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THE RECIPROCAL INTERACTION OF ANGIOSPERM EVOLUTION AND TETRAPOD HERBIVORY

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Abstract

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We have interpreted the history of angiosperm–herbivorous tetrapod interactions based on the fossil record of the two groups. This history can be divided conveniently into four stages. Stage 1, lasting ~40 Ma (Barremian–Campanian), was characterized by diverse large herbivores, few species of small herbivores, and *r*-selected angiosperms. The dominant interaction between herbivores and angiosperms during this stage was generalized herbivory. During Stage 2 (~10 Ma, Campanian – Maestrichtian), small herbivores increased in diversity; larger angiosperms and larger angiosperm diaspores became more common. Generalized herbivory was still the dominant interaction in this stage, but frugivory/dispersal of angiosperm diaspores by small herbivores became more important. In Stage 3 (~25 Ma, Paleocene – mid-Eocene) large angiosperms and large angiosperm diaspores were diverse; large herbivores were initially absent, later low in diversity. Frugivory/dispersal was common during this stage, generalized herbivory much less so. During Stage 4 (~30 Ma, Oligocene – Recent), the relative importance of large vs. small herbivores and large vs. small angiosperms has varied by community, as has the relative importance of generalized herbivory vs. frugivory/dispersal.

We infer the following evolutionary effects of angiosperms and tetrapods on each other. During Stage 1 generalized herbivory/disturbance by dinosaurs favored angiosperms that remained relatively small and *r*-selected. Increasing abundance and geographic spread of these *r*-selected angiosperms fueled the Late Cretaceous diversification of low-browsing ornithopod dinosaurs. The rarity of angiosperms with large diaspores provided little resource for a radiation of small herbivores. The low diversity of small herbivores created few opportunities for the evolution of small herbivore dispersal syndromes among angiosperms. The stability of angiosperm–vertebrate herbivore interactions during Stage 1 suggests this system of ecological relationships had internally self-reinforcing properties.

The modest radiation of small herbivores during Stage 2 may indicate increased frugivory/dispersal. More common large angiosperm axes and diaspores show some angiosperm lines were becoming more *K*-selected. These imply a modification of the stable system formed during Stage 1.

Extinction of all large herbivores at the K/T boundary destroyed Stage 1 ecological interactions and changed selective pressures on angiosperms. In the early Paleocene, generalized herbivory/herbivore disturbance was absent or uncommon. Denser vegetation, increased competition between plants, and increased seed dispersal/predation by small animals resulted in selection for larger seeds, diaspores and sporophytes. The distribution of resources in closed angiosperm vegetation permitted the radiation of small, arboreal, frugivorous birds and mammals, which in turn were important to the success of angiosperms with large, animal-dispersed seeds. Spread of arborescent angiosperm vegetation reduced resources and evolutionary opportunities available to larger mammalian herbivores, retarding their diversification, and in turn perpetuating low levels of generalized herbivory/disturbance. Stage 3 was another period during which angiosperm–vertebrate herbivore interactions were stabilized by self-reinforcing behavior of the system.

During Stage 4 increased seasonality began to favor shorter life cycles among angiosperms; herbaceous plants diversified and spread. Open, high-productivity vegetation was better exploited by large herbivores, which diversified, increasing generalized herbivory/disturbance that in turn created more habitat for *r*-selected angiosperms.

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Introduction

One of the dominant interactions between terrestrial vertebrates and plants is phytophagy — animals eat plants. However, evolution of this basic trophic relationship has resulted in vertebrate herbivores that specialize on particular types of plant organs, as well as on different plant species and vegetational types. These feeding specializations are reflected in our terminology: folivore, frugivore, granivore, browser, grazer, arboreal herbivore. Herbivory is also categorized according to its effect on the plant; if the animal eats the plant it is simple herbivory, but if the animal also moves seeds to good germination sites the interaction is called dispersal.

In many ecosystems herbivores have a strong influence on the structure and composition of the vegetation. For example, elephants may create sufficient disturbance to limit the establishment of woody plants in grasslands, maintaining the community in an early to mid-seral state (e.g. Croze, 1974). Arboreal folivores may influence the reproductive success of temperate and tropical forest canopy trees (Rockwood, 1973; Coley, 1983; Crawley, 1983). Frugivores may become an integral part of the life history of a plant (Howe and Smallwood, 1982), influencing the shape of its seed rain (Janzen, 1983, and references therein), and therefore its reproductive success (e.g. Janzen, 1969, 1971, 1983 and references therein; Harper, 1977).

