

Evolutionary aspects of life forms in angiosperm families

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SUMMARY

The distribution patterns of life forms among extant families, subclasses and classes are described with the aim of detecting evolutionary trends. The explosive diversification of angiosperms constrains the possibilities for detecting such trends. Moreover, the extant groups of seed plants are only a small sample from the historical diversity. Nevertheless, we could distinguish between common, scattered, clustered, and rare distribution patterns among groups of families in subclasses. The rare category may represent specialized life forms, including epiphytes, carnivorous plants, (hemi)parasites, saprophytes, succulents, xerophytes, halophytes, aquatics and marsh plants. Geophytes and lianas have a more scattered distribution pattern among the families. Trees, shrubs and herbaceous plants are very common, dwarf shrubs show a more clustered distribution. These patterns may be indicative of the potential for trends and reversals. At a finer scale, it was concluded that biennials did emerge from annuals, whereas the reverse is difficult. All biennials are dicots.

Key-words: evolutionary trends, distribution patterns, life forms, morphology, plant strategies.

INTRODUCTION

Interest in plant life forms (Raunkiaer 1934; Szujkó-Lacza & Fekete 1972), growth habits (Stebbins 1950, 1974) and growth forms (Barkman 1988) seem to have been outcompeted by debates on plant strategies (Grime 1979; Tilman 1988). However, these interests are essentially similar, because life forms are types of plants having the same kind of morphological and/or physiological adaptations to one or more ecological factors. Interest in frequency distributions of life forms in plant communities (Joenje 1978) or biomes (Crawley 1986; Ingrouille 1992) has remained, as well as interest in the ecophysiology of plant life forms (Schulze 1982), but the evolutionary aspect has been paid scant attention.

The present paper describes distribution patterns of life forms among angiosperm families, subclasses and classes with the aim of detecting evolutionary trends. Interpretation of our screening results largely depends on the extent to which the classification system used really reflects the phylogenetic relationships between taxa. Chase *et al.*

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Table 1. Life forms distinguished for the present screening (indications of related terms in parentheses)

1. Woody and herbaceous life forms	
T	Trees (woody phanerophytes)
S	Shrubs (woody phanerophytes)
D	Dwarf shrubs (chamaephytes)
L	Lianas (woody or herbaceous, phanerophytic)
H	Herbaceous plants (including phanerophytic plants)
2. Life cycles	
G	Geophytes (perennial [hemi]cryptophytes)
1	Annuals
2	Biennials
3. Habitat type	
a	Aquatic freshwater plants (hydrophytes)
m	Aquatic marine plants (hydrophytes)
w	Marsh plants (helophytes)
s	Succulents
x	Xerophytes
h	Halophytes
4. Life style	
e	Epiphytes
c	Carnivorous plants
p	Parasites
hp	Hemiparasites
q	Saprophytes

(1993) screened the nucleotide sequence of *rbcL*-DNA in about 500 angiosperm species, and showed a great deal of evidence for this. When De Queiroz & Gauthier (1994) stated that the current nomenclature system is clearly non-evolutionary, they referred to the naming of taxa, rather than to the classification.

We made use of the classification system of Heywood (1978), which is mainly in accordance with Cronquist's (1968) system. We will keep an eye upon the view of Cronquist (1981) as far as the arrangement of orders in subclasses is concerned. While compiling our screening results, we will reconsider some trends and discuss at which level of classification the trends can usefully be deduced. We should emphasize that we only considered actually occurring plant species.

Schulze (1982) presented a survey of plant life-form classifications and made a selection for his ecophysiological approach. For the present purpose, we distinguished four groupings of life-forms (Table 1). Recognizing that a single species or family can combine life-forms from different groupings, we are also interested in particular combinations, e.g. whether there are aquatic annuals.

TRENDS DESCRIBED SO FAR

Stebbins (1974) tentatively described some trends in the evolution of growth habits.

Phanerophytes (trees, woody vines and herbaceous phanerophytes) are the most generalized and heterogeneous group, having in common only the characteristic that

their buds and apical shoots are far above-ground and do not die back during seasons unfavourable for growth (cold, drought). The first angiosperms originated in the tropics and were probably small, slender shrubs rather than massive trees. Most, if not all modern dicotyledonous trees have evolved from these shrubby ancestors. This trend is followed by that of shrubs to perennial herbs, in response to cold or drought. Finally, the trend results in evolution from perennials to annuals and biennials.

