

ECOLOGICAL ASPECTS OF THE CRETACEOUS FLOWERING PLANT RADIATION¹

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ABSTRACT

The first flowering plant fossils occur as rare, undiverse pollen grains in the Early Cretaceous (Valanginian-Hauterivian). Angiosperms diversified slowly during the Barremian-Aptian but rapidly during the Albian-Cenomanian. By the end of the Cretaceous, at least half of the living angiosperm orders were present, and angiosperms were greater than 70% of terrestrial plant species globally. The rapid diversification of the group, and its dominance in modern vegetation, has led to the idea that the Cretaceous radiation of angiosperms also represents their rise to vegetational dominance.

Paleoecological data cast a different light on the Cretaceous radiation of angiosperms. Analyses of sedimentary environments indicate that angiosperms not only originated in unstable habitats but remained centered there through most of the Cretaceous. Morphology of leaves, seeds, and wood is consistent with the status of most Cretaceous angiosperms as herbs to small trees with early successional strategy. The diversification of flowering plants in the Cretaceous represents the evolution of a highly speciose clade of weeds but not necessarily a major change in global vegetation.

INTRODUCTION

Flowering plants, or angiosperms, are presently the most dominant group of terrestrial autotrophs. They span an array of habits including very large trees,

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lianas, epiphytes, smaller trees and shrubs, scrambling vines, a variety of herbs, and an assortment of floating aquatic and submerged plants. Their life histories vary from slow-maturing species with individuals having life spans of centuries or millenia to annual herbs that complete generations in a single growing season. With the exception of high-latitude and montane conifer forests, most of the world's major biomes, from wet tropical forest to temperate deciduous forest to steppe to tropical grassland and desert, are overwhelmingly occupied by angiosperms, both in terms of biomass and number of species. Furthermore, the interactions between flowering plants and their pollinators, dispersers, and herbivores are a major feature of the ecological web in most regions, and these interactions play an important role in the generation and maintenance of biological diversity in terrestrial communities.

Despite the singular ecological significance and species diversity of angiosperms, they are not in a genealogical sense one of the major branches of land plants and did not originate with other major land plant clades (e.g. lycopsids, ferns, conifers, cycads, ginkgos) during the middle or late Paleozoic. The occurrence of fossils of the angiosperm sister groups Gnetales and Bennettitales in the early Mesozoic implies that the ancestors of angiosperms may have been a distinct lineage as early as the Late Triassic. Angiosperms *sensu stricto* (i.e. the group including all extant flowering plants and their last common ancestor) could have arisen at any time between the Late Triassic and the Early Cretaceous. The oldest reliably identified angiosperm fossils are Early Cretaceous (Valanginian-Hauterivian), and the stratigraphic appearance of increasingly complex forms makes it clear that the primary radiation of the group occurred during the late Early Cretaceous. The importance of angiosperms in modern vegetation is thus in striking contrast with the relatively recent origin and diversification of the group.

The spectacular diversity and dominance achieved by the angiosperms since the Early Cretaceous generally has been explained in terms of possible "key innovations" that distinguish most angiosperms from other plants, such as double fertilization, pollen tube competition, or presence of vessels in vascular tissue. The potential importance of ecological interactions has also been considered, mostly with regard to the development of insect pollination, animal dispersal of seeds, and increasing complexity of secondary compounds involved in defending plants against herbivory. Most of the hypotheses based on key innovations and the development of new ecological interactions (e.g. Regal 1977, Burger 1981) are inadequate in that they treat the angiosperms as a monolithic group that succeeded for a single reason. The high species-level diversity of angiosperms by the mid-Cretaceous, and the presence of many major, ordinal-level subclades by the Campanian, almost necessitates that there were multiple reasons for the success of flowering plants, with different reasons applying to

different subgroups. This point is reinforced by the lack of increase in branching rate associated with the appearance of putative key innovations at the base of the angiosperm phylogenetic tree (Sanderson & Donoghue 1994).

Our goals in this paper are to summarize where Cretaceous angiosperms lived and how they made a living, and to consider the implications of these factors for their evolutionary success. We discuss the data in three sections. The first contains a brief summary of the taxonomic radiation of flowering plants, the genealogical plot we are trying to put in ecological context. The second section has information on the distribution of Cretaceous angiosperms on both local and global scales. These distributions are the basis for inferring the habitat and climatic preferences of Cretaceous angiosperms. The third section contains data on the ecomorphology (ecologically significant features) of Cretaceous flowering plants. Functional interpretation of fossil leaves, wood, seeds, flowers, and pollen gives information on the habits and ecological strategies of Cretaceous angiosperms. Distributional and ecomorphological lines of evidence can be compared to see if they indicate similar habitats and ecological strategies for Cretaceous angiosperms. In the Discussion section we place the inferred ecological strategies of Cretaceous flowering plants in the context of strategies observed in living plants and relate the inferred ecological strategies to the evolutionary history of the group.

THE TAXONOMIC RADIATION OF CRETACEOUS ANGIOSPERMS

A brief review of the systematic relationships of angiosperms and the timing of their evolution is a necessary preface for discussing the ecological context of the angiosperm radiation. Although angiosperms almost certainly originated in the Mesozoic (see Sytsma & Baum 1996 for a critical review of molecular clock studies indicating a Paleozoic origin), their distinctness from other living plants has made their relationships obscure. Recent phylogenetic analyses have all tended to support the hypothesis that the closest relatives of flowering plants are the Gnetales (extant but with only three genera) and two extinct groups, the Bennettitales and Pentoxylales (e.g. Crane 1985, Doyle & Donoghue 1986a,b, 1987, 1993, Hamby & Zimmer 1992, Nixon et al 1994) (Figure 1). Together, the Gnetales, Bennettitales, and angiosperms have been called the anthophytes because they share the tendency to cluster their reproductive organs into flower-like structures and to enclose their seeds in more than one layer of tissue (Doyle & Donoghue 1986b, Crane et al 1995). Strong evidence exists for insect pollination and animal dispersal in some Bennettitales (Crepet 1972, Crepet & Friis 1987, Crane 1987), and insect pollination has been observed in extant Gnetales (Friedman 1996).

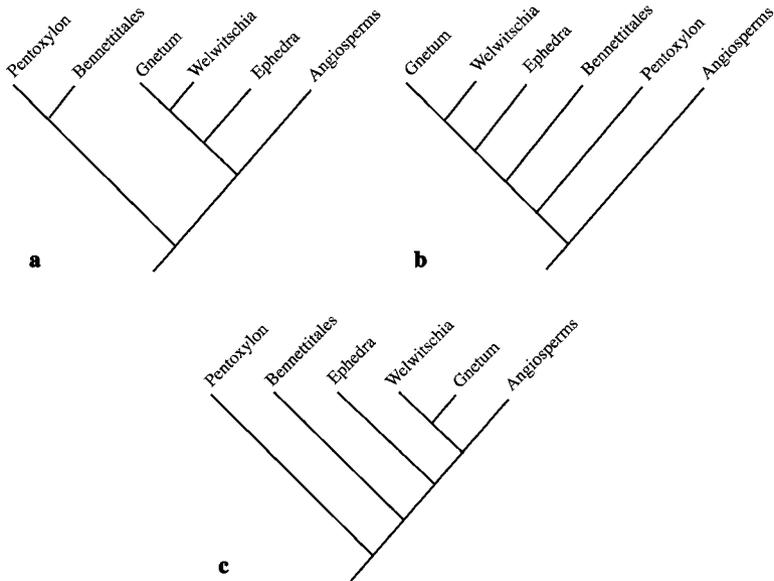


Figure 1 Alternative relationships for angiosperms and related seed plants (anthophytes). (a) Gnetales as the sister group to angiosperms (Crane 1985), (b) Gnetales + Bennettitales + Pentoxylales as the sister group to angiosperms (Doyle & Donoghue 1993), (c) *Gnetum* + *Welwitschia* alone as the sister group to angiosperms (Nixon et al 1994). Alternatives *a* and *b* imply a long lag time between splitting of angiosperms from other anthophytes and the Early Cretaceous diversification of crown group angiosperms; alternative *c* is consistent with an Early Cretaceous origin and diversification for angiosperms.

In spite of the general agreement that the anthophytes form a natural group, there is no consensus on which taxon is most closely related to angiosperms. All three putative sister groups to the angiosperms are known from earlier in the Mesozoic than are angiosperms themselves. Gnetales may be as old as Permian, and pollen and megafossils document many occurrences of this group in the Triassic through Cretaceous (Crane 1988). Bennettitales are known from the Late Triassic through mid-Cretaceous (Crane 1987, 1988), and Pentoxylales are known from the Early Jurassic and Early Cretaceous (Drinnan & Chambers 1985, Doyle & Donoghue 1993). The existence of all the probable sister taxa to the angiosperms by the Jurassic implies that the angiosperm lineage was also distinct by this time (Doyle & Donoghue 1993). This lineage, termed the angiophytes, is not equivalent to angiosperms as we know them from Cretaceous to Recent forms. The “stem angiophytes” of the Late Triassic and Jurassic may have lacked many of the derived features of the crown group, but to date no

taxa have been assigned to the group. Possible members include Late Triassic pollen grains with “angiospermoid” features (Cornet 1989a) and the enigmatic Late Triassic megafossil *Sanmiguelia* (Cornet 1989b).

The existence of a long latent period between the divergence of the angiosperm line from other anthophytes in the Late Triassic and the explosive radiation of the angiosperms proper in the Early Cretaceous counts as one of the major puzzles in seed plant evolution (Doyle & Donoghue 1993). Two categories of explanations have been offered for the latent period: The diversity enhancing features of crown group angiosperms had not yet evolved in stem angiosperms, or diversity among angiosperms was inhibited during the Jurassic by environmental conditions or biotic interactions (Doyle & Donoghue 1993).

One recent phylogenetic analysis of angiosperms does not imply a Triassic origin for angiosperms. Nixon et al (1994) concluded that the extant gnetalean genera *Gnetum* and *Welwitschia* were the sister taxa to crown group angiosperms, with the third extant gnetalean, *Ephedra*, an outgroup to *Gnetum*, *Welwitschia*, plus the angiosperms (Figure 1c). This hypothesis would allow angiosperms to have originated in the Early Cretaceous, since there is no earlier fossil record for *Gnetum* or *Welwitschia*. In this context, it is interesting to note that early Mesozoic gnetalean pollen is ephedroid in appearance (Crane 1988). The earliest appearance of *Gnetum*-like pollen is approximately coeval with the earliest angiosperm pollen (Brenner 1996), making the stratigraphic record of pollen consistent with this hypothesis of angiosperm relationships.

All recent systematic analyses recognize two major monophyletic lineages within the angiosperms: the monocots and the eudicots (Crane et al 1995). These two groups also contain the vast majority of living angiosperm species. Less clear are the relationships of groups that retain a large number of primitive characters: Laurales, Winterales, Magnoliales, Aristolochiales, Nymphaeales, Piperales, Lactoridaceae, and Chloranthaceae (Figure 2). Some analyses unite monocots with Aristolochiales, Nymphaeales, Piperales, and Chloranthaceae in a group called the paleoherbs that is considered to be the sister group to the rest of the angiosperms (Zimmer et al 1989, Taylor & Hickey 1992). Others consider the Magnoliales to be the basal sister group, with Laurales (including Chloranthaceae) and Winterales the next branches, and the paleoherbs as the sister group of eudicots (Doyle & Donoghue 1993). Still other analyses have inferred the outgroup to all other angiosperms to be the Nymphaeales (Doyle et al 1994), a single genus within Nymphaeales, *Ceratophyllum* (Les et al 1991), and a subgroup within the Laurales, the families Calycanthaceae and Idiospermaceae (Loconte & Stevenson 1991, Loconte 1996).