Plants, and particularly angiosperms, have an enormous range of morphologies, chemistries and phenologies that function in part to deter herbivores or to encourage dispersers. Such features as the intercalary meristem of grasses, the toxins and textures of the mature foliage of tropical forest trees, the fleshy coverings of many fruits and seeds, and the timing of maturation of many plant parts are apt responses to various kinds of vertebrate herbivores and dispersers.

Although vertebrate herbivores have a directly observable effect on plant communities, and there is a great array of plant features that function to modify vertebrate feeding behavior, there are few if any case studies that demonstrate the evolution of a particular plant feature as a response to selective pressures generated by a specific vertebrate herbivore or disperser. In spite of the absence of such studies, we think that the ubiquitous presence of the plant morphologies and herbivore effects outlined above is itself strong evidence that vertebrate herbivores and dispersers have had a powerful influence on plant evolution. This kind of broad evolutionary effect of one set of lineages on another set of lineages has been termed "diffuse coevolution" (Herrera, 1984).

The results of diffuse coevolution are common in present-day ecosystems, yet there has been comparatively little attention given to the possible effect of phytophagous vertebrates on the evolution of flowering plants, or to the development and long term history of current interactions between the two groups of organisms (although see Regal, 1977; Bakker, 1978; Tiffney, 1984). Rather, paleobotanists have tended to emphasize the importance of climatic and edaphic conditions for flowering plant evolution (e.g. Axelrod, 1952; Doyle and Hickey, 1976). When paleobotanists have considered the role of biotic factors in shaping plant evolution they have usually emphasized plant–plant competition or pollination biology (Doyle and Hickey, 1976; Knoll, 1984). In this paper we examine the history and evolutionary significance of the interaction between phytophagous vertebrates and angiosperms. We emphasize the importance of herbivores and dispersers for angiosperm evolution, not because other biotic and abiotic factors are unimportant, but because we feel the effects of herbivorous vertebrates on angiosperm evolution (and vice versa) need fuller discussion.

Methods

Reconstructing the history of an ecological relationship is necessarily a somewhat speculative endeavor. The processes of herbivory and dispersal cannot be fossilized. Therefore we must rely on preservable attributes of ecosystems and organisms; e.g. the shapes and sizes of organisms and the diversity and spatial distribution of species. Fortunately there is a large body of ecological work that relates such attributes to the ecological roles of individual species and the organization of communities.

Our method has been to review the ecological literature on herbivory and dispersal, extracting from it a set of correlations that can be used as tools to explore the fossil record and interpret extinct communities. This is a standard uniformitarian approach, and if applied too strictly can give a false impression that past and present communities are similar. We have tried to avoid this pitfall by using correlations that arise from basic mechanical and physiological constraints on organisms rather than by making analogies directly at the level of community organization.

Correlational tools for interpreting extinct communities

Five attributes were chosen to characterize the nature of angiosperm–herbivore interactions in extinct communities: herbivore body size, herbivore dentition, herbivore locomotion, angiosperm diaspore size, and angiosperm stature. These attributes were chosen because they are important in present-day communities and because they can be measured or inferred from fossil remains. Clearly it would be desirable to include many other features, for instance the amount and kind of angiosperm secondary compounds, but such information is not generally available for fossil organisms. Two parameters, herbivore body size and angiosperm diaspore size, were quantified.

Herbivore body size

Body size in tetrapods controls or is correlated with a variety of ecologically significant traits (Western, 1979; Damuth, 1981a,b; Peters, 1983). Basic physiological processes and mechanical factors dictate that larger herbivores will have greater total energy requirements but lower metabolic rates than smaller herbivores (Peters, 1983; Demment and Van Soest, 1985). Together these factors have important consequences for the dietary requirements of large as opposed to small herbivores.

