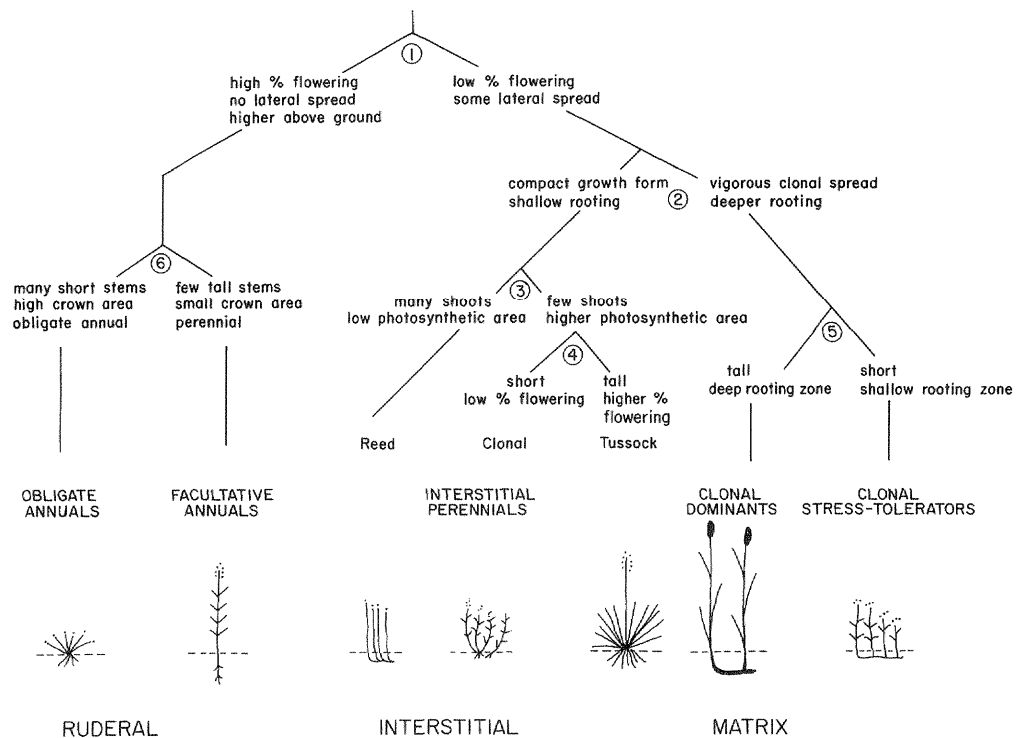


Fig. 4. Summary of the dendrogram given in Fig. 2, emphasizing plant traits and major functional groups. The number at each bifurcation corresponds to the analysis given in Table 3.

annuals' were tall with an erect, fast-growing main stem (e.g. *Verbena hastata*). Shoots emerged from the base of this stem the next year, again producing tall plants with a narrow, erect growth form topped by an inflorescence.

Within the 'perennials', there was a clear distinction between species which spread clonally and species with a more clumped growth form. The clonally spreading species had a deep and massive below-ground structure, which produced the high below-ground to above-ground biomass ratio. Probably, this also accounts for the high biomass to volume ratio of this group of species since roots and rhizomes are usually more dense than leaves and stems. The species with a clumped growth form were more compact in their growth with shallow and rather smaller below-ground structures. We have called these two types 'matrix species' and 'interstitial species' respectively (sensu Grubb 1986). At a finer scale, the 'matrix species' further comprised two groups. One consisted of tall and robust species with vigorous lateral spread that frequently produce large monospecific stands in fertile habitats (e.g. *Typha glauca*); we have called them 'clonal dominants'. The other group had a similar growth pattern but was much smaller and consequently did not produce dense canopies; these were species more typical of infertile sand and gravel shorelines (e.g.

Scirpus torreyi); we have therefore called them 'clonal stress tolerators'.