The fossil record shows that many of the lineages considered to be basal in the phylogenetic analyses were present by the Barremian. The earliest records of crown group angiosperms are based on pollen. Rare inaperturate

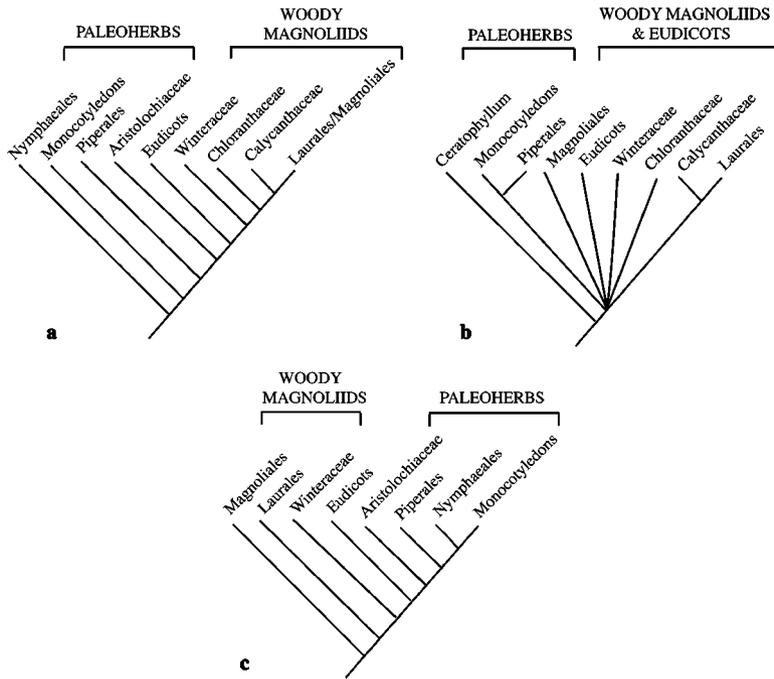


Figure 2 Alternative relationships for major clades within angiosperms. (a) Nymphaeales as the sister to other angiosperms with several paleoherb groups separating early from the eudicots and woody magnoliids (Doyle et al 1994). (b) *Ceratophyllum* rooting with unresolved relationships between paleoherbs, magnoliids, and eudicots (Albert et al 1994). (c) Magnoliid rooting with eudicots and paleoherbs as sister taxa (Doyle & Donoghue 1993).

pollen grains from the late Valanginian to Hauterivian of Israel are probably the oldest angiosperms, and they are most similar to pollen of extant Piperales (Brenner 1996). By the late Hauterivian, pollen assemblages from Israel contain four types of angiosperms: pre-*Afropollis* (*Afropollis* is thought to have been produced by angiosperms similar to Winteraceae or Illiciaceae), Spinatus group similar to *Brenneripollis* (possibly Chloranthaceae), *Clavatipollenites* (proto-Chloranthaceae), and *Liliacidites* (monocot pollen) (Brenner 1996). Late Barremian and Aptian pollen from Israel also contains the oldest true *Afropollis*, which became widespread at low latitudes during the Aptian through Cenomanian (Doyle et al 1982).

Friis et al (1994) have reported a number of three-dimensionally preserved reproductive structures from the Early Cretaceous of Portugal. Most significant is the putatively Valanginian-Hauterivian site of Torres Vedras, which contains

forms tentatively assigned to lauraleans, chloranthoids, and lower hamamelids (eudicots). If validated as Valanginian-Hauterivian, this site would predate the first occurrence of abundant dispersed tricolpate (eudicot) pollen in the early Aptian of Israel (Brenner 1996) by some ten million years. The earliest fossils of Magnoliales are probably the pollen *Lethomasites*, from the Aptian (Ward et al 1989); possible magnolialean leaves also are present in the Aptian of the Potomac Group of eastern North America (Hickey & Doyle 1977, Upchurch 1984). Other proposed basal branches of the angiosperms, such as *Ceratophyllum* and Calycanthaceae, also have first occurrences in the Aptian or Albian (Dilcher 1989, Friis et al 1994).

Piperalean and chloranthaceous pollen appear to predate other types of angiosperm remains by as much as 4–5 million years, with winteraceous pollen appearing next. This pattern of stratigraphic occurrence is more consistent with the “paleoherb” than with the magolialean hypothesis for basal angiosperms (Taylor & Hickey 1996), but the difference in appearance times is not so great that it unambiguously favors any of the alternative hypotheses (Doyle & Donoghue 1993, Crane et al 1995). Regardless of which living group represents the first lineage to diverge from the rest of the angiosperms, there appears to be only 10–12 million years between the first record of angiosperms and clear documentation of all of the major lines of flowering plants in the Aptian. Clearly the basal radiation of flowering plants was rapid, and it occurred during a period when their pollen and megafossils were rare components of terrestrial floras and species diversity was relatively low (Doyle & Donoghue 1993, Crane et al 1995, Taylor & Hickey 1996).

If the Hauterivian-Aptian radiation of flowering plants was characterized by low numbers of species representing a few basal lineages, the Albian-Cenomanian shows a very different pattern. Compilations of fossil angiosperm species document a dramatic increase in flowering plant diversity between the Albian and the Cenomanian at a global scale (Lidgard & Crane 1988, 1990, Crane & Lidgard 1989, 1990) (Figure 3a). At the local scale, angiosperms expanded from just a few percent of the species in most local floras during the Aptian to more than 70% of the species in typical Cenomanian through Maastrichtian floras (Figure 3b). The increase in angiosperm species diversity was accompanied by the appearance of extant orders and families that document most of the major sublineages within the eudicots (Table 1). Approximately 42 of the 94 extant orders (44%) and 63 of the 439 extant families (14%) of flowering plants have first occurrences during the Cretaceous.

By the Maastrichtian, relatively “advanced” families such as Amaranthaceae/Chenopodiaceae, Graminae, Bombacaceae, Myrtaceae, Proteaceae, Fabaceae, and Zingiberaceae were already present (Muller 1981; Table 1). However, there were also notable absences, including all of the asterid orders: Dipsacales,

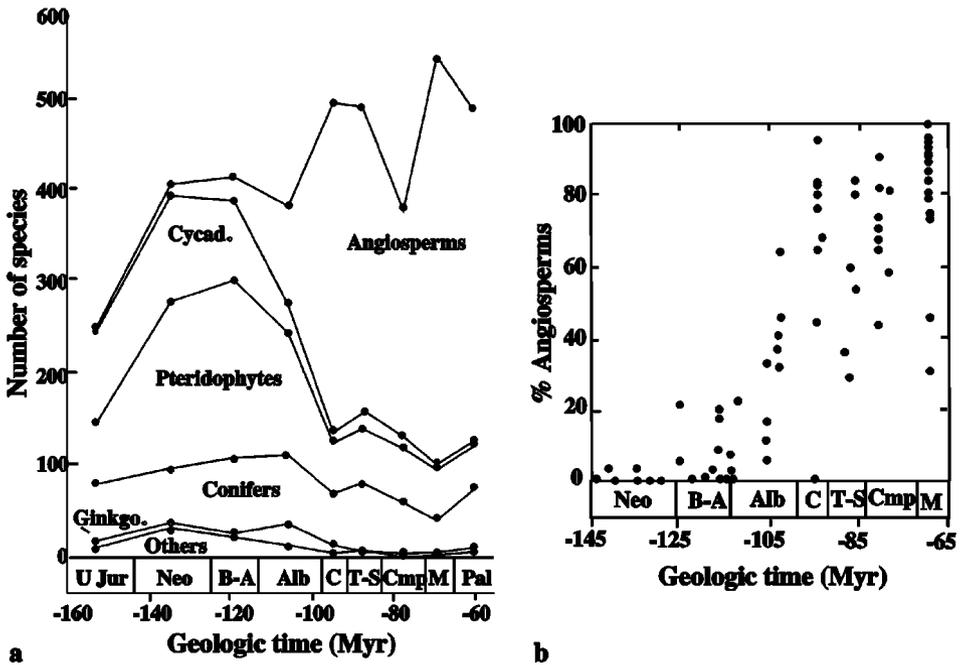


Figure 3 (a) Global species diversity of major land plant groups during the Cretaceous, showing the dramatic increase in angiosperm diversity during the Albian and Cenomanian (redrawn from Lidgard & Crane 1988). (b) Percentage of species in local megafloras that are flowering plants, showing a sharp increase in the Albian and Cenomanian, and relative stability in the Late Cretaceous (redrawn from Crane & Lidgard 1990).

Gentianales, Polemoniales, Scrophulariales, Lamiales, Campanulales, and Asterales. These are among the most diverse extant clades of angiosperms, and are major contributors to both herbaceous (e.g. Lamiaceae, Asteraceae) and woody (e.g. Rubiaceae, Apocynaceae, Bignoniaceae) vegetation. Also absent or poorly represented in the Cretaceous fossil record are palmate dilleniids (sensu Hickey & Wolfe 1975) such as Malvales, Violales, Passiflorales and Euphorbiales (with the possible exception of Buxaceae).

Given the rapid rate of discovery of Cretaceous fossils with close affinities to extant families in the last 10 years, it is highly probable that many or even most angiosperm families will eventually be found to have originated in the Cretaceous. This is especially true because isolated fossil organs generally have not been assigned to extant families unless they have features that clearly demonstrate affinities to extant genera within a family (Collinson et al 1993). The

Table 1 Angiosperm taxa recorded from the Cretaceous (arrangement of Takhtajan 1969)

Order and Family	Organ, Genus	Stage ^a	Reference
Magnoliales			
Magnoliaceae?	Inflorescence, <i>Archaeanthus</i>	CE	Dilcher & Crane 1984, Crane 1989
	Inflorescence, <i>Lesqueria</i>	CE	Crane & Dilcher 1984
Eupomatiaceae	Flower, "Taxon A"	TU	Crepet & Nixon 1994
Annonaceae	Pollen, <i>Foveomorphomonocolpites</i>	MA	Muller 1981
Winteraceae?	Pollen, <i>Lethomasites</i>	AP	Ward et al 1989
Laurales			
Amborellaceae	Fruit	AP?	Friis et al 1995
Monimiaceae?	Leaf	SA	Knappe & Ruffle 1975
Trimeniaceae	Pollen, <i>Cretacaeporites</i>	AL	Muller 1981
Chloranthaceae	Pollen, <i>Clavatipollenites</i>	VA?	Friis et al 1986
	Pollen, <i>Asteropollis</i>	AP	
	Pollen, <i>Stephanocolpites</i>	AL	
	Fruit, <i>Couperites</i>	CE	Pedersen et al 1991
	Flower, <i>Chloranthistemon</i>	TU	Herendeen et al 1993
Calycanthaceae	Flower, <i>Virginianthus</i>	AL	Friis et al 1994
	Flower, "Taxon B"?	TU	Crepet & Nixon 1994
Lauraceae	Flower, <i>Perseanthus</i>	TU	Herendeen et al 1994
	Wood, <i>Paraphyllanthoxylon</i>	AL	Herendeen 1991
	Flower, <i>Mauldinia</i>	CE	Drinnan et al 1990
Priscaeae	Inflorescence, <i>Prisca</i>	CE	Retallack & Dilcher 1981
incertae sedis	Leaf	CE	Upchurch & Dilcher 1990
Piperales			
Piperaceae?	Pollen, pre- <i>Afropollis</i>	HA	Brenner 1996
	Leaf and inflorescence, <i>Koonwarraphyton</i>	AP	Taylor & Hickey 1990
Nymphaeales			
Ceratophyllaceae	Seed	AP	Dilcher 1989
Nymphaeaceae	Pollen, aff. <i>Nymphaea</i>	MA	Muller 1981
incertae sedis	Leaf	AP	Hickey & Doyle 1977
Illiciales			
Illiciaceae	Pollen, aff. <i>Illicium?</i>	MA	Muller 1981
Schisandraceae	Pollen	MA	Muller 1981
Ranunculales			
Menispermaceae	Seed and leaf	CA?–MA	Collinson et al 1993
Circaeasteraceae?	Fruit, <i>Appomatoxia</i>	AL	Friis et al 1995
Papaverales			
Papaveraceae?	Fruit, <i>Paleoaster</i>	CA	Smith 1996
Trochodendrales			
Trochodendraceae?	Leaf	CE	Hickey & Doyle 1977
	Leaf	CA	Crabtree 1987