Large herbivores tend to feed on a wide range of plants and plant parts, and much of the diet is high in fiber and low in energy (Jarman and Sinclair, 1979; Peters, 1983). The lack of selectiveness is related to the need for large herbivores to eat large quantities of food to fulfill their energetic needs — they cannot meet their requirements by seeking out rare or widely dispersed high energy food. The ability of large herbivores to survive on high fiber diets is largely the result of a low metabolic rate, which permits them to retain cellulose in the gut for long periods, deriving energy from it through microbial fermentation (Janis, 1976; Demment and Van Soest, 1985).

Because of their higher metabolic rate, small herbivores have effectively less gut capacity for meeting their metabolic requirements; this requires them to obtain a higher energy diet (Demment and Van Soest, 1985). As a result, most small herbivores eat fruits or seeds, and there are no mammalian herbivores smaller than 0.75 kg that are exclusive folivores (Kay and Hylander, 1978). This point is reinforced by the anomalously low metabolic rates observed in many smaller folivorous mammals (McNab, 1978).

These relationships between body size and diet are based on physiological and physical principles that apply to all tetrapods, and so they should hold true for extinct as well as living forms (Damuth, 1982). We will assume that size of an extinct herbivore gives a rough approximation of the "quality" (energy per weight) of its diet and the degree to which it specialized on higher energy plant parts such as fruits and seeds.

For extinct herbivores body size was estimated to order of magnitude in grams (Fig.1). The order-of-magnitude precision of the data is a result of our inability to make more precise estimates based on fossils. However, the relationship between body size and diet is such that small differences in body size do not have a large effect on diet.

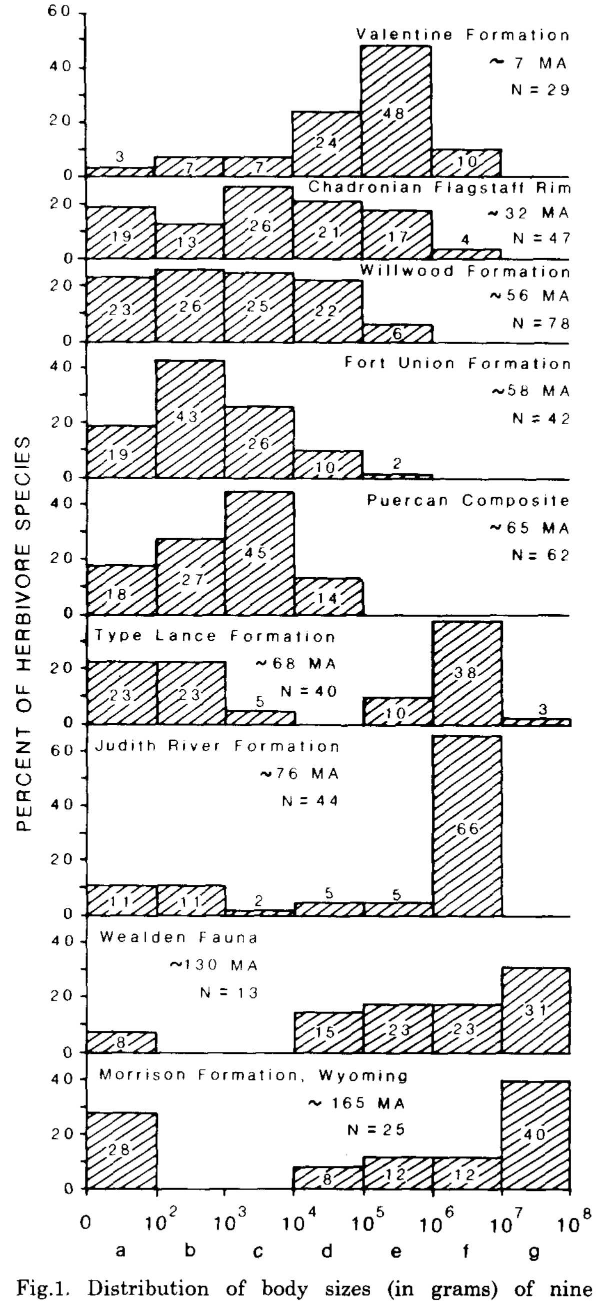


Fig.1. Distribution of body sizes (in grams) of nine herbivorous tetrapod faunas during the last 160 million years. "*N*" is the number of herbivore species in a given fauna. Note the sharp contrast between the body size distribution of the Mesozoic and early Cenozoic faunas.