Woody monocots usually have an unbranched stem with a terminal crown of large leaves, a habit which is rare in dicots. These differences in habit are partly a result of the absence or poor development of cambium in monocots, in contrast to its usual presence in dicots (Cronquist 1968). Absence of cambium greatly restricts the ability of the stem to increase in thickness. Such increase can come about only through the expansion of leaf bases at a relatively early stage in the ontogeny, as in palms, or through the origin of a generalized cambial tissue that permits the differentiation of new vascular bundles, as in *Dracaena*. The palm method apparently suppresses or greatly restricts the ability of the stem to form branches, whereas that found in *Dracaena* is associated with much slower growth than that of arboreal dicots. Furthermore, the absence of a solid vascular cylinder makes the young stems so weak that they can grow upward successfully only if they have previously acquired great thickness, as in the larger palms, or if they are supported by massive surrounding leaf sheaths, as in Musaceae and the larger grasses, including bamboos. Another consequence of the absence of cambium is that the shoots of the monocots can elongate more rapidly than those of most dicots. In the tropics this favours evolution in the direction of herbaceous climbers, as in the monocotyledonous families Araceae, Commelinaceae, some climbing Palmae and Gramineae. Data supporting this statement are not available, since the herbaceous or woody origin of many lianas was often not traceable.

In conclusion, evolution of woody monocotyledons from their herbaceous ancestors is rather difficult. It might be better compared with the rare reversion of herbaceous dicots to woody plants than to the common and easy origin of herbs from woody ancestors.

Evolutionary trends in the monocots are, more than in dicots, associated with vegetative differentiation. The predominant trend has been from thicker and shorter to more elongate stems, with respect to both the aerial and subterranean parts of the plant. Examples are the climbing phanerophytes, the deep water aquatics and the most extensively rhizomatous monocots. This trend to slenderness is by no means irreversible. The rosette trees, such as the Palmae, *Yucca* and *Dracaena*, and the larger bamboos are almost certainly derived from more slender representatives of the order and are considered secondary derivatives. The same holds for aquatic and xeric forms.

The trend in life forms of dicots can be explained to a large part by reduction (Stebbins 1951; Cronquist 1968): decrease in size of the mature plant and decrease in age. Determinate vegetative-reproductive shoots of spring-blooming perennials and annuals are an example of reduction. The shift from a woody to a herbaceous life form involves reduction of secondary growth (loss of cambium) and is often connected with the replacement of the main root by an adventitious root system (Ehrendorfer 1973). Neoteny is probably also important in the general trend of reduction (Cronquist 1968).

Reversals have occurred very frequently. Terrestrial monocots, which originated from aquatic premonocots, have themselves repeatedly given rise to groups that have

returned to the water. Among the modern Alismatidae there appears to be progressive adaptation to an aquatic (eventually even marine) habitat. In the Arecidae, the terrestrial family Araceae has some secondarily aquatic forms, which gave rise to the thalloid aquatic Lemnaceae. In the Commelinidae aquatic families such as Mayacaceae, Sparganiaceae, and Typhaceae appear to be derived from terrestrial ancestors within the group. In the Liliidae, the aquatic habitat of the Pontederiaceae must be secondary (Cronquist 1968).

Though most of the dicotyledonous trees have evolved from shrubby ancestors, the reverse direction of evolution, from trees to shrubs, has undoubtedly occurred many times, e.g. in *Magnolia*, *Quercus*, *Acer* and *Salix* (Stebbins 1974). The size of an adult plant is easily reversible, as compared to the trend from woody to herbaceous plants, for example, which implies the loss of cambial meristem. Among the monocots, palms and bamboos have been documented as reversals; among the dicots, reversals have been recorded in some oceanic islands genera of the Compositae, Boraginaceae, Goodeniaceae and Campanulaceae, as well as in continental genera of the Scrophulariaceae, Phytolaccaceae, Myrtaceae, Compositae and Chenopodiaceae. The latter were associated with a climate change from mesic to xeric in the early and mid Tertiary period.