(Continued)

Table 1 (Continued)

Order and Family	Organ, Genus	Stage ^a	Reference
Cercidiphyllales			
Cercidiphyllaceae	Pollen	CA	Muller 1981
incertae sedis	Leaf	CA	Crabtree 1987
Hamamelidales			
Hamamelidaceae	Seed	LK	Collinson et al 1993
	Inflorescence	TU	Crepet et al 1992
	Inflorescence, <i>Archamamelis</i>	CA?	Endress & Friis 1991
	Inflorescence	CA	Magallon-Puebla et al 1997
Platanaceae	Leaf, <i>Sapindopsis</i>	AL	Hickey & Doyle 1977
	Inflorescence	AL	Crane et al 1986, Friis et al 1988
Myrothamnaceae	Pollen	CE	Ward & Doyle 1988
Urticales			
Ulmaceae	Pollen, aff. <i>Ulmus</i>	MA	Muller 1981
	Pollen, aff. <i>Celtis</i>	TU	Muller 1981
	Leaf	SA-CA	Manchester 1989
Urticaceae??	Seed	CA-MA	Collinson 1989
Fagales			
Fagaceae	Pollen, aff. <i>Castanea?</i>	SA	Muller 1981
	Pollen, aff. <i>Nothofagus?</i>	SA	Muller 1981
	Fruit	CA	Herendeen et al 1995
	Flower	TU	Crepet 1996
Betulales			
Betulaceae	Pollen, aff. <i>Alnus</i>	SA	Muller 1981
	Pollen, aff. <i>Betula</i>	SA	Muller 1981
Myricales			
Myricaceae	Pollen, aff. <i>Myrica</i>	SA	Muller 1981
Juglandales			
Juglandaceae?	Inflorescence, <i>Manningia</i>	CA	Friis, 1983
	Pollen, <i>Momipites</i>	CA	Muller 1981
Caryophyllales			
Amaranthaceae	Seed	SA/CA	Collinson et al 1993
Amaranthaceae/ Chenopodiaceae	Pollen	MA	Muller 1981
Theales			
Clusiaceae?	Flower	TU	Crepet et al 1992
	Seed	CE	Collinson et al 1993
Capparales			
Moringaceae?	Flower	TU	Crepet et al 1992
Ericales			
Actinidiaceae	Flower, <i>Parasarauia</i>	CA	Keller et al 1996
Cyrtillaceae/ Clethraceae	Pollen, aff. <i>Clethra</i>	MA	Muller 1981
Ericaceae?	Flower, <i>Paleoenkianthus</i>	TU	Nixon & Crepet 1993

(Continued)

Table 1 (Continued)

Order and Family	Organ, Genus	Stage ^a	Reference
Diapensiales			
Diapensiaceae?	Flower, <i>Actinocalyx</i>	CA	Friis 1985
Ebenales			
Symplocaceae	Pollen	MA	Muller 1981
Sapotaceae	Pollen	MA	Muller 1981
Malvales			
Bombacaceae	Pollen, aff. <i>Bombax</i>	MA	Muller 1981
incertae sedis	Flower	TU	Crepet 1996
Euphorbiales			
Buxaceae	Inflorescence, <i>Spanomera</i>	AL	Drinnan et al 1991
	Pollen, aff. <i>Pachysandra</i>	CA	Muller 1981
Saxifragales			
incertae sedis	Flower, <i>Scandianthus</i>	CA	Friis & Skarby 1982
(Escalloniaceae?)			
	Flower, <i>Silvianthemum</i>	CA	Friis 1990
	Flower	TU	Crepet 1996
Araliales			
Araliaceae	Fruit	MA	Collinson et al 1993
Mastixiaceae	Fruit	MA	Collinson et al 1993
Rhamnaceae	Leaf	MA	Collinson et al 1993
Rosales			
Rosaceae?	Leaf	MA	Collinson et al 1993
Sabiaceae	Seed	MA	Collinson et al 1993
incertae sedis	Flower	CE	Basinger & Dilcher 1984
	Flower	TU	Crepet 1996
Fabales			
Caesalpinaceae	Pollen, aff. <i>Sindora</i>	MA	Muller 1981
	Wood	TU-SA	Giraud & Lejal-Nicol 1989, Herendeen et al 1992
Myrtales			
Myrtaceae	Pollen	SA	Muller 1981
Onagraceae	Pollen, aff. <i>Epilobium</i>	MA	Muller 1981
Combretaceae	Flower and leaf, <i>Esgueiria</i>	CA-MA	Friis et al 1992
Hippuridales			
Gunneraceae	Pollen	TU	Muller 1981
	Leaf	MA	LJ Hickey & D Fuller, unpublished data
Sapindales			
Sapindaceae	Pollen, aff. <i>Cupanioipsis</i>	CO	Muller 1981
	Seed	MA	Collinson et al 1993
Geraniales			
Malpighiaceae	Pollen, aff. <i>Ctenolophon</i>	MA	Muller 1981
Celastrales			
Aquifoliaceae	Pollen, aff. <i>Ilex</i>	TU	Muller 1981
	Seed	MA	Collinson et al 1993

(Continued)

Table 1 (Continued)

Order and Family	Organ, Genus	Stage ^a	Reference
Santalales			
Olacaceae	Pollen, aff. <i>Anacolosa</i>	MA	Muller 1981
Santalaceae??	Pollen, <i>Aquilapollenites</i>	MA	Muller 1981
Proteales			
Proteaceae	Pollen	LK	Dettmann & Jarzen 1991
Zingiberales			
Musaceae	Seed	CA	Rodriguez-de la Rosa & Cevallos-Ferriz 1994
Zingiberaceae	Seed, <i>Spirematospermum</i>	CA	Friis 1988
	Leaf, <i>Zingiberopsis</i>	MA	Hickey & Peterson 1978
Restionales			
Restionaceae	Pollen	MA	Linder 1987
Poales			
Poaceae	Pollen	MA	Linder 1987
Arecales			
Arecaceae	Pollen	TU	Christopher 1979
	Leaf	SA	Read & Hickey 1972
	Leaf	CA	Crabtree 1987
Arales			
Araceae?	Seed	AL?	Herendeen & Crane 1995
	Seed, <i>Epipremnum</i>	CA-MA	Friis et al 1992
Pandanales			
Pandanaceae	Pollen	MA	Muller 1981
Typhales			
Sparganiaceae?	Pollen, aff. <i>Typha</i>	CA	Herendeen & Crane 1995
	Fruit	CE	Collinson et al 1993

^aStage: AL = Albian; AP = Aptian; CA = Campanian; CE = Cenomanian; CO = Coniacian; MA = Maastrichtian; SA = Santonian; TU = Turonian; VA = Valanginian.

families represented by Cretaceous fossils are also widely distributed among the major subgroups of angiosperms. Estimating the true proportion of angiosperm families that originated during the Cretaceous is complicated by the absence of a generally accepted higher-level phylogeny for angiosperms and the many paraphyletic families and orders (e.g. Judd et al 1994). This makes it difficult to infer the presence of sister taxa to those documented by fossils. Complete systems of angiosperm classification have been proposed by botanists relying on "evolutionary systematic" techniques (e.g. Takhtajan 1969), and many of the relationships proposed by these authors have been confirmed or only slightly modified by more recent, explicit cladistic analyses (e.g. Judd et al 1994). As a heuristic device to show the wide taxonomic distribution of families with Cretaceous fossil records, we have modified the dendrogram of angiosperm orders from Takhtajan (1969) and indicated those known from Cretaceous fossils (Figure 4).

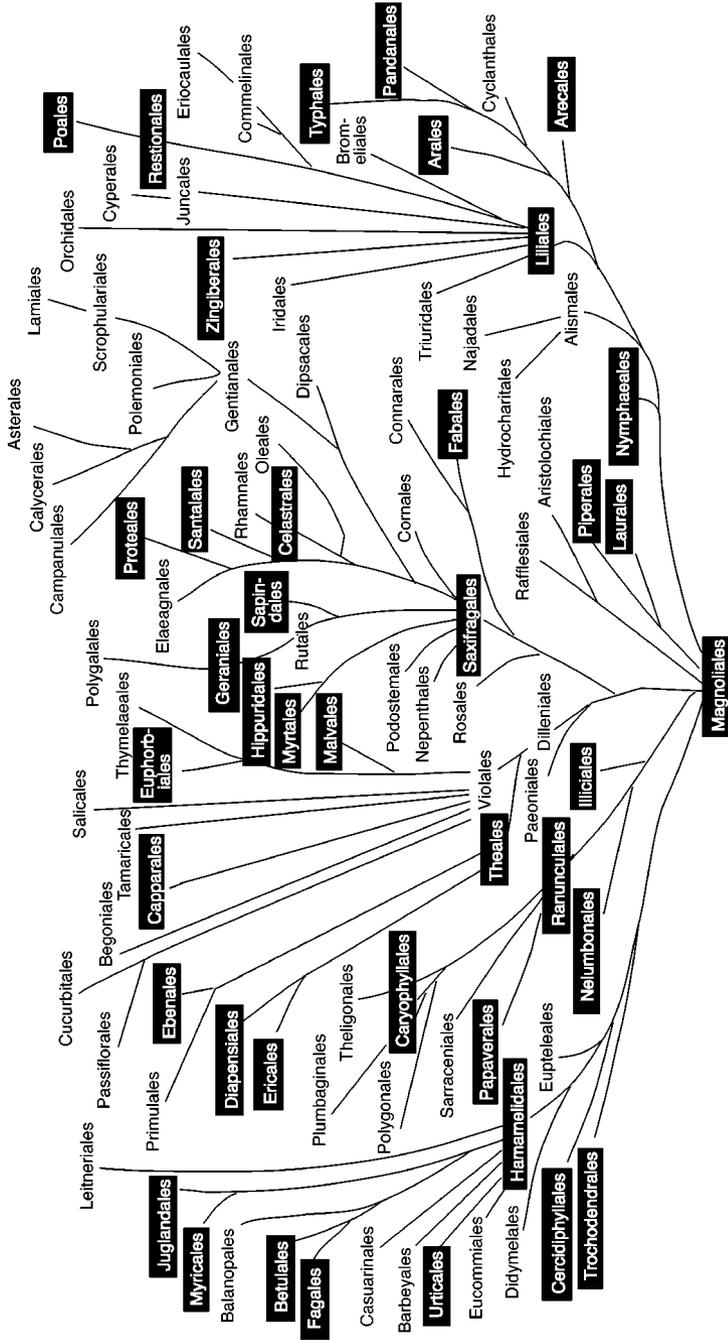


Figure 4 Dendrogram showing the wide systematic spread of angiosperm orders with Cretaceous fossil records (shown in reverse type). Records for Cretaceous fossils are in Table 1. Dendrogram redrawn from Takhtajan (1969).

ENVIRONMENTS AND ABUNDANCE OF CRETACEOUS ANGIOSPERMS

Although there are thousands of palynological and megafossil records of Cretaceous angiosperms from around the world, relatively few floras have been described in terms of their sedimentological and environmental context, or the relative abundance (as opposed to the relative diversity) of major land plant groups. With the exception of some studies in the high southern latitudes (Specht et al 1992, Cantrill 1996, Cantrill & Nichols 1996), and Asia (Krassilov 1975), most of the detailed sedimentological and paleoenvironmental work on Cretaceous floras containing angiosperms has been carried out in North America.