Herbivore diet

The dental and postcranial morphology of extinct vertebrates provide an additional basis for inferring their dietary requirements. For many extinct herbivores the masticatory apparatus is known well enough to permit a functional analysis that in turn can be used to reconstruct some of the mechanical properties of the diet. This type of analysis has been widely used in studying fossil mammals (e.g. Kay, 1977; Krause, 1982a), and more recently has been applied to some groups of dinosaurs as well (Weishampel, 1984a; Norman and Weishampel, 1985).

In this study we have assembled data on a sequence of faunas and roughly characterized the herbivores according to their masticatory adaptations. Dinosaur dietary inferences were taken from Coombs (1975) (sauropods); Weishampel (1984a,b) and Norman and Weishampel (1985) (hadrosaurids); and Ostrom (1966) (ceratopsians). Dietary inferences for mammalian herbivores were taken from the literature or based on cusp height and "crestiness" of molar teeth, and degree of specialization of incisors and/or premolars.

Only three broad dietary categories were recognized on the basis of dentition: frugivore/omnivores, folivore/browsers, and grazers.

Herbivore locomotion

The locomotory capabilities of an herbivore species are of clear significance in determining the kinds of plant resources it can reach. For example, in tall forest vegetation much of the usable plant biomass is in the canopy, and therefore available only to arboreal and volant herbivores.

Inferring locomotory function from skeletal remains partly depends on the size of the organism and its degree of specialization. One can predict that very large tetrapods will be exclusively terrestrial. In contrast, small tetrapods can adopt a wide range of locomotory styles even if they have a generalized postcranial structure. Even among small animals, however, those that can fly and most that are highly arboreal have specialized limbs.

We have used three locomotory categories in analyzing the fossil record of herbivorous tetrapods: terrestrial, arboreal, and volant. These three categories express the most important differences in the ways herbivores obtain plant food without stretching too far our ability to infer mode of locomotion from fossil remains.

Angiosperm diaspore size

In living plants propagule size is highly correlated with two classes of ecological traits: habit/habitat of parent plant, and dispersal syndrome. Early successional plants and plants of small stature tend to have smaller seeds than larger species occupying later successional vegetation (Salisbury, 1942; Harper et al., 1970; Silvertown, 1981; Strauss and Ledig, 1985). The smaller seeds of early successional plants presumably reflect a lower need for stored nutrients in an environment with high light levels. The correlation of diaspore size with dispersal syndrome is more complicated, but generally wind-dispersed diaspores are small, while those that are dispersed by endozoochory are larger and possess some sort of reward or attractant, the nature of which depends on the dispersal agent (Ridley, 1930; Van der Pijl, 1982), but note that small diaspores may be dispersed by large herbivores (Janzen, 1984). In this study we will follow methods and use data presented by Tiffney (1984).

Angiosperm stature

Plant stature is an important constraint on the ecological role of individual species, but it also determines characteristics of vegetation (e.g. light availability, nutrient flow, distribution of herbivore food) that in turn influence the composition of an area's biota. The height of extinct trees can almost never be directly measured, only inferred from the dimensions of fossilized trunks. Published reports of Cretaceous angiosperm wood are not abundant, and usually focus on taxonomically important anatomical features rather than on size. Here we have assembled scattered data on diameter of fossil angiosperm axes from published and unpublished sources.

Patterns in the fossil record

Before discussing historical patterns in detail, we note two general aspects of the data set. First, the fossil data are widely spaced stratigraphically, with the result that only long-term trends can be detected. Second, most of the information on the fossil record comes from the Northern Hemisphere, and from North America and Europe in particular. This geographic limitation is unfortunate but unavoidable. The climatic bias imposed by this geographic restriction is not as severe as might be imagined because world climate during the Cretaceous and Paleogene was much more equable than it is now and latitudinal temperature gradients were greatly reduced (e.g. Wolfe, 1978). Furthermore, the limited data from low latitudes and the Southern Hemisphere do not seem to contradict our conclusions.