The trend from perennial to annual/biennial seems almost irreversible. Monocarpic flowering behaviour is associated with rather inflexible allocation patterns, resulting in death after reproduction.

SCREENING RESULTS AND INTERPRETATION

Life-form spectra within monocot and dicot classes (Table 2)

Meeuse (1987) suggested that the monocots diverged from their magnoliid precursors at some early stage of evolution, and recognized the possibility of a polyphyletic descent, i.e. a parallel evolution of monocotyledonous lineages. Crane *et al.* (1995), in their review of current hypotheses of angiosperm evolution, recognized two large clades (monocotyledons and eudicots) embedded within a poorly defined basal assemblage (grade of magnoliid dicots). They defined the monocotyledons as monophyletic, based on their single cotyledon and other features, eudicots being circumscribed by the production of triaperturate or triaperturate-derived pollen. This is in agreement with the results from phylogenetic analyses on the basis of *rbcL*-DNA (Chase *et al.* 1993).

Here we question what percentage of the families listed by Heywood (1978) contain species with each of the life forms distinguished in Table 1, with the aim of comparing the frequency distribution among families of the monocotyledonous and dicotyledonous classes (Table 2). It should be noted that many plant species have been categorized into more than one of the life forms defined.

Woody species are present in over 50% of the dicotyledonous families, whereas a low percentage (<10%) of monocot families contains these life forms. Most of the latter belong to the single larger family of Palmae (Cronquist 1968). However, the woody plants of the monocots are not trees and shrubs. Palms, *Pandanus* species, some Agavaceae and bamboos have special growth forms that have evolved only among the monocotyledons (Porter 1959). The frequency of dwarf shrubs is about the same in the two classes (11% in dicots and 14% in monocots). Lianas are more frequent in the dicots (27%) than in the monocots (17%).

Table 2. Life-form spectra of monocotyledonous and dicotyledonous subclasses, indicated as the percentage of families that contain species with the life form

Life forms (see Table 1)	Percentage of families	
	monocots (<i>n</i> =58)	dicots (<i>n</i> =248)
1. Woody and herbaceous life forms		
Trees	7	60
Shrubs	14	63
Dwarf shrubs	14	11
Lianas	17	27
Herbaceous plants	81	48
2. Life cycles		
Geophytes	74	16
Annuals	24	24
Biennials	—	8
3. Habitat type		
Aquatic freshwater plants	20	8
Aquatic marine plants	10	—
Marsh plants	24	2
Succulents	5	4
Xerophytes	12	3
Halophytes	5	2
4. Life style		
Epiphytes	2	5
Carnivorous plants	—	2
Parasites	—	3
Hemiparasites	—	2
Saprophytes	5	1

Herbaceous plants are much more common among monocots (the vast majority) as compared to dicots (only half). This difference is mainly due to the number of geophytes. The striking number of geophytes in the monocot families can be a consequence of the presence of numerous vascular bundles, particularly in the leaf bases, and the development of leaves with broad sheathing bases. This condition can serve as an initial modification that promotes evolution of bulb and corm geophytes (Stebbins 1974).

Annuals are evenly frequent in both classes. Biennials, however, are much less frequent and only present in dicot families.

Epiphytes, saprophytes and xerophytes are present in low frequencies within both classes. Carnivorous plants and parasites are all dicotyledonous.

Freshwater aquatics and marsh plants are much more common among monocotyledonous families compared with dicots. According to Cronquist (1981), Liliopsida are sometimes supposed to be of aquatic origin. Submerged marine plants are all monocots, they are present in >10% of the monocot families. This phenomenon can be explained by differences in shoot growth. Seed plants such as *Zostera*, *Phyllospadix* and *Posidonia*,

Table 3. Distribution of life forms within the subclasses of angiosperms (number of screened families in parentheses). Category p includes hp