Earliest Records

The earliest angiosperm pollen has been recovered from bore holes in the Valanginian-Hauterivian Helez Formation of Israel (Brenner 1996). The Helez Formation is a near-shore to non-marine unit consisting of shales, aeolian sands, limestones, and dolomite. The pollen-bearing sediments are carbonaceous shales containing carbonized plant fragments and siderite nodules, and they are thought to represent lagoonal or fluvial deposition in fresh to brackish water (Brenner 1996). Angiosperms in these deposits occur as fewer than two grains per thousand palynomorphs, but the rarity is not associated with poor preservation or marine conditions and may indicate that the parent plants were insect pollinated (Brenner 1996) or that there were few individuals. The palynoflora associated with the earliest angiosperms lacks bisaccate pollen of Podocarpaceae and Pinaceae (indicative of subtropical to temperate, moist climates), but it is lower in *Classopollis* (xeromorphic conifer) and ephedroid pollen, and higher in fern spore diversity, than coeval floras from Brazil that probably grew in a dry paleoclimate (Brenner 1996). Brenner (1996) inferred the climate of the earliest angiosperms to be humid tropical.

A much more geographically extensive record of early angiosperms is known from Barremian through Cenomanian sediments in the South Atlantic Rift sequence (Doyle et al 1982). Although these rift sediments contain large amounts of halite, indicating greater evaporation than precipitation and possibly an arid equatorial paleoclimate (Ziegler et al 1987), the earliest angiosperms in this sequence (Barremian *Afropollis*) are not associated with *Classopollis* and halite but with palynological and sedimentary indicators of more mesic conditions (Doyle et al 1982). However, by the Late Aptian, some species of *Clavatipollenites* were associated with *Classopollis*, ephedroids, and halite, all indicators of aridity (Doyle et al 1982). Results from both Israel and West Africa suggest that angiosperms initially evolved in relatively moist or seasonal tropical

climates but that within the first 10 million years of their appearance, some species had colonized more arid climates and some lineages had expanded poleward.

North America

The Aptian-Cenomanian Potomac Group of eastern North America contains the earliest angiosperm megafossils that have been documented in sedimentary context (Doyle & Hickey 1976, Hickey & Doyle 1977, Taylor & Hickey 1996). Angiosperm fossils are rare, local, and undiverse in Zone I, the early Aptian part of the section (Doyle & Hickey 1976, Doyle 1992), and are confined to coarser sediments (medium to very fine sand) with primary stratification indicating within or near-channel deposition. Nearby flat-bedded or massive clay and mud rocks lack angiosperms and are dominated by conifer, fern, and cycadophyte foliage (Doyle & Hickey 1976, Hickey & Doyle 1977). Zone I of the Potomac group is about 10 million years after the earliest occurrences of angiosperms in paleoequatorial regions and postdates the separation of the monocot, chloranthoid, and magnoliacean lineages. Doyle & Hickey (1976) interpreted disorganized pinnately veined leaves in Zone I as being of magnoliacean "grade" but not necessarily with affinities to Magnoliales. Indefinite pinnate/palmate leaves in Zone I may represent Saururaceae/Piperaceae or other paleoherb taxa (Taylor & Hickey 1996). Highly lobate leaves in Zone I resemble some Ranunculales, and tricolpate pollen is present though rare (Doyle 1992).

By the middle to late Albian (mid Subzone II-B), Potomac Group palynofloras contain a diversity of tricolpate (eudicot) pollen; angiosperms are locally abundant in some leaf assemblages and occur in a somewhat wider variety of facies as well (Doyle & Hickey 1976). The first abundant angiosperm leaves are forms related to Platanales, such as *Sapindopsis* and *Araliaephyllum*. As with the Zone I dicots, these early sycamore relatives are associated with coarser fluvial deposits indicative of channel margin environments and/or with fusain, burned plant material (Doyle & Hickey 1976). The platanoids are absent from backswamp deposits of the same age, but other angiosperm leaf types similar to floating aquatic plants like Nymphaeales are found in clay/silt sediments with parallel lamination, indicating deposition in standing water. The somewhat increased range of depositional environments is consistent with the expansion of angiosperms into a slightly wider range of habitats than in the Aptian to early Albian, and their abundance in channel and pond sediments suggests dominance in some high-light and well-watered settings that supported few other woody plants. The early affinity of platanoids for stream margin environments continued throughout the Cretaceous and Cenozoic and is still seen in living *Platanus* species. This is a striking example of habitat fidelity in a very long-lived lineage.

By the late Albian-Cenomanian (upper Subzone II-B to Zone III), truly pinnately compound types of *Sapindopsis* are found in abundance in sites indicating fluvial channel deposition or associated with fusain (Doyle & Hickey 1976, Hickey & Doyle 1977). In living dicots, pinnately compound leaves such as these are associated with rapidly growing, early successional trees (Givnish 1979). Platanoids are also more common in the channel deposits of this time; some of these are relatively large leaved (up to 15 cm) and show petiole features consistent with regular abscission of leaves. Some Latest Albian and early Cenomanian floras from finer-grained sediments in the Potomac Group also contain a fairly high diversity of simple, pinnate leaves with venation relatively disorganized compared with contemporaneous platanoids (Doyle & Hickey 1976). These simple leaves may indicate that magnolialean lineages were beginning to be more important and diverse on stable flood basin substrates.

Upchurch et al (1994) recognized three “megafloral facies” consistent with the sedimentological observations of Hickey & Doyle (1977): the platanoid facies, the *Sapindopsis* facies, and the *Nelumbites/Populophyllum* facies. The first is defined by abundant platanoid leaves and few other floral remains and is found in coarse-grained channel deposits. Assemblages of the second type are mono-specific occurrences of *Sapindopsis* leaves in slightly finer-grained crevasse-splay or abandoned channel deposits. The *Nelumbites* megafloral facies occurs in laminated clays deposited in abandoned channels and is typically dominated by nearly in situ floating aquatic *Nelumbites* and a variety of conifer foliage, presumably derived from surrounding floodplain trees. A detailed study of one *Nelumbites*-dominated site (Quantico, upper Subzone II-B) revealed that roughly one third of the specimens were *Nelumbites* but that no other angiosperm was more than 1 or 2% of the specimens, and even in aggregate they were only 8% (Upchurch et al 1994). Conifer foliage of several types accounted for most of the remaining specimens. Several of the dicot taxa present at this site were either lauraleans or magnolialeans.

Angiosperm pollen and megafossils are regular members of assemblages throughout the northern Rockies by the middle of the middle Albian, and they are widespread by the late middle Albian except in the far north (Crabtree 1987). However, many compression fossil assemblages in the northern Rocky Mountains do not have abundant dicot leaves. A large assemblage from the Wayan Formation of southeast Idaho (late Albian to early Cenomanian?) is dominated by ferns and contains a single angiosperm—a species of *Sapindopsis*. Deltaic sediments in the Albino Member of the Mowry Formation (late Albian) also document a fern-dominated vegetation (Crabtree 1987). One relatively northern flora that does show high dicot abundance is a dispersed cuticle assemblage from a coal in the upper Albian Longford Member of the Kiowa Formation in eastern Kansas, at 38°N paleolatitude (Upchurch 1995). One sample from the

coal has approximately equal numbers of conifer and dicot cuticle fragments; the other has almost exclusively dicots. Fusainized wood fragments are also abundant in these samples, and most of them are coniferous, as is the palynoflora (Upchurch 1995). Upchurch interpreted the regional vegetation as conifer dominated, with abundant herbaceous or small woody dicots (Chloranthaceae and Laurales) in areas of the peat that had recently burned.

The importance of magnoliids on more stable substrates in the early Late Cretaceous is reinforced by the Cenomanian Rose Creek flora from Nebraska. This assemblage is derived from fine-grained facies possibly influenced by brackish water and may represent the inland side of mangrove vegetation (Upchurch & Dilcher 1990). Magnoliid or magnoliid grade leaves comprise 70% of the angiosperm species and 90% of the angiosperm specimens at Rose Creek. Rosid and incertae sedis leaves comprise 10 and 20% of the angiosperm species and few specimens. This contrasts sharply with the dominance of platanoids and hamamelids in the sandier Dakota floras described by Lesquereux (1892). Retallack & Dilcher (1981, 1986) recognized two types of Dakota Group assemblages from Kansas and Nebraska: stream-side and lake margin environments dominated by platanoids and more paludal settings with a higher abundance of magnoliids (e.g. *Liriophyllum*, *Magnoliaephyllum*). Of the leaf cuticle fragments in an associated lignite, 85% are assignable to Lauraceae, indicating the importance of this group of dicots in peat-forming environments (Upchurch 1995).

The tendency for angiosperm dominance to be low except in fluvial and other disturbed environments continued through the Late Cretaceous, particularly north of about 45° paleolatitude in North America. Cenomanian assemblages from the North Slope of Alaska have moderately abundant dicots in channel and channel-margin settings, but the assemblages from distal floodplain areas are dominated by conifers, ferns, cycadophytes, and ginkgos (Spicer 1987). Lower Campanian floras in the Milk River, Eagle, and Two Medicine Formations from Alberta and Montana contain an abundance of araucarian, taxodiaceous, and cupressaceous foliage. The Two Medicine flora has 30 angiosperm, 2 conifer, and 6 fern species (Crabtree 1987). Although the angiosperms are the most diverse element of the flora, swamp facies are dominated by taxodiaceous and cupressaceous conifers, palms are abundant in the channel margin facies, and the levees and crevasses are dominated by dicots, especially hamamelids. Nonhamamelid dicots are only about 10% of the leaves. Campanian leaf assemblages from the Black Hawk Formation in Utah show greater dominance of angiosperms in channel-margin than in coal swamp settings, where conifers and ferns were more abundant (Parker 1975).

Even in the early Maastrichtian of northern North America, dicot dominance tended to be limited to depositional environments indicating disturbed sites.

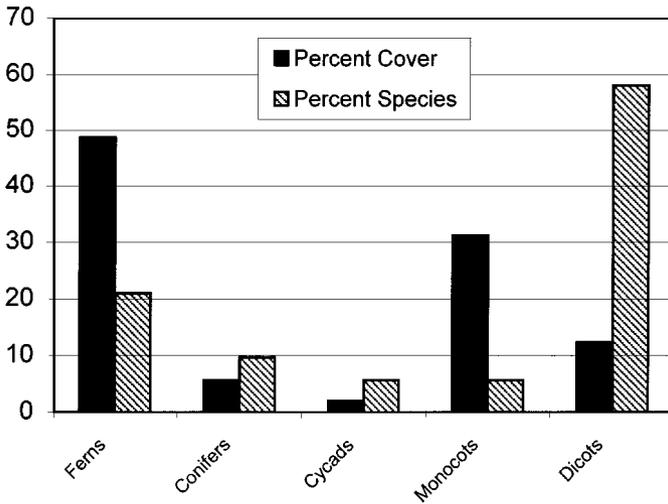


Figure 5 Diversity and abundance of major plant groups in the Big Cedar Ridge flora, Meeteetse Formation, early Maastrichtian of Wyoming. Updated from Wing et al (1993).