Herbivore body size

During the time since the origin and radiation of the angiosperms there have been dramatic changes in the sizes of herbivorous tetrapods. (Fig.1). In Late Jurassic and Early Cretaceous herbivore faunas, most species were in the largest size categories (> 1000 kg), few or none in the middle size categories (1–1000 kg), and a small number were in the smallest size category (< 1 kg). Low diversity of small and mid-body sizes distinguishes these distributions from all Cenozoic herbivore faunas.

The relative diversity of small herbivores increased during the Campanian and Maestrichtian, primarily because of the radiation of the Multituberculata. The anomalously high diversity of very small herbivores in the Late Jurassic Morrison fauna is due to probable oversplitting of the genus *Docodon* (Jenkins, 1969). The late Maestrichtian herbivore fauna of the Lance Formation (Estes and Berberian, 1970; Clemens, 1973; D.B. Weishampel, pers.

comm., 1985) had almost equal numbers of herbivorous mammal and dinosaur species. The strong bimodality of the body-size distribution reflects the lack of size overlap between mammals and adult dinosaurs.

Herbivore body size distribution changed dramatically with the extinction of the dinosaurs; all herbivores larger than ~10 kg were eliminated. During the early Paleocene herbivorous mammals radiated rapidly into mid-size categories, but in spite of this rapid radiation, it was not until the late Eocene or early Oligocene, some 30 Ma after the K/T boundary, that a substantial percentage of herbivore diversity was again made up by species 100 kg and larger. The low diversity of medium to large herbivores in the three Paleocene and Eocene faunas plotted in Fig.1 appears to be typical of most faunas of this age, although diversity of large herbivores may have begun to increase somewhat earlier (late Eocene) in South America than in other parts of the world (Patterson and Pascual, 1968; Stebbins, 1981).

In the Oligocene and Miocene faunas (Webb, 1969; Emry, 1973) plotted here, much of the herbivore diversity was in species between 10 and 1000 kg. The near absence of small herbivores in the Miocene Burge Fauna is probably a taphonomic or collecting bias, since there are only two rodents. This high diversity in the middle to large size categories is typical of modern faunas of open vegetation, such as that of the Serengeti, but not of forested areas (Fleming, 1973; Fig.2).

The data on herbivore body size distribution can be summarized as follows. Late Jurassic and Early Cretaceous faunas were most diverse in the 1000 kg range and above for body weights. In the Campanian and Maestrichtian, herbivores below 1 kg body weight became more diverse, being as diverse as the large dinosaurian herbivores in one late Maestrichtian fauna. In the earliest Paleocene all herbivores were <10 kg body weight. Mammalian herbivore faunas were dominated by species under 100 kg for most of the Paleocene and Eocene (~30 Ma). Some Oligocene and