	Life form (see Table 1)																	
	T	S	D	L	H	G	1	2	a	m	w	s	x	h	e	c	p	q
Dicots																		
Magnoliidae (32)	1	1	4	2	3	4	4	4	4	—	—	—	4	—	4	—	—	—
Hamamelidae (11)	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Carophyllidae (13)	3	1	3	2	1	2	3	4	—	—	—	3	—	2	4	—	—	—
Dilleniidae (60)	1	1	3	2	2	4	4	4	4	—	—	—	—	—	4	—	—	4
Rosidae (88)	1	1	3	2	2	2	2	2	2	—	2	4	4	—	—	4	3	4
Asteridae (44)	2	1	2	2	1	2	1	2	2	—	2	4	4	—	2	—	4	—
Monocots																		
Alismatidae (16)	—	1	—	—	1	2	2	—	1	2	—	—	—	4	—	—	—	4
Arecidae (21)	—	—	3	—	1	1	2	—	2	—	2	—	—	—	—	—	—	—
Commelinidae (5)	2	—	4	1	3	4	—	—	4	—	4	—	—	3	—	—	—	—
Liliidae (16)	4	2	2	2	1	1	4	—	—	—	2	—	2	—	—	—	—	—

1 Common; present in >50% of subclass families.

2 Scattered through the subclass families; present in <50% of the families.

3 Clustered; not common; present only in related families or orders.

4 Rare and only present in unrelated families.

have greatly elongated internodes and leaves (Stebbins 1974). The majority of halophytes are dicotyledonous.

Distribution patterns of life forms among families within subclasses (Table 3)

Dicots

Magnoliidae. This most primitive subclass is the basal complex from which all other angiosperm subclasses have been derived. The Magnoliales are among the three most primitive orders and do not include lianas. All three primitive orders are woody, and predominantly tropical in distribution.

Herbaceous life forms in the Magnoliidae are represented by epiphytes, carnivorous plants, aquatics, geophytes, annuals and biennials. Combinations between these occur in the Lauraceae (parasitic lianas), Peperomiaceae (epiphytic succulent geophytes), Nepenthaceae (epiphytic herbaceous lianas), and Sarraceniaceae (carnivorous geophytes). These are all very special life forms.

The general trend can be reconstructed as follows: the woody Magnoliales gave rise to the Piperales with herbaceous succulent epiphytes (Peperomiaceae), to the Aristolochiales with carnivorous epiphytes, to the aquatic Nymphaeales, and to the geophytic Ranunculaceae. The Ranunculales gave rise to the Papaverales with geophytes, annuals and biennials.

Hamamelidae. These are considered to be derived from the Magnoliidae and represent remnants of a very early line of specialization. All the families of the Hamamelidae are woody, either trees or shrubs, and are temperate in distribution. However, if the order Urticales is attributed to the Hamamelidae (Cronquist 1981) rather than to the Dilleniidae (Heywood 1978), herbaceous plants do also occur in this subclass.

Carophyllidae. This subclass has its origin in the Magnoliidae, probably in or near the Ranunculaceae.

The Caryophyllales show an almost complete spectrum of life forms. They are especially rich in dwarf shrubs, geophytes and annuals, and probably more than half of the total number of species are succulents and halophytes. Though the Phytolaccaceae are considered the most primitive family, this family already contains all perennial life forms (group 1, Table 1). Biennials only occur in the Caryophyllaceae. An interesting feature is the occurrence of epiphytic Cactaceae, which are considered to be derived from non-epiphytic Cactaceae.

Dilleniidae. This subclass again has its origin in the Magnoliidae, the Dilleniales being the connecting link. This subclass contains also a broad range of life forms, showing a general trend of diversification. Most families contain trees, shrubs, lianas and herbaceous plants. There is a high proportion of dwarf shrubs, e.g. in the Capparales and Ericales. Special features are epiphytic lianas in the Marcgraviaceae and epiphytic trees or shrubs in the Guttiferae. Geophytes are found in the relatively primitive Paeoniaceae and the more advanced Begoniaceae, Cucurbitaceae, Pyrolaceae and Primulaceae. Annuals occur in most orders, especially in the Capparales, while biennials are restricted to the Malvaceae, Cruciferae and Resedaceae. Aquatics are found in the Cruciferae. Halophytes are only represented in the interrelated Tamaricaceae and Frankeniaceae. Xerophytes occur in the Crossomataceae, Cistaceae and Fouquieriaceae. Saprophytes are among the mycotrophic Ericaceae.