Study of the Big Cedar Ridge flora, an in situ early Maastrichtian assemblage from the Meeteetse Formation in central Wyoming, has shown that gleicheniacean fern foliage is dominant at sites where the substrate was highly organic (Wing et al 1993). Dicots are dominant at only a few of the 100 sites where relative abundances were measured, and all of the dicot-dominated sites are associated with paleochannels. Overall, although angiosperms comprise 80% of the species at Big Cedar Ridge, they are only 12% of the material identified on bedding planes (Wing et al 1993; Figure 5). The one abundant angiosperm at Big Cedar Ridge is a species of coryphoid palm, perhaps indicating that palm thickets grew on muck soils in this deltaic setting. Leaf assemblages from other areas of the Meeteetse Formation have also been quantified in terms of relative cover of different major plant groups, and similar patterns of dominance have been found. Of an additional 40 sites in four different areas, dicots are only abundant in those where there is clear sedimentological evidence for deposition in abandoned fluvial channels (Tiver et al 1994). Other sites are dominated by conifers, ferns, or monocots. An approximately coeval flora from the Almond Formation in southern Wyoming occurs in an ashfall within a coal and is similar to the Meeteetse floras both in species composition and dominance by non-angiosperms (Tiver et al 1994). Further north, megaflores from the Late Cretaceous of Alberta found in the Horseshoe Canyon Formation are dominated by conifers (McIver & Aulenback 1994).

Late Campanian–early Maastrichtian floras from the Fruitland and Kirtland Formations in the San Juan Basin of northern New Mexico (about 38°N paleo-latitude) illustrate a different pattern of dominance among major plant groups. Dicot leaves are dominant across a variety of flood plain habitats with the exception of some organic distal swamp environments (Boucher & Wing 1997, Boucher et al 1997). Only floras preserved in ashfalls within coals are dominated by ferns. Distal areas of floodplain swamps that were disturbed by sediment influx subsequently developed floras dominated by dicots or, in a few places, conifers. Fossil wood also shows the importance of dicots in this area. Fossil dicot wood is more abundant than coniferous wood in mudstone paleosols of the Kirtland Formation (Boucher et al 1997), and some dicot trunks are 0.5–1 m in diameter (Wheeler et al 1995), showing that dicots were large plants that dominated floodplain vegetation across a range of habitats.

Late Maastrichtian megaflores and dispersed cuticle assemblages from the Raton Basin of northern New Mexico are dominated by angiosperms, and conifers are essentially absent from peat-forming environments, even as pollen (Wolfe & Upchurch 1987, Upchurch 1995). Although ferns are absent from the cuticle assemblage, probably because their thin cuticles are not easily preserved, they may have played a significant role in peat substrate vegetation based on the abundance of their spores (up to 25%) in coals (Upchurch 1995). As with the Meeteetse megaflores, however, much of the abundance of angiosperms consists of just a few types of monocots (44% of fragments), while the much more diverse eudicots make up only 18% of the cuticle fragments across all samples (Upchurch 1995). Magnoliid dicots are 38% of the cuticle sample and more than half the species (Upchurch 1995).

Late Maastrichtian megaflores from the Hell Creek Formation of North Dakota also are dominated by dicots, with ferns and taxodiaceous conifers making up more than 5% of the specimens at only 2 of 15 sites (Johnson 1992). However, the dominant dicots in this assemblage are mostly platanoids and hamamelids, and well-preserved leaves were derived largely from channel and near-channel sedimentary environments (Johnson 1992). The relative importance of dicots in more stable floodplain habitats during the late Maastrichtian in the northern Rocky Mountains has not yet been clearly established.

Geochemical Evidence

A further source of information on the abundance of flowering plants in the geological past comes from oleananes. Oleananes are compounds that are today produced exclusively by angiosperms, and their abundance in near-shore marine rocks can be taken as an averaged signal of the importance of angiosperms in the terrestrial vegetation of nearby continents (Moldowan et al 1994). Moldowan et al (1994) found 0–10% oleanane in Jurassic and Lower Cretaceous rocks,

0–15% in Late Cretaceous and Paleocene rocks, and mostly higher levels in Eocene and younger rocks. These data suggest that angiosperms may have been a smaller part of the biomass of terrestrial vegetation in the Cretaceous than in the Cenozoic.

Global Paleogeographic Distribution

The poleward migration of angiosperms during their early evolution was first recognized by Axelrod (1959) on the basis of megafossils and subsequently more rigorously defined using palynofloras (Brenner 1976, Hickey & Doyle 1977). The earliest records of angiosperm pollen are inaperturate forms from the Valanginian-Hauterivian of the Northern Gondwana province at about the paleoequator (Brenner 1996). Monosulcate pollen has its first occurrence in the same region in the late Hauterivian to Barremian (Brenner 1996). The oldest angiosperm pollen records from Laurasia are small monosulcates from the late Hauterivian of England (Hughes 1994). Monosulcates (presumably magnoliids) rapidly occupied a broad band of paleolatitude (roughly 30°N to 60°S) in the late Barremian–early Aptian (Hickey & Doyle 1977). Tricolpate angiosperm pollen tends to occur earlier at low latitudes and then at successively higher latitudes through the Albian and Cenomanian (Brenner 1976, Hickey & Doyle 1977). The earliest records of angiosperm pollen in the mid-latitudes of western North America are tricolpate grains from the Loon River Formation (early middle Albian) of northwest Alberta and monosulcates from the Cloverly Formation of Wyoming (Crabtree 1987). The oldest angiosperm megafossils from Alaska are from the late Albian part of the Chandler Formation in fluvially deposited sediments (Scott & Smiley 1979).

Latitudinal migration of angiosperms followed a similar pattern in the Southern Hemisphere. As in the Northern Hemisphere, there appear to be two phases: initial appearances of monosulcate magnoliid angiosperms rapidly transgressing southward in the Barremian to the Aptian, followed by a wave of increasing eudicot pollen diversity beginning in the Aptian at paleoequatorial latitudes and moving to higher latitudes by the Cenomanian (Drinnan & Crane 1990). The earliest records of angiosperms in the middle to high latitudes of Australia are Barremian pollen from the Eromanga Basin in southern Queensland (Burger 1988) and a single megafossil from the Aptian or early Albian Koonwarra flora of southeastern Victoria (Taylor & Hickey 1990). The oldest angiosperm megafossil from southern South America is Aptian (Romero & Archangelsky 1986). Monosulcate pollen was not floristically or numerically important in Australian floras until the mid-Albian, at about the same time as the first occurrence of triaperturate eudicot pollen in this region (Burger 1988). The earliest angiosperm pollen known in Antarctica is a monosulcate, *Clavatipollenites* species (Chloranthaceae), from the early Albian (Truswell 1990).

First occurrences of angiosperms suggest that they originally had a low-latitude distribution and expanded their range poleward over many millions of years. There was also a latitudinal pattern to the spread of floras in which angiosperms made up a predominance of species (Lidgard & Crane 1988, 1990, Crane & Lidgard 1989, 1990). For example, in equatorial palynofloras of Maastrichtian age, greater than 80% of the species are angiosperms, whereas in palynofloras from 65–80°N of the same age, only about 40% of the species are angiosperms.

Palynological assemblages have also been studied with respect to the abundance of angiosperm pollen through time and across latitude (Lupia et al 1997). As with first occurrences and diversity, there is a clear poleward spread of angiosperm dominance through the Cretaceous. By the Maastrichtian, 80–100% of grains in equatorial palynofloras were from angiosperms, whereas in coeval assemblages from 80°N, only about 35% of grains belonged to angiospermous taxa (Lupia et al 1997). Palynological data reveal substantial declines in angiosperm abundance and diversity north of about 40°, and other groups also show substantial changes in diversity and abundance at approximately the same latitude, which suggests that in the Late Cretaceous there were relatively sharp vegetational and floristic boundaries in spite of low latitudinal temperature gradients (Upchurch & Wolfe 1993).

Late Early and early Late Cretaceous megafloras also demonstrate low angiosperm abundance at high southern paleolatitudes. Most Albian and Cenomanian-Campanian floras on the Antarctic Peninsula continued to be dominated by ferns and/or conifers (Truswell 1990, Rees & Smellie 1989, Chapman & Smellie 1992, Cantrill 1996, Cantrill & Nichols 1996). Detailed paleoecological study of in situ late Albian megafloras from Alexander Island near the Antarctic Peninsula has demonstrated the presence of fern thickets with subdominant conifers (Cantrill 1996); angiosperms occurred in significant abundance (40% of specimens) at only 3 localities out of 76 (Cantrill & Nichols 1996). These 3 localities offer sedimentological evidence of overbank deposition adjacent to channels (Cantrill & Nichols 1996). At southern middle paleolatitude, the Cenomanian Winton Formation flora from the Eromanga Basin in central Queensland, Australia, is derived from a low-energy fluvio-lacustrine setting. The flora is mixed ferns, conifers, Pentoxylales, and angiosperms, and seven of the eight angiosperm taxa are of hamamelid (eudicot) affinities (McLoughlin et al 1995).

Angiosperm dominated palynofloras and megafloras are not common at high southern paleolatitudes until the Campanian-Maastrichtian (Truswell 1990, Dettmann & Jarzen 1988, Askin 1988, Zastawniak 1994, Hill & Scriven 1995). A probable Campanian megaflora from King George Island off the Antarctic Peninsula is dominated both in species and specimens by a range of dicots, including probable Fagaceae, platanoids, magnolialeans, and lauraleans

(Zastawniak 1994), although the lack of information on depositional environment and the small sample size of only 102 specimens casts doubt on the generalizability of these observations. Santonian-Maastrichtian pollen and spore assemblages from southeast Australia and Antarctica have been interpreted to represent tall, open forest with conifers and angiosperms in the canopy, shrubby angiosperms in the understory, and waterlogged sites dominated by ferns (Specht et al 1992). Pollen from a mid-Cretaceous fluvial site in Patagonia indicates that mosses were dominant in this moist setting, followed by gymnosperms and primitive angiosperms (Archangelsky et al 1994).

The latitudinal spread of angiosperms, in terms of first occurrence, diversity, and abundance, took place over a period of at least 10–20 million years in the Early and early Late Cretaceous. Even now, angiosperms are less important and diverse in the vegetation of high latitudes than they are in middle and lower latitudes. The slow increase in angiosperm diversity and abundance at higher latitudes clearly indicates that they were limited by aspects of their biology that changed through evolution rather than simply by slow rates of migration resulting from limited land connections between low and high latitudes during the Cretaceous.

THE ECOMORPHIC RADIATION OF CRETACEOUS ANGIOSPERMS

Taxonomic compilations have clearly demonstrated a rapid diversification of flowering plants during the Albian and Cenomanian (e.g. Lidgard & Crane 1988, 1990, Crane & Lidgard 1989, 1990). Below we review the functional morphology of Cretaceous angiosperms in order to assess the degree to which this taxonomic radiation yielded angiosperms with new growth architectures and new ecological roles.

Flowers and Pollen—Inferences on Reproduction

Insect pollination is thought to have been widespread in angiosperm relatives such as Gnetales and Bennettitales (Crepet et al 1991), and even the earliest known angiosperm pollen is of a size and has sculptural characteristics that are consistent with insect pollination (Doyle & Hickey 1976, Brenner 1996). The earliest known flowers with tricolpate pollen grains (eudicots) have pollen that is too small for effective wind pollination (Friis et al 1994, Crane et al 1995). Furthermore, pollen found in situ in one Early Cretaceous flower has a substance like the pollen kitt that sticks pollen together in some living insect-pollinated plants (Crepet et al 1991). Insect pollination was probably a retained primitive feature of reproductive biology in early angiosperms but was not associated with morphological specializations for particular insect vectors. Barremian, Aptian, and Albian flowers are small, simple, and tend to be aggregated into

inflorescences (Taylor & Hickey 1990, Crane et al 1986, 1989, Crepet et al 1991). No specimens are known that indicate large numbers of floral parts or showy bracts or petals to attract insect pollinators, and Crepet et al (1991) have suggested that Early Cretaceous angiosperms attracted pollinators with pollen and possibly brightly colored or odoriferous connective tissue in the stamens. Even the early relatives of some wind-pollinated extant forms like Platanaceae may have been insect pollinated.