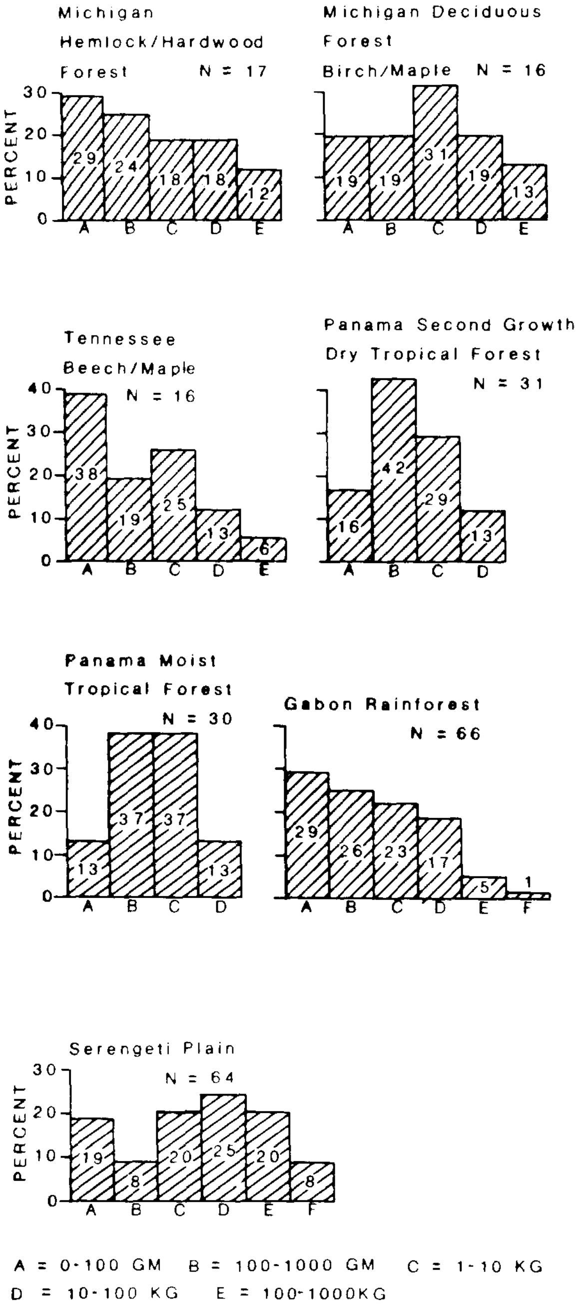


Fig.2. Distribution of body sizes (in **grams**) of terrestrial herbivorous/omnivorous mammals in a variety of present-day vegetational types. "*N*" is the number of species in a given fauna. Note the greater diversity of large herbivorous mammals in the open vegetational setting of the Serengeti. North and Central American data from Fleming (1973); Gabon data from Emmons et al., (1983); Serengeti data from field guides.

later faunas achieve considerable diversity of herbivore species larger than 100 kg.

Herbivore diet and locomotion

Late Jurassic

Large sauropods were the dominant herbivores of the Late Jurassic (e.g. Morrison Fauna). Large bodies and long necks would presumably have permitted them to browse 10–12 m above the ground (Bakker, 1978). Many sauropods appear to have been terrestrial (Dodson et al., 1980), and their feeding behavior is thought to have involved removing shoots or branches with their rake-like dentitions (Coombs, 1975). Sauropods probably lacked chewing capabilities, the teeth being widely separated and showing no signs of tooth-to-tooth occlusion. Food was probably processed in a gastric mill. Because of their large body size, sauropods would presumably have had low metabolic rates (Hotton, 1980; Ostrom, 1980; Spotila, 1980; Weaver, 1983), and therefore, slow passage of food through the gut.

Stegosaurids, the other common herbivores of the Late Jurassic, also lacked chewing teeth. Sauropods and stegosaurids together make up 95% of the preserved biomass in Middle to Late Jurassic faunas (Bakker, 1978).

Among mammals of the Late Jurassic only multituberculates and docodonts were probable herbivores or herbivore/omnivores, and their generalized dentitions do not permit a more precise reconstruction of diet (Clemens and Kielan-Jaworowska, 1979; Kron, 1979). However, the small size of these mammals suggests they would have relied, in part, on relatively rich foods like seeds or insects.

Cretaceous

The Lower Cretaceous Wealden fauna has 12 species of herbivorous dinosaurs, of which four are sauropods and one a stegosaurid (Ostrom, 1970; D.B. Weishampel, pers. comm., 1985). Most of the rest of the herbivores are ornithopods, and the most abundant forms are the iguanodontids. Thus there seems to have been a shift in diversity and abundance from the Late Jurassic to the Early Cretaceous. The newly dominant ornithopods were smaller and shorter than the sauropods, and most possessed occluding dentitions. These differences in size and dentition suggest that the ornithopods would have had higher metabolic rates than sauropods, and divided plant food into smaller pieces before swallowing. Little is known about Early Cretaceous mammalian herbivores, although one multituberculate is reported from the Wealden.

The Late Cretaceous saw a continued diversification of the ornithopod dinosaurs, with hadrosaurs and ceratopsians becoming the dominant groups in relative abundance and diversity. Hadrosaurs had two rows of occluding teeth that formed a complex and efficient chewing apparatus (Weishampel, 1984a; Norman and Weishampel, 1985). They also had webbed feet (Currie, 1983), and though their locomotion is reconstructed as quadrupedal, they were presumably capable of an upright feeding stance (Ostrom, 1964). Ceratopsians had one row of vertically occluding teeth, and quadrupedal locomotion (Ostrom, 1966). Like most ornithischians, ceratopsians and hadrosaurs had a beak but no anterior dentition. The long, narrow occlusal surfaces of hadrosaur dentitions suggest they would have been better suited to shredding foliage than to breaking and grinding harder plant parts.