The finer scale of guilds in the interstitial group was not so well-defined, but three sub-groups could be found. One sub-group consisted largely of 'reeds', plants with numerous but essentially leafless aerial shoots (e.g. *Eleocharis smallii*); we have called them 'reed interstitials'. The remaining two sub-groups differed only in that one group was consistently larger in the field and flowered later; many had a large tussock growth form (e.g. *Carex crinita*). We have called these plants 'tussock interstitials'. The smaller guild consisted of neither reed-like nor tussock growth forms, and tended to be weakly spreading (e.g. *Penthorum sedoides*). The greater flowering in this group suggests that some of these interstitial species possessed traits tending towards the ruderals discussed above. We called them 'clonal interstitial species'. A sketch of each guild is shown in Fig. 4. Given the heterogeneity of the interstitial group, it may be best to consider it as one group until additional species and traits in this group are evaluated.

Table 2. Mean values 95% confidence interval for 27 traits in 7 guilds of wetland plants.

Traits (see Table 1)	Guilds						
	Ruderal		Interstitial			Matrix	
	Annual obligate (8) ¹	Annual facultative (5)	Reed interstitial (6)	Clonal interstitial (9)	Tussock interstitial (9)	Clonal stress tolerator (4)	Clonal dominant (6)
Measured in the garden							
1. Lifespan	1.12 ± 0.29	2.4 ± 0.69	3.83 ± 0.43	3.4 ± 0.69	4.0 ± 0	4.0 ± 0	3.83 ± 0.4
2. % flower	100.0 ± 0	92.8 ± 15.6	20.0 ± 29.2	42.8 ± 43.3	3.11 ± 4.7	7.25 ± 23.0	14.33 ± 23.7
3. Height (cm)	38.4 ± 28.2	43.5 ± 11.5	23.4 ± 11.9	15.5 ± 13.8	19.9 ± 6.1	16.8 ± 23.5	59.0 ± 13.9
4. Rate of shoot extension (cm/day)	0.039 ± 0.005	0.065 ± 0.011	0.50 ± 0.009	0.047 ± 0.02	0.050 ± 0.007	0.047 ± 0.013	0.046 ± 0.018
5. Total biomass (g)	23.8 ± 18.0	12.2 ± 6.5	6.8 ± 8.9	1.6 ± 1.3	2.3 ± 1.0	2.3 ± 4.9	15.6 ± 8.7
6. Above-ground biomass (ab) (g)	15.7 ± 12.0	5.3 ± 2.4	1.9 ± 1.7	0.72 ± 0.55	0.91 ± 0.42	0.81 ± 1.50	4.4 ± 2.7
7. Below-ground biomass (be) (g)	8.0 ± 6.0	6.8 ± 4.1	4.9 ± 7.4	0.96 ± 0.78	1.4 ± 0.65	1.5 ± 3.5	11.1 ± 6.2