Some floral specializations for insect pollination appear to have evolved by the Cenomanian, including bisexuality, some differentiation of petals and sepals, and larger flowers (Basinger & Dilcher 1984, Crepet et al 1991). Still, most flowers were small, had few parts, and had open radial form. One lauraceous flower had modified stamens that may have served as pollinator rewards (Drinnan et al 1990), and in some rosids, the attractive function may have been taken over by the corolla of the flower, but pollen was still probably the main reward in magnoliids and hamamelids (Crepet et al 1991).

Diversity of floral form increased greatly in the Turonian-Maastrichtian as rosids, dilleniids, and higher hamamelids radiated. Floral features such as sympetally, clawed petals/nectary complexes, bilateral symmetry, prolonged calyx tubes, elongate stamen filaments, inverted anthers, pseudoterminal short-slit anther dehiscence, anther appendages, viscin threads, polyads, and nectar and resin rewards appeared by the Turonian and probably reflect specialization for pollination by bees (Crepet 1996). Many-parted flowers of Magnoliales from the Turonian may indicate the evolution of specialized beetle pollination in this group. Most fossil flowers of this age were small, however. The presence of ginger and banana family fossils in the Campanian-Maastrichtian (Hickey & Peterson 1978, Friis 1988) may indicate mammalian pollination, since that is inferred to be the primitive state for this order of plants (Kress 1990). Flowers and dispersed pollen of the *Normapolles* group may indicate the development of specialized wind-pollinated angiosperms during the Late Cretaceous, although the oldest fossils of some modern wind-pollinated families, such as the oaks, have features that suggest insect pollination (Herendeen et al 1995). In living angiosperms, wind pollination is common among both early and late successional trees.

Research on fossil flowers over the last 10–15 years has substantially revised our understanding of the evolution of pollination modes among angiosperms. Generalized insect pollination is now seen as a basal feature among angiosperms and their closest relatives. Early angiosperms appear to have had small flowers with few parts that probably were pollinated by a variety of insect taxa but specialized for none. The reward for pollinators in these early angiosperms was the pollen itself. Cenomanian flowers do not yet provide strong evidence for greater specialization of pollination syndromes, but by the Turonian, flowering plants show a wide variety of features that are today closely associated with

several types of specialized insect pollination and high species diversity within angiosperm subclades.

Seeds and Fruits—Inferences on Dispersal and Establishment

Seed size is one of the most ecologically revealing traits of plants. Seed size is directly correlated with seedling growth rate under heavily shaded conditions and inversely correlated with death rate (e.g. Grime 1979). Large seeds are thus strongly associated with the ability to establish seedlings under a forest canopy, although there are small-seeded species that regenerate in forest gaps created by windfalls or other disturbance. Small seed size is also highly positively correlated with invasive behavior in trees (Marzluff & Dial 1991).

The seed size distribution of Cretaceous angiosperms only encompasses the smallest part of the size range seen in Paleocene through Recent flowering plants, and there was relatively little change in angiosperm seed size during the Cretaceous (Tiffney 1984; Figure 6). This is consistent with weedy biology

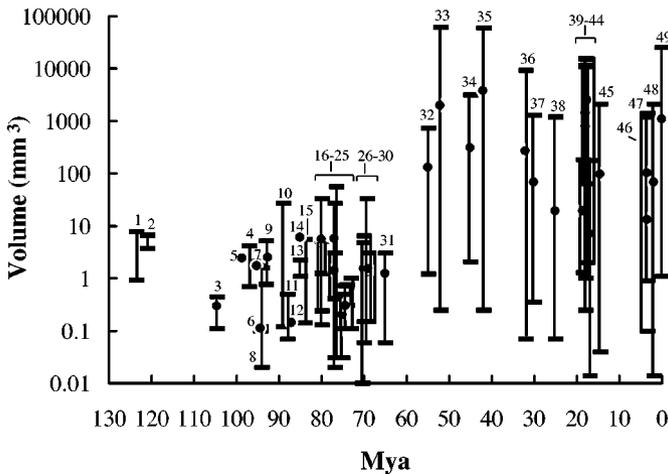


Figure 6 Plot of log of diaspore volume against time for 49 Cretaceous and Tertiary seed floras, showing the small size range of Cretaceous angiosperm diaspores in contrast to the large range of Cenozoic fossils and Recent angiosperms. The vertical lines represent the range of diaspore volume; the filled dots represent the average diaspore volume. Note that in some floras, the average volume or the range of volume is not available, and in some cases more than one flora occurs at a single time. Values for 19–23 and 28–49 are taken from Tiffney (1984). For new records (1–18, 24–27), diaspore size was calculated following the methods of Tiffney (1984) and references are as follows: 1, Friis et al (1994); 2, Pedersen et al (1993); 3, Friis et al (1995); 4, Dilcher & Crane (1984); 5, Crane & Dilcher (1984); 6, Pedersen et al (1991); 7, Crane & Herendeen (1996); 8, 10–15, 24–27, Knobloch & Mai (1986); 9, 16, Frumin & Friis (1996); 17, Friis (1988); 18, Rodriguez-de la Rosa & Cevallos-Ferriz (1994).

and abiotic dispersal for the majority of Cretaceous flowering plants. The morphology of young fruits and winged seeds also suggests that seed dispersal was passive or by wind previous to the Turonian. Among tricolpate taxa, a large number of capsular fruits with small winged seeds have been found (Crepet & Nixon 1994). The evolution of larger seed size in many angiosperm lineages during the early Cenozoic indicates that this was the time when animal dispersal and shade-tolerant life history strategies became common among flowering plants (Tiffney 1984, Wing & Tiffney 1987).

Wood—Inferences on Size and Growth Rate

A number of ecologically important traits can be inferred from wood, which serves to support plants and to transport water and photosynthate. The diameters of fossil wood specimens give a rough indication of the height and size of the plants that produced them. Anatomical features of wood are correlated with the rate and efficiency of fluid transport, with the vulnerability of the vascular tissue to embolism, and with patterns of growth (e.g. Carlquist 1975). There are also strong phylogenetic trends in vascular anatomy: For example, tissue in which vessels and fibers are less differentiated is considered more primitive than that in which there is stronger differentiation of cell types (Wheeler & Baas 1991). The relationships between ecological traits and wood anatomical features observed in living angiosperms may not apply to all fossil angiosperms because wood tissue has become more specialized through evolution (Wheeler & Baas 1991).

The most striking feature of the Cretaceous record of angiosperm wood is the rarity of specimens. Wheeler & Baas (1991) surveyed the fossil record of dicotyledonous wood worldwide for the Cretaceous and Cenozoic and tabulated approximately 1200 records; fewer than 100 (8%) of these were from the Cretaceous, although the Cretaceous represents about 40% of the duration over which records were tabulated. Almost all of the Cretaceous records were from the Maastrichtian or Campanian, with only a handful from the Albian through Cenomanian (e.g. Cahoon 1972, Serlin 1982, Thayne et al 1983, 1985). There is no dicot wood reported from the Hauterivian-Aptian. Even in Late Cretaceous floras, dicot wood, as well as monocot wood, is a rare component—assemblages are almost exclusively conifer (e.g. Ramanujan 1972). This pattern continues into the Maastrichtian in northern North America, while in areas farther south, dicot wood is at least locally more abundant (Wheeler et al 1987, Boucher & Wing 1997, Boucher et al 1997). The rarity of dicot wood in the Cretaceous when compared to the Cenozoic suggests that large dicot trees were substantially less common for most of the Cretaceous than they were during the Cenozoic.

Dicotyledonous woods from the San Juan Basin illustrate combinations of features representing hydraulic strategies that are rare in the Cenozoic (Wheeler

et al 1995). *Aplectotremas*, a wood from the Albian of Texas (Serlin 1982), has been inferred to represent a large, fast-growing tree by Upchurch & Wolfe (1993), based on its large vessels arranged in groups of two or three, large volume of soft tissue, and high vulnerability to embolism. Upchurch & Wolfe (1993) inferred that Albian woods described by Thayne et al (1983, 1985) were small to medium trees because of the low conductivity of vasculature and abundant soft tissue. In general, Late Cretaceous woods from southern North America are characterized by large vessel elements, high vulnerability, high conductivity, and large volume of soft tissue, whereas wood samples from farther north are smaller in diameter, with lower conductivity and lower vulnerability (Wolfe & Upchurch 1987). Based on these observations, Wolfe & Upchurch (1987) inferred that there were larger, faster growing dicot trees in the south and smaller shrubby dicots in the north.

In general, the anatomy of Cretaceous dicot wood is very different from that of Cenozoic dicot wood (Wheeler & Baas 1993). Cretaceous dicot woods tend not to have growth rings, a characteristic of less seasonal climates, but they also have relatively small-diameter vessels, which are associated with cool or dry climates in the Recent (Wheeler & Baas 1993). This sort of apparent conflict between characters suggests that there were substantial functional differences between Cretaceous and post-Cretaceous dicot vascular function. Generally, Cretaceous wood anatomy suggests less efficient, more vulnerable vasculature and confirms that earlier dicot wood had less division of function among different cell types (Wheeler 1991, Wheeler & Baas 1991, 1993). Wheeler & Baas (1993) suggested that the transition to more efficient vascular systems among dicots in the Cenozoic is consistent with the development of taller-statured vegetation.

Leaves—Inferences on Growth Form and Phenology

VENATION, SIZE, AND SHAPE Extant angiosperms show a great variety of leaf size, shape, and venation patterns. Leaf size and shape are strongly correlated with precipitation and temperature (Wolfe 1993), but some kinds of leaf form also are typical of plants with specific growth architecture. Among living dicots, pinnately and palmately compound leaves are commonly, though not uniquely, seen in early successional and deciduous trees and shrubs (Givnish 1978, 1979). Deeply cordate leaves with peltate or infundibulate bases, somewhat disorganized venation, and in some cases very large teeth, are commonly seen in extant herbaceous angiosperms (Hickey & Doyle 1977, Givnish 1986). Peltate and deeply cordate leaves are also common among floating aquatic plants. Extant lianas typically have leaves with deeply cordate bases, rounded shape, and well-organized venation, although there are many exceptions (Givnish & Vermeij 1976). Simple, unlobed, pinnately and palmately veined leaves are seen today

in trees and shrubs with a wide variety of habits and growing in many different environments. The overall degree of organization of the leaf vein net also correlates with tree vs herb habit as well as with phylogenetic advancement (“leaf rank” of Hickey 1979). Although leaf morphology provides few characters that can be unambiguously interpreted in terms of the growth architecture and life history strategy of the plant, these correlations are informative when combined with information from other plant organs and from sedimentary environments of the fossils.

Aptian to earliest Albian (Zone I) dicot leaves are small (<5 cm long), thin-textured, and poorly organized; some are highly lobed, others are indefinite pinnate/palmate, and still others are pinnate and entire with very disorganized venation. The morphology of the reniform and lobate leaves is consistent with their being herbaceous (Taylor & Hickey 1996). Monocot leaves of this age are also indicative of herbaceous growth architecture. A single dicot leaf type from the early Albian part of the Potomac sequence has features that could be consistent with tree growth form; *Eucalyptophyllum* has a leaf margin reinforced by a vein, thick cuticle with sunken stomata, and an elongate shape (Upchurch & Wolfe 1993).