Several other groups of herbivorous dinosaurs are also found in Late Cretaceous faunas: hypsilophodonts, pachycephalosaurs, fabrosaurs, and ankylosaurs. Hypsilophodonts and fabrosaurs were relatively small (10–100 kg?) ornithopods with weak dentitions and a primitive retention of premaxillary teeth. Ankylosaurs were a group of large (> 1000 kg) low-statured, armored dinosaurs with weak or absent dentition. Pachycephalosaurs were generally in the 100 kg range. Of these groups only fabrosaurs and hypsilophodonts were in a size class consistent with a diet containing a large proportion of fruits and seeds, furthermore the dental apparatus in these groups was generalized and less suited for shredding vegetation than that of the larger hadrosaurs (Weishampel, 1984a). Sauropod remains are found rarely even in upper Maestrichtian sediments.

Mammalian herbivores first attained significant diversity in the Late Cretaceous (Campanian), largely as a result of the radiation of multituberculates. Some Paleocene multituberculates are thought to have been arboreal on the basis of postcranial morphology, and their dentitions were suited for slicing and processing discrete, hard objects such as fruits and seeds (Krause, 1982a; Krause and Jenkins, 1983), but Cretaceous multituberculates are less completely known. Campanian faunas of North America typically contain five to seven genera of possibly herbivorous multituberculates, and one to three species of possibly omnivorous marsupials (Clemens, 1979; Clemens and Kielan-Jaworowska, 1979; Clemens et al., 1979). During the Maestrichtian both the size and diversity of herbivorous mammals increased. Eight to nine families of multituberculates were present by the end of the Cretaceous (Clemens and Kielan-Jaworowska, 1979). The late Maestrichtian Lance Formation fauna contains larger multituberculates (~1 kg) and *Glasbius*, a possibly frugivorous marsupial (Clemens, 1966, 1973). Primitive ungulates (the condylarth *Protungulatum*) and primates appeared in the latest Maestrichtian or earliest Paleocene (Clemens et al., 1979).

Paleocene

Following the extinction of the dinosaurs there was pronounced taxonomic and ecological radiation of herbivorous mammals in the Paleocene. During this Paleocene radiation multituberculates continued to diversify, reaching a peak of generic diversity (13) in the Torrejonian, even though their relative abundance in most assemblages decreased from the Lancian onward (70% of minimum number of individuals in Lancian, 55% in Puercan, 20% in Torrejonian, ~20% in Tiffanian, ~15% in Clarkforkian, ~5% in Wasatchian) (Krause, 1982b). The coincidence of this decrease in relative abundance with a phylogenetic and morphological diversification (some multituberculates got larger, more herbivorous; some smaller, more insectivorous) suggests some sort of evolutionary "release", involving the radiation of multituberculates into new niches even as they were becoming increasingly rare in comparison to other mammals.

As mentioned above, the Paleocene diversification of mammals was largely confined to smaller body sizes (1–10 kg). A variety of lines of evidence suggest that many of these small herbivores were arboreal. Some multituberculates and primates had postcranial adaptations for arboreality (Rose, 1977; Krause and Jenkins, 1983). Other groups of Paleocene herbivores, such as rodents and the smallest condylarths, were of a size to be facultatively arboreal, and Paleocene dermopterans have a living arboreal relative, *Cynocephalus* (the "flying lemur").

Dental evolution in Paleocene mammals also gives evidence of ecological specialization among herbivores. Species of the multituberculates, primates, and rodents all developed gliriform dentitions that probably functioned at least partly to process fruits and/or seeds. Probably folivorous dentitions evolved in the dermopterans, condylarths and pantodonts (Rose, 1981; Rose and Krause, 1982). Among the larger terrestrial herbivores taeniodonts may have been specialized for rooting (Coombs, 1983), but most of the condylarths and pantodonts retained fairly generalized herbivorous dentitions.

Eocene

Among the smaller herbivores, rodents and primates both increased their taxonomic and ecological diversity during the early Eocene. The Eocene also brought the first appearance and subsequent radiation of the artiodactyls and perissodactyls, presently the most diverse groups of mid-size to large mammalian herbivores. Condylarths and pantodonts continued to be abundant and fairly diverse during the early Eocene, but