Rosidae. These are a large subclass, derived from the Magnoliidae, parallel with the Dilleniidae. Here again a general trend of diversification is shown. Trees and shrubs are common in nearly all the families of the Rosidae. Dwarf shrubs are very common in the Rosales, while lianas are scattered through the whole subclass. The latter holds also for the geophytes and annuals. In some families with annuals there are also biennials. Aquatics and marsh plants are frequent in the Fabales, Podostemales (submerged and extremely modified freshwater aquatics) and most families of the Halogorales and Myrtales. Succulents are restricted to the Crassulaceae, Euphorbiaceae and Oxidaceae, xerophytes to the Fabales and Proteales. Carnivorous plants occur in the Rosales, epiphytes are restricted to the Melastomaceae and Santalaceae, parasites and half-parasites to most of the families of the Santalales and Rafflesiales, while saprophytes are found only in the Polygalaceae.

Asteridae. This subclass is derived from the Rosidae (especially the Rosales), and is the most advanced subclass of the dicots. A large spectrum of life forms is shown. Most families contain shrubs, and to a lesser degree trees and lianas as well. Dwarf shrubs are restricted to a few families. Almost every family of the Asteridae contains herbaceous forms. Geophytes are especially frequent among the Polemoniales and Scrophulariales. The majority of families contain annuals, a few of these also biennials. Freshwater aquatics are not frequent, but still numerous. Succulents and xerophytes are not very frequent, and neither are epiphytes, saprophytes and parasites. Succulent epiphytes occur in the Asclepiadaceae and Gesneriaceae. Some families (Acanthaceae, Lobeliaceae, Compositae) contain both aquatics and xerophytes.

Monocots

Alismatidae. This is the most primitive subclass of the monocotyledons (Cronquist 1981). However, they are not considered to be on the main line of evolution of the class, but a near-basal sidebranch, a relictual group which has retained many primitive characters. They are considered to be connected to the dicotyledons with the Magnoliidae, more specially the order Nymphaeales.

The Alismatidae are very restricted in their life forms. They are all freshwater aquatic or semi-aquatic herbaceous plants, except for the saprophytic and less related Triuridales. They are the only subclass of the angiosperms in which (submerged) marine plants have evolved. The presence of geophytes, and to a lesser degree annuals (together with the aquatic habit) is very common, too.

Arecidae. These are considered as an early, specialized sidebranch of the main line of evolution of the monocotyledons. A loose affinity among the four orders is widely recognized (Cronquist 1981).

Half of the species are arborescent, especially the Palmae and Pandanaceae. Lianas are also frequent, except for the Lemnaceae which are aquatic plants (derived from the Araceae). The Cyclanthaceae and Araceae show the unusual combination of shrubby plants, lianas, geophytes and epiphytes.

Commelinidae. The vast majority of this subclass are terrestrial herbs, often occurring in moist sites. Though all the families of the Commelinidae express the herbaceous habit, and nearly all of them are geophytic as well, they are ecologically much more divergent than the Alismatidae. Most families, except for the Bromeliales and Zingiberales, contain marsh plants. Submerged aquatic plants are less common and scattered through the subclass. Succulence is only known from the Commelinaceae. Epiphytism and xerophytism both occur in the Bromeliaceae. The arborescent or shrubby habit (megaphytes) is shown in the Gramineae, Juncaceae, Bromeliaceae, and especially in most families of the Zingiberales.

Liliidae. This most advanced subclass of the monocots is more related to the Commelinidae than to any other subclass. They are supposed to have a common ancestor. The arborescent (megaphytic) habit and lianas occur frequently. Nearly all the families of the Liliidae contain geophytic herbs, e.g. the bulbous habit of the Liliaceae and Iridaceae. Annuals occur only in the Pontederiaceae and Burmanniaceae. Freshwater aquatics are only known from the Pontederiaceae. Xerophytism is very common, while succulence occurs in the Liliaceae and Agavaceae. Among the mycotrophic Orchidales there are saprophytes, xerophytes and epiphytes.