Increasing size and variation in morphology of angiosperm leaves is a clear trend through the Albian and Cenomanian Potomac Group (Hickey & Doyle 1977). Later Albian dicots have somewhat better organized venation than the earliest Albian forms, indicating better ability to withstand mechanical stresses, more efficient distribution and retrieval of water and solutes, and perhaps larger plant size and a wider range of life forms, including tree and shrub architecture (Hickey & Doyle 1977). Pinnately and palmately lobed leaves probably were derived from early successional shrubs or small trees. Peltate and deeply cordate leaves were most likely derived from terrestrial herbs or floating aquatic plants (Hickey & Doyle 1977, Upchurch et al 1994), indicating that by the Albian, flowering plants also occupied open, sunny habitats with unlimited water and perhaps shaded understory areas. Pinnately compound leaves also appeared during the late Albian, probably indicating small, fast-growing deciduous trees (Hickey & Doyle 1977). Such leaves remained a common element of Cretaceous megaflores through the Maastrichtian (e.g. Crabtree 1987).

New leaf types appearing in the late Albian or Cenomanian include strongly bilobed forms, bifurcately compound leaves, and simple pinnately veined leaves with emarginate apices (Upchurch & Wolfe 1993). This latter leaf type and the increased diversity of other simple, pinnate leaves have been taken to indicate the expansion of dicots in late-successional habitats (Upchurch & Wolfe 1993). At least one Cenomanian assemblage (from the Dakota Group) has leaves that have been interpreted as vines or lianas (Upchurch & Wolfe 1993). It appears that all of the major functional types of dicot leaves were present by

the Cenomanian in North America, although liana-type leaves remained rare through the Late Cretaceous, perhaps an indication that complex, storied, rain forest vegetation was rare or absent (Wolfe & Upchurch 1987). Late Cretaceous angiosperms from lower middle latitudes also retained small leaves, relative to those of extant tropical and subtropical floras, which has been interpreted as a response to subhumid climate rather than reflecting the evolutionary advancement or ecological strategies of flowering plants at that time (Wolfe & Upchurch 1987). The early "saturation" of dicot leaf morphospace may reflect the relatively few distinct types of leaves that can be recognized even in extant vegetation, as well as the lack of complete distinctness of leaves from plants with different growth architecture and ecological strategies. The relatively primitive state of angiosperm wood and diaspores in the Late Cretaceous makes it unlikely that the attainment of a modern range of leaf physiognomy by the Cenomanian reflects a modern suite of growth architectures and life history strategies among flowering plants.

CUTICLE CHARACTERS Leaf cuticles present another set of features that can be interpreted in a functional/morphological context (Upchurch 1995). Thick cuticle, sunken stomata, and dense hairs are all features that retard evapotranspiration in living plants and are typical of evergreen plants that face intermittent or continual water stress. Thinner cuticles, and stomata on both lower and upper surfaces, are typical of deciduous plants that experience wetter or more humid conditions, as well as some floating aquatics. Cuticular hairs may also be present as an anti-herbivore device.

Although cuticle characters are informative about the evapotranspirative environment of the plant, interpreting them in terms of ecological strategies is subject to the same problems found in interpreting leaf morphology. For example, xeromorphic cuticular features may be present in living angiosperms that are tropical canopy trees, desert tree/shrubs, and small plants growing on low-nutrient substrates. In these different environments and strategies, the potential benefit of higher photosynthetic rate achieved through exposed stomata appears to be lower than the cost of water loss. Ecological interpretation of cuticle features is most revealing when combined with information on leaf morphology and sedimentary environments.

The occupation of cuticle morphospace during the Cretaceous angiosperm radiation is only beginning to be studied (e.g. Upchurch 1984, 1995, Upchurch & Wolfe 1993). However, cuticles of *Sapindopsis* and early platanoids are "mesomorphic," showing no particular features to retard water loss (Upchurch 1984). Leaf cuticles of Albian and Cenomanian lauraleans and chloranthoids are thick, as is typical of broad-leaved evergreens (Upchurch & Dilcher 1990, Upchurch 1995), and have some features related to reducing water loss, possibly

indicating that they occupied water-stressed or nutrient-limited habitats. A middle Albian (?) plant assemblage from the Edwards Limestone of central Texas is dominated by conifers, ferns, and seed ferns, but it also contains a few angiosperms that show xeromorphic features such as thick leaves, stomata restricted to the underside of the leaf, and dense hairs (Serlin 1982). This may be the oldest record of a xeromorphic angiosperm.

DISCUSSION

An Ecological Framework

Grime (1977, 1979) advanced the idea that there are three primary life history strategies for plants: ruderal, competitive, and stress tolerating (Figure 7a). Ruderals are plants that have short life spans, low investment in individual offspring, high potential growth rate, and little ability to withstand limited resources except as seeds. Ruderals excel at growth in disturbed habitats, where there is frequent partial or total destruction of plant biomass but where resources may be plentiful. Competitors tend to have longer life spans, to have greater investment in individual offspring, high potential growth rate, and to respond rapidly through differential growth to changes in critical resources such as light and water. Competitive plants are able to succeed in physically stable habitats where resource levels may be reduced because of the growth of other plants. Stress tolerators have variable life spans, variable investment in offspring, low potential growth rate, and high tolerance of low light or low nutrient conditions. Stress tolerators exist in relatively stable environments with chronically low availability of some of the resources necessary for photosynthesis. Grime

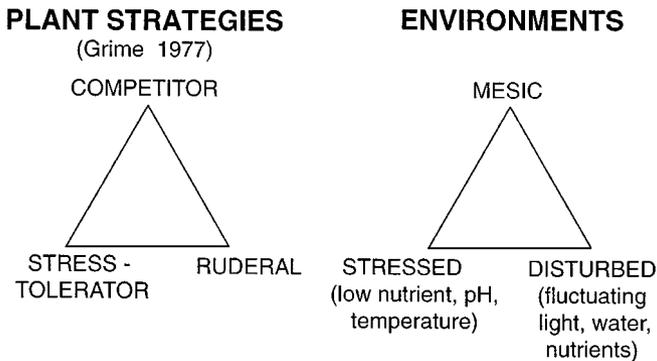


Figure 7 (a) Primary plant strategies proposed by Grime (1977, 1979) and (b) environments in which these strategies are most successful.

(1979) considered all shrubs and trees to be competitors or stress tolerators compared with herbs, but ecological strategies vary enormously within woody plants, and we consider some trees to be ruderal by virtue of their rapid growth, short life spans, and shade intolerance, at least compared with other woody plants.

Grime's triangle can be used as a heuristic for environments as well as for life history strategies (Figure 7*b*). Habitats corresponding to the strategies are disturbed (ruderal), mesic (competitor), and stressed (stress tolerator). Disturbed habitats include stream channel margins or other areas subject to frequent high-energy flooding, fires, or mass wasting and also most deserts. Deserts might seem naturally to belong among the "stressed" habitats because of the scarcity of water. However, low annual precipitation is associated with short, intense episodes of precipitation, and water is abundant in most deserts for short periods of time (MacMahon 1985), so that deserts are similar to disturbed habitats in having short periods of abundant resources. Other disturbed habitats include marshlands with variable water level, sea shores subject to large tidal fluctuation, and many grasslands (Grime 1979).

Mesic habitats include areas where water, major nutrients, light, and temperature permit growth on a more or less continuous basis. Where water and nutrients are the most available, standing biomass tends to be high and plants compete for light, nutrients, and water. In some mesic habitats, the growth of a dense canopy may create shade and resource limitations for smaller plants.

Stressed environments include peat bogs, white sand, and other low-nutrient soils, all places where major nutrients are continually suboptimal for most plants. Arctic and high-alpine climates can also be considered stress inducing because low temperatures inhibit growth and nutrient release from decay of organic matter (Grime 1979). Of course all three types of environments intergrade with one another: Nutrient levels may be low in a tropical forest where other resources are abundant; peat bogs occasionally burn, temporarily releasing nutrients that are otherwise limiting; some deserts may have chronically low precipitation without storms, thus making them more continuously stressful.

Grime's three primary strategies form a useful framework in which to consider the ecological radiation of flowering plants during the Cretaceous. Grime (1977) listed some morphological features associated with each of the three primary strategies, and we have added to his table features that can be assayed in the fossil record (Table 2).

Ecological Strategies in Cretaceous Angiosperms: Congruence or Lag?

For the last 20 years, views of Cretaceous angiosperm paleoecology have been shaped strongly by studies of the Aptian-Cenomanian Potomac Group floras

Table 2 Morphological correlates of ecological strategies in plants (based on Grime 1977)

	Competitive	Stress tolerant	Ruderal
Life form	Herb/tree/shrub	Herb/tree/shrub	Herb
Shoot morphology	Dense canopy, high and wide	Variable	Small, narrow spread
Longevity	Long or short	Long to very long	Very short
Leaf longevity	Short	Long	Very short
Leaf phenology	Peaks of leaf production	Evergreen	Short phase leaf production
Flower phenology	Flowers after productive period	Unpredictable	Flowers early in life
Flower frequency	Annual	Intermittent	Frequent
Percent production to seeds	Small	Small	Large
Perennation	Buds and seeds	Leaves and roots	Seeds
Growth rate	Potentially high	Slow	High
Defense of leaf	Moderate	High	Low
Stress response	Growth	None	Reproduction
Traits Available for Study in the Fossil Record			
Seeds	Large, variable	Variable	Small
Leaf size	Moderate to large	Small	Variable
Leaf shape	Simple	Simple	Compound or deeply lobed
Leaf texture	Mesomorphic	Thick	Variable, thin
Cuticle	Moderately thick	Xeromorphic, hairs	Thin, dense stomata
Vasculature	Moderately conductive	Low conductivity	High conductivity

by Doyle & Hickey (Doyle & Hickey 1976, Hickey & Doyle 1977). These authors proposed that early angiosperms were small trees with high growth rates and rapid reproduction that grew along stream courses where light, water, and nutrients would have been at high levels. In these environments, competition from other plants would have been reduced by frequent physical disturbance. Retallack & Dilcher (1981, 1986) largely concurred with the view that early angiosperms were early successional, and they added that early angiosperm migration might have been along coastal corridors. Retallack & Dilcher also applied Grime's terminology of ecological strategies, referring to early angiosperms as ruderals. More recently, Taylor & Hickey (1992, 1996) have argued that the oldest angiosperms were scrambling or rhizomatous perennial herbs that lived on unstable, nutrient-rich sites; still, the capacity for rapid growth and maturation is seen as critical to their early success. Most studies of the last 20 years seem to agree that the first angiosperms and their Early Cretaceous descendants had many features of ruderal life histories and occupied disturbed habitats.

The ecological strategies and environmental settings of Late Cretaceous angiosperms have been more disputed, and two alternate interpretations of the record currently exist. In one, the range of angiosperm ecological strategies and growth forms expands at roughly the same rate and time as their taxonomic diversity; we call this pattern congruency. The alternate interpretation is that the expansion of ecological strategies and growth forms occurred in the Campanian-Maastrichtian or possibly Paleocene, about 30 million years after their rapid taxonomic diversification; we call this pattern lag. Congruency was implicit in the study of Hickey & Doyle (1977), who recognized angiosperm floating aquatics, understory herbs, shrubs and trees, and early successional trees in the Aptian and Albian and late successional canopy trees in the Cenomanian. They also observed that the range of depositional environments containing angiosperms expanded to include finer-grained, presumably more stable settings by the Cenomanian (Hickey & Doyle 1977). Retallack & Dilcher (1986) cited examples of angiosperm stress tolerators and competitors from the Cenomanian, also implying congruency. Upchurch & Wolfe (1993) argued that one Cenomanian Dakota Group fossil assemblage represented rain forest vegetation with angiosperms as canopy trees. Crane (1987) also thought that the vegetational dominance of angiosperms was achieved more or less in concert with their taxonomic diversification. Lag, or delayed ecological expansion, has been argued based on the small size of angiosperm diaspores throughout the Cretaceous (Tiffney 1984, Wing & Tiffney 1987), on the rarity, small size, and inefficient anatomy of Cretaceous angiosperm wood (Wing & Tiffney 1987, Wheeler & Baas 1991), and on the abundance of conifer and fern fossils in Late Cretaceous assemblages derived from fine-grained sediments in the northern Rocky Mountains (Wing et al 1993, Tiver et al 1994, Taylor & Hickey 1996).