8. Ratio be/ab	0.54 ± 0.12	1.3 ± 0.22	2.0 ± 2.0	1.4 ± 0.56	1.8 ± 0.37	2.2 ± 1.2	2.8 ± 0.93
9. Photosynthetic area (Pa) (cm ²)	709.1 ± 334.0	501.0 ± 322.2	126.1 ± 142.6	86.2 ± 77.0	127.5 ± 64.2	80.7 ± 153.8	319.0 ± 247.6
10. Pa / total biomass (cm ² /g)	36.0 ± 7.6	37.5 ± 7.2	31.0 ± 14.4	56.2 ± 10.5	59.0 ± 11.3	31.5 ± 12.5	20.7 ± 7.0
11. Pa / volume (cm ² /mL)	4.9 ± 1.3	5.1 ± 1.5	2.8 ± 0.5	5.5 ± 1.6	5.3 ± 0.8	5.2 ± 2.5	2.6 ± 1.3
12. Total biomass / volume (g/mL)	0.135 ± 0.026	0.137 ± 0.044	0.098 ± 0.028	0.106 ± 0.040	0.102 ± 0.021	0.191 ± 0.150	0.128 ± 0.040
13. Number of shoots	98.4 ± 98.0	1.0 ± 0	148.0 ± 265.0	9.6 ± 16.0	4.1 ± 4.0	5.9 ± 6.0	13.8 ± 8.8
14. Crown area (cm ²)	0.134 ± 0.090	0.030 ± 0.025	0.028 ± 0.020	0.013 ± 0.011	0.027 ± 0.030	0.030 ± 0.070	0.132 ± 0.080
15. Stem diameter (cm)	0.45 ± 0.27	0.61 ± 0.16	0.21 ± 0.12	0.26 ± 0.17	0.62 ± 0.25	0.46 ± 0.45	0.64 ± 0.33
16. Rooting depth (cm)	1.2 ± 0.35	2.7 ± 2.4	3.4 ± 2.8	2.0 ± 1.8	2.9 ± 0.88	4.9 ± 8.9	14.3 ± 9.0
17. Diameter below-ground (cm)	0.10 ± 0.05	0.45 ± 0.29	0.18 ± 0.07	0.19 ± 0.13	0.40 ± 0.33	0.22 ± 0.07	0.57 ± 0.27
18. Shortest distance (cm)	0.062 ± 0.043	0 -	0.106 ± 0.009	0.053 ± 0.095	0.057 ± 0.057	2.366 ± 0.404	0.59 ± 0.344
19. Longest distance (cm)	0.062 ± 0.043	0 -	0.587 ± 0.784	0.733 ± 1.96	0.617 ± 1.45	7.29 ± 6.31	4.43 ± 1.86
Measured in the field							
20. Total height (cm)	30.9 ± 21.0	77.6 ± 55.0	57.2 ± 23.1	38.4 ± 24.4	106.0 ± 28.5	49.0 ± 51.6	138.0 ± 39.0
21. Number of shoots	22.3 ± 28.5	2.6 ± 3.7	31.2 ± 18.7	3.6 ± 4.0	6.0 ± 4.2	3.7 ± 4.2	5.4 ± 4.6
22. Stem diameter (cm)	0.3 ± 0.2	0.6 ± 0.3	0.3 ± 0.3	0.3 ± 0.3	0.7 ± 0.2	0.7 ± 0.6	0.9 ± 0.3
23. Shortest distance (cm)	0.1 ± 0	0.2 ± 0.3	0.1 ± 0	1.4 ± 2.2	1.0 ± 1.1	2.7 ± 4.0	3.1 ± 3.6
24. Longest distance (cm)	0.1 ± 0	0.9 ± 2.2	1.5 ± 1.0	5.4 ± 11.1	1.7 ± 1.4	6.2 ± 7.0	9.2 ± 3.1
25. Diameter below-ground (cm)	0 ± 0	0.7 ± 0.3	0.3 ± 0.5	0.3 ± 0.3	0.9 ± 0.5	0.3 ± 0.3	0.8 ± 0.3
26. Rooting depth (cm)	0.7 ± 0.2	1.9 ± 1.0	1.4 ± 0.5	1.1 ± 0.8	1.7 ± 0.9	2.6 ± 2.5	4.6 ± 1.5
Measured in the greenhouse							
27. RGR (g-g/day)	0.253 ± 0.031	0.258 ± 0.005	0.195 ± 0.059	0.280 ± 0.130	0.189 ± 0.030	0.203 ± 0.120	0.170 ± 0.051