Combinations of life forms within dicotyledonous families

Table 4 presents the results of a screening of the frequencies of combinations of four selected life forms (trees, shrubs, lianas, herbaceous plants) among species within a large number of dicotyledonous families. Note that the combinations are not entirely exclusive among one another. The actual relative frequency index of a combination may result from both directional trends and reversals in the past. The large number of families containing TS (the only index > 1) might indicate that this transition is relatively easy (in both directions). The index for SH is also relatively high (c. 1). All other

Table 4. Absolute number (N) and frequency index (x) of combinations of life forms (trees, shrubs, lianas, herbaceous plants) within dicotyledonous families. The frequency index is the ratio between the number of families with a combination of life forms as compared to the sum of the number of families with each of the relevant components (given below each of the combinations)

Life form	N	x	Life form	N	x
TS	51	>1	TSL	20	<1
T	22		TS	51	
S	12		TL	3	
			SL	3	
TL	3	≪1	TSH	21	<1
T	22		TS	51	
L	3		TH	2	
			SH	31	
TH	2	≪1	TLH	2	<1
T	22		TL	3	
H	28		TH	2	
			LH	0	
SL	3	<1	SLH	5	≪1
S	12		SL	3	
L	3		SH	31	
			LH	0	
SH	31	c.1	TSLH	26	<1
S	12		TSL	20	
H	28		TSH	21	
			TLH	2	

combinations are not frequent as compared to the components, which suggests rather difficult transitions. The most infrequent combinations are TL and TH. These screening results are largely in accordance with Stebbins' (1951) view.

Further screening revealed that biennials do not occur in families without annuals (19 families), while annuals are more frequently present in families without biennials (51 families). This result, in support of the view that biennials originated from annuals, is in agreement with the screening results of European dicot families by Schat *et al.* (1989). Indeed, monocots have no potential to form a taproot, which characterizes the majority of biennials. The trend from perennial to annual and the trend from annual to biennial are probably irreversible, although Gottlieb (1984) has shown that the difference between annuals and biennials within a species may be governed by only one or two genes.

With respect to the other herbaceous life forms, the frequencies of the combinations were too low to allow conclusions to be drawn.

CONCLUDING REMARKS

The explosive diversification of angiosperms restricts the possibilities of detecting trends in life forms. This problem holds even stronger if we recognize that the extant groups of

seed plants are only a poor sample of the total historical diversity of the seed plant clade (Crane *et al.* 1995). Actually, directional trends and reversals cannot be distinguished and together come under the umbrella of transitions in the past. Only in the case of trends from woody to herbaceous plants and of perennials to annual and biennial plants can we assume irreversibility. Once lost, cambium and polycarpy are relatively difficult to regain.

As far as life forms are concerned we distinguished different levels of classification for our screening. At the level of classes, we can see that there is a lack of biennials, carnivorous plants and parasites among the monocots, while submerged marine plants are all monocotyledonous. The majority of woody plants occur in dicot families.

At the level of subclasses, it became clear that there is a lot of differentiation in life forms within each of the subclasses, which restricts the possibilities of detecting trends. Trees, shrubs and herbaceous plants have a very common distribution in most of the subclasses. Geophytes, marsh plants and lianas have a more scattered distribution. Only dwarf shrubs show a more clustered distribution. Epiphytes, saprophytes, xerophytes, annuals and biennials are rare throughout. Aquatics are rare or show at least a scattered distribution pattern among the families. The remaining life forms are only present in a few subclasses. Transitions may become more difficult in the order from common to scattered to clustered to rare (see the four categories distinguished in Table 3). Thus, epiphytes, carnivorous plants, parasites, saprophytes, succulents, xerophytes, halophytes, aquatics and marshplants—all showing a rare pattern among the families of the subclasses—may represent highly specialized life forms, difficult to reverse. For example, (hemi)parasites occur in only a few lineages, which have been classified in separate (sub)families or even orders, due to a drastic and complex divergence. Consequently, the future evolutionary potentiality of lineages with such life forms are severely curtailed, which in turn suggests a high degree of canalization in these lines.

Some trends could be detected at the level of orders or families. Biennials do not occur in families without annuals, suggesting that biennials derived from annuals after the latter had been evolved from perennial herbs. Combinations of freshwater aquatics, marine, and marsh plants in mesic habitats, and of succulents, xerophytes and halophytes in xeric habitats are expected to be more common than combinations of mesic and xeric forms. Something similar may be true for hemiparasites, parasites, saprophytes and mycotrophic forms. However, the family level screening resulted in frequencies too low to draw conclusions about the reality of these potentialities.

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