In either congruent or lag models, the ecological expansion of angiosperms took place along at least four identifiable gradients: time, phylogeny, latitude, and local environmental/edaphic conditions. Most authors have considered only two or three of these simultaneously, and some of the apparent conflict between congruency and lag is resolved when additional dimensions are considered. Early Cretaceous angiosperms are easily characterized ecologically because near the base of the radiation there had been less opportunity for different sublineages to expand geographically and evolve different ecological strategies and growth architecture. By the Cenomanian, angiosperms were a globally distributed, highly diverse group, comprised of sublineages separated from one another by 20–30 million years of independent evolution. This degree of phylogenetic separation almost ensures that any generalization about Late Cretaceous flowering plants as a whole will be incorrect. Whether ecological expansion appears to lag or be congruent with taxonomic radiation depends on what sublineages are being considered and what regions and environments are studied.

There appear to be several intersecting trends in the abundance of Late Cretaceous angiosperm remains and the inferred size and ecological strategies of the plants that produced them. 1. At lower paleolatitudes, angiosperms became abundant and occupied a broader range of habitats earlier than at higher latitudes. 2. Within a given paleolatitudinal belt, angiosperms appear to have dominated disturbed habitats earlier and more completely than stressed and mesic habitats in the same region. 3. At low to middle paleolatitudes, woody magnoliids appear to have reached stressed and mesic habitats earlier than eudicots such as platanoids, lower hamamelids, and lower rosids.

Thus, lag vs congruency hypotheses must be evaluated in paleogeographic and phylogenetic context. The occupation of stressed and mesic habitats by tree-form magnoliids may have been congruent with the primary taxonomic diversification of angiosperms during the Albian and Cenomanian at low to middle paleolatitudes. This does not necessarily conflict with the possibility that eudicots remained ruderal small trees and a minor component of vegetation on stressed and mesic sites at middle to high paleolatitudes until long after the primary mid-Cretaceous diversification was over.

Escalation in Angiosperm Evolution

The data reviewed above show that angiosperm abundance expanded across both paleolatitude (low to high) and local environments (disturbed to mesic or stressed). These two gradients have an underlying similarity in that potential rates of growth decrease from higher to lower nutrient sites and from lower to higher latitudes. Equatorial regions with high levels of solar insolation, high temperatures, and adequate precipitation are favorable to ruderal strategies except in areas where soil nutrient levels are low (Grime 1979). If the Cretaceous tropics were seasonally wet rather than ever wet (Ziegler et al 1987), then ruderal strategies might have been even more advantageous in the tropics than they are today because tree biomass would probably have been less and the structure of vegetation more open. The success of Early Cretaceous angiosperms in the tropics may have been related not only to their ability to maintain dispersed populations and avoid species-specific predation/parasitism, but also to their rapid growth rates and life cycles (Bond 1989, Midgley & Bond 1991, Taylor & Hickey 1996).

The slow movement of angiosperms into higher-latitude vegetation is consistent with the generally more stressed conditions that pertain in regions where temperature and/or light limit growth through a substantial part of the year. In these conditions, the existing conifer and fern vegetation would have offered few opportunities for growth to ruderals, which explains the strong tendency for angiosperms to be restricted to freshly disturbed areas at higher latitudes. High growth rates are basic to the ruderal strategy and require habitats with high levels of light, water, and nutrients. Such habitats are, almost by definition,

unstable or disturbed environments because stable habitats with ample resources develop a heavy cover of plants that reduces the availability of resources through competition (Grime 1979). Plants that grow faster and have shorter generation times succeed in disturbed habitats because they use the resources of the open patch more quickly and are better able to locate the next patch through rapid reproduction and high fecundity.

Ruderals conform to one type of escalation, as defined by Vermeij (1987), in that they are opportunists with high rates of energy use. If organisms have become generally more escalated through the Phanerozoic (Vermeij 1987), then successive waves of evolutionary radiations in land plants might be expected to have arisen from the most ruderal groups present at any given time. Vermeij (1987) argued that high-energy environments favor escalated forms. On a global scale, the environments most likely to favor highly escalated forms such as ruderals are the tropics. More light and more precipitation generally make faster growth rates possible. The great limiting factor in tropical growth is likely to be nutrient levels—these are typically low in soils that are leached by high rainfall and utilized by continuous growth of vegetation. The most productive areas in the world will therefore be regions that are tropical, but that have higher soil-nutrient levels because the parent material is fresh (e.g. recent volcanic soils and fluvial sediments) or nutrients have been released by fire or other disturbances. Tropical weeds should be the most highly escalated plant forms.

Ruderals are, by definition, unable to do well in the most nutrient- and light-limited habitats, which may explain why stressed environments can become “museums” that retain older lineages; groups with slower metabolic rates persist because under stressed conditions high growth rates are not advantageous (Grime 1977, Vermeij 1987). As long as these stressed environments have a continuous distribution in space and through time, their stress-tolerant and competitive incumbents would be difficult to displace. The limited diversification of angiosperms with stress-tolerant or competitive strategies during most of the Cretaceous, and the apparently rapid development of these strategies in many distantly related angiosperm lineages during the early Cenozoic, suggest that environmental disturbance near the K/T boundary may have been important for breaking the dominance of older stress-tolerant and competitive lineages (Wing & Tiffney 1987). If this is a general pattern, then episodes of mass extinction or environmental disruption should precede periods during which escalated groups of plants take over more stressed environments, a pattern that has also been seen in Carboniferous swamp forests (DiMichele et al 1987).

Taxonomic Diversity vs Ecological Dominance

In many paleontological studies, taxonomic diversity is considered a proxy for ecological importance. The implicit assumption is that more species in a lineage indicate greater biomass in the lineage as well. Diverse groups are often

referred to as “dominating” the biota of a given time interval or geographic area. Although this generalization may apply in animals, there are strong reasons to think that among plants there is no strong correlation between biomass dominance and species diversity (Bond 1989, Eriksson & Bremer 1992, Tiffney & Mazer 1995). Even a casual glance at the diversities of extant families of flowering plants shows that the most diverse (e.g. Asteraceae, Graminae) are largely herbaceous and ruderal and achieve high biomass in areas marked by disturbance or highly seasonal climate. More rigorous systematic comparisons confirm that there is a strong association between herbaceous habit and high species diversity when arborescent groups are compared to their smaller-statured sister taxa (Judd et al 1994). Considering land plants as a whole, the most diverse group outside of angiosperms is the largely herbaceous and ruderal ferns, whereas the more stress-tolerant cycads and conifers have low species diversity, even though the conifers in particular have very high standing biomass in some regions. There are low diversity herbaceous groups (club mosses and horsetails), but these seem to be stress-tolerant herbs rather than ruderals (Grime 1979).

Although the taxonomic diversification of angiosperms during the middle of the Cretaceous has generally been considered to mark the rise to vegetational dominance of a competitively superior group, the evidence presented here raises other possibilities. The taxonomic diversification of angiosperms in the Cretaceous appears to have been largely a radiation of herbaceous and woody plants with ruderal strategies. In this theory, the vegetation of stressed and competitive environments would have remained dominated by conifers, ferns, and cycads throughout the Cretaceous, particularly in less species-rich higher latitudes. Ruderal angiosperms would not necessarily have outcompeted older groups of plants because of key innovations in vegetative or reproductive biology; they may simply have filled in disturbed gaps that would previously have been lightly vegetated. In this scenario, Cretaceous angiosperms would have competed for space, light, and nutrients mostly with other ruderals—perhaps Gnetales and some groups of ferns, as has been suggested on the basis of taxonomic diversity and palynological abundance data (Crane & Lidgard 1990, Lupia et al 1997).

If angiosperms did not outcompete older lineages in stressed or competitive environments, how did they come to dominate global vegetation the way they do now? At least two possibilities exist. The spread of angiosperms to non-ruderal habitats and strategies may have been a passive consequence of higher rates of speciation in this smaller statured group. Replacement of competitors and stress tolerators belonging to other higher taxa would have taken place as the pool of lineages available to replace extinct species became increasingly angiospermous. This should have produced a gradual pattern of increasing angiosperm dominance, though the increase in angiosperm dominance might have been delayed from the increase in diversity. Alternatively, extrinsic events such as

the mass extinction at the K/T boundary, or other global environmental change, may have preferentially caused extinction of non-angiosperms or increased the success of the already diverse angiosperms. Such a cause might have produced a relatively sharp shift in vegetational dominance, and if it was associated with the K/T extinction, the rise to vegetational dominance of angiosperms may have been largely a Cenozoic rather than Cretaceous event. Regardless of the accuracy of this scenario, the weak or even negative correlation between diversity and biomass dominance in plants is a strong reason for incorporating both measures in future paleontological studies of lineage histories.

CONCLUSIONS

1. The earliest (Valanginian-Hauterivian) angiosperms were probably tropical ruderal plants, possibly herbaceous, but certainly of small stature.
2. The diversification of angiosperms in the Barremian-Cenomanian produced many species but limited expansion into different ecological strategies. Some clades of angiosperms (particularly woody magnoliids) developed large tree growth forms and more stress-tolerant or competitive ecological strategies by the Cenomanian, but most angiosperms (eudicots such as hamamelids and rosids) remained ruderal herbs, shrubs, or small trees that were important in disturbed habitats. The poleward spread of flowering plants was geologically slow.
3. During the Turonian-Maastrichtian, many extant orders of flowering plants first appeared, probably becoming recognizable because of specializations in floral morphology related to advanced insect pollination systems. Even though reproductive morphologies began to look more modern, dispersal remained largely abiotic, and many angiosperm lineages continued to have ruderal ecological strategies. At middle to high paleolatitudes, angiosperms played a relatively subordinate role in conifer- and fern-dominated vegetation of stable and low-nutrient land surfaces and dominated only in disturbed environments. At lower paleolatitudes, angiosperms played a greater role in vegetation across the spectrum of environments; they were major contributors to biomass not only in disturbed habitats but also in some stressed and stable competitive conditions. In low to middle latitudes, ruderal angiosperms may have competitively displaced ruderal ferns and gymnosperms. The importance of angiosperms in Late Cretaceous vegetation growing on stable land surfaces in the tropics is unknown, but knowledge of it would be a useful index of the degree to which they had evolved a modern range of ecological strategies.

4. By the close of the Cretaceous, although angiosperms were by far the most diverse group of terrestrial plants in terms of species, they still lacked the biomass dominance of global vegetation and range of ecological strategies that they achieved during the Cenozoic. On local environmental gradients, they were least important in stressed or competitive habitats, and on a global scale, they were least important at paleolatitudes higher than about 40°–45°N and S, probably because their success was related to fast growth and high rates of resource use.
5. The angiosperm radiation provides a major example of decoupling of taxonomic diversity and ecological dominance. The tendency, seen also in extant plants, for herbaceous groups with ruderal life histories to have high diversity suggests that species diversity in the fossil record is likely to be a poor predictor of ecological importance. Angiosperms may have displaced older groups of land plants in part through competition, but also through replacement following preferential extinction of other groups and/or through higher rates of speciation. The best evidence for competitive replacement is in the reciprocal pattern of abundance of angiosperms and ferns at low to middle paleolatitudes in the Late Cretaceous.
6. The angiosperms may be but one example of a general phenomenon in plants in which successive major groups evolved first as small ruderals and only later in their evolutionary history invaded competitive and stressed habitats. This pattern is consistent with patterns of escalation that have been described in animal evolution, since ruderals grow and reproduce more rapidly than other plants. The continued dominance of earlier-evolving, presumably less-escalated taxa in stressed settings is consistent with the advantages of incumbency in environments where rapid growth and reproduction is not tenable.

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