¹ = The number in brackets is the number of species assigned to that functional group.

Traits	Division in dendrogram					
	1	2	3	4	5	6
Measured in the garden						
Lifespan	0.000 *	-	-	0.012	0.003 *	-
% flowering	0.000 *	-	-	0.012 *	-	-
Height	-	-	-	-	-	0.025 *
Rate of shoot extension	-	-	-	-	0.003 *	-
Total biomass	0.000	-	-	-	-	0.025 *
Above-ground biomass	0.000 *	-	-	-	0.008 *	0.025 *
Below-ground biomass	0.009	-	-	-	-	0.025 *
Ratio below / above-ground biomass	0.000 *	0.033 *	-	-	0.003 *	-
Photosynthetic area	0.000 *	-	-	-	-	0.053 *
Photosynthetic area / total biomass	-	0.004	0.007 *	-	-	0.053 *
Photosynthetic area / volume	-	-	0.003 *	-	-	0.053 *
Dry weight - volume	0.031	0.045 *	-	-	-	-
Number of shoots	-	-	0.003 *	-	0.037 *	0.025 *
Crown area	0.025	-	-	-	0.013 *	-
Stem diameter	-	-	0.018	-	-	-
Rooting depth	0.008	-	-	-	0.014 *	-
Below-ground diameter	-	0.011	-	-	0.005 *	0.025 *
Shortest distance	0.002	0.000 *	-	-	0.030 *	0.025 *
Longest distance	0.002 *	0.000 *	-	-	0.030 *	-
Measured in the field						
Total height	0.044	-	-	0.020 *	0.040 *	0.025 *
Number of shoots	-	-	0.003 *	-	-	-
Stem diameter	-	0.037	0.027	0.020 *	0.022 *	-
Shortest distance	0.007	0.025 *	-	-	-	-
Longest distance	0.001 *	0.003 *	-	-	-	-
Diameter below-ground	0.025	-	-	-	0.001 *	0.024 *
Rooting depth	0.044	0.005 *	-	-	0.033 *	0.025 *
Measured in the greenhouse						
Relative growth rate	0.003	-	-	-	-	-

Table 3. The traits found significantly different (using the Mann-Whitney *u* test) among groups at each division of the dendrogram shown in Fig. 4. *P*-values are given and those values marked with asterisks identify the traits where there was a significant difference among groups and no overlap in the trait means of the groups.

Discussion

The principal objective of this paper was to present a general rationale and methodology for constructing guilds in plant communities. A major obstacle encountered in studying patterns and processes in plant communities is the large number of species that are present which generate undue complexity (Wimsatt 1982; Rigler 1982). One route around this obstacle is to amalgamate groups of species into guilds or functionally similar groups which share ecological traits and which presumably play similar roles in ecological communities. In our example, the number of components in the wetland vegetation was reduced from 43 species to 7 guilds. Of course, since these 43 species were selected from a much larger pool of wetland plants, the 7 guilds actually represent much of the variation in this larger pool of hundreds of species.

Our data set did not include a distinctive group of evergreen rosette species (e.g. *Lobelia dortmanna*, *Eriocaulon septangulare*, *Isoetes* spp.), termed 'isoetids' (Hutchinson 1975). Unfortunately, these species are very difficult to germinate and grow. Perhaps an additional guild of 'stress tolerators' (sensu Grime 1973, 1977, 1979) should be created to include such species. Evidence supporting this comes from data on their physiology (Boston & Adams 1986, 1987), relative growth rates (Shipley & Peters 1990), competitive ability (Wilson & Keddy 1986; Gaudet & Keddy 1988) and field distribution (Moore et al. 1989; Wisheu & Keddy 1989a).

A few anomalies were noteworthy. Given its life form and habitat, we expected that *Asclepias incarnata* would be classified near species such as *Verbena hastata* and *Mimulus ringens* ('facultative annuals'), but it did not flower in the first year as did the remainder of these species. We were also surprised that *Epilobium ciliatum* was classified as an obligate annual, since it often grew with facultative annuals in the field. The data for the classification did not include whether or not a species overwintered, so ability to overwinter provided a good independent test of membership in this guild. All of the individuals of this species died after a single year of growth, contrary to our expectations, but consistent with the classification.

Our results appear consistent with other studies of guilds. For example, species which colonize gaps in existing vegetation have been called ruderals by Grime (1974, 1977) and have been described in habitats ranging from prairies (Platt & Weis 1977) to wetlands (van der Valk 1981; Day et al. 1988). Grubb (1986) has described the distinction between matrix and interstitial species in chalk grassland. Similarly, van der Valk (1981) has drawn attention to the dichotomy between

mud flat annuals and long-lived perennials in prairie wetlands. Each of these (and the many others reviewed in the introduction) draw attention to different sets of traits, different functional groups, and different ecological processes. Our work suggests that these views can be combined to describe the many types of guilds which occur in a single habitat: temperate zone wetlands.

Most of the guilds appear to fall along a continuum of life histories adjusted to different light regimes. This is consistent with the growing body of literature proposing that light gradients are of over-riding importance in the evolution of plant traits and the functioning of plant communities (e.g. Grime 1977, 1979; Givnish 1982; Tilman 1982, 1986, 1988; Keddy 1989a). It is also consistent with the role which disturbance and gaps play in the non-equilibrium coexistence of plants (Grubb 1977; Pickett 1980; Pickett & White 1985). This has been specifically discussed for wetland plants in Shipley et al. (1989). Lastly, it is also consistent with the growing body of literature showing that standing crop gradients can predict species richness and life form in plant communities (e.g. Grime 1973, 1979; Al-Mufti et al. 1977; Moore et al. 1989; Wisheu & Keddy 1989b). This suggests that light:nutrient ratio models, standing crop models, and guild models are all different representations of an underlying generality in the structure and function of plant communities.

Guilds as a tool for predictions

The major emphasis of guild studies is still upon description and comparison (e.g. Terborgh & Robinson 1986), but guilds may also be valuable tools for prediction. For instance we may wish to predict how a specified perturbation will convert one vector of species abundances to another (Lewontin 1974; Keddy 1989b). Here the 43 species we studied (which represent the range of variation found in hundreds of other wetland plant species), might be reduced to a column vector of only 4 guilds. We might then explore how changes in different sets of environmental factors would transform the abundances of these guilds through time. For example, any factor which increases productivity or decreases disturbance would reduce light availability and reduce regeneration opportunities; we would then predict a gradual shift away from obligate and facultative annuals to clonal dominants. Conversely, if the wetland were subjected to fluctuating water levels, grazing, or recreational development, we would expect a shift towards the ruderal and gap colonizer end of the continuum. If the disturbances created only small gaps - say due to increased population sizes of a small mammal, then only the interstitial species and facultative annuals would be predicted to increase.

An example of this approach can be found in van der Valk (1981)'s study of prairie wetlands. Species were divided into 12 'life history types' and a series of rules derived for converting the vegetation from one life history type to another. Similarly, Noble & Slatyer (1980) used series of 'vital attributes' to recognize 30 different 'species types'. They then present a series of rules for predicting changes in vegetation after fire.

Conclusion

Since we are in the early phase of objectively classifying plants into functional groups, there are many opportunities for research, especially in relation to conservation and models for predictions. Unanswered questions would include: 1. What are the best traits for measuring the functional roles of plants in vegetation? 2. What are the minimum number of traits we need to measure to produce accurate and useful classifications of functional groups? 3. What are the most efficient methods for screening for the above traits? 4. How many functional groups are necessary for particular levels of accuracy? 5. Across how many vegetation types can one extrapolate with a particular model?

As the need for models for conservation continues to grow (e.g. Myers 1985; Starfield & Bleloch 1986) we have suggested that one possible way of dealing with this situation is to move away from species oriented models to guild oriented models. The growing number of such studies in the literature suggest that this may not only be an expedient measure for conservation biology, but a promising one for predictions.

Acknowledgements. We thank P. Fricker, C. Gaudet, S. McCanny, D. Moore, B. Shipley, I. Wisheu for helpful discussions as the work progressed. We are grateful to B. Shipley for access to the relative growth rate data from his experiments. We appreciated comments on drafts of this manuscript provided by P. Grubb, M. Johansen, D. Larson, S. McCanny and B. Shipley. We also thank J. Belcher and C. McJannet for looking after our plants in the screening experiments, and A. Payne, I. Wisheu, E. Weiher and J. Helie for assistance in preparing this manuscript. This research was supported by the Canadian Shield Foundation, by a Strategic Grant from the Natural Sciences and Engineering Research Council of Canada, and by the 'Fond pour la Formation de Chercheurs et l'Aide à la Recherche'.

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Received 9 January 1992;

Revision received 30 March 1993;

Accepted 2 April 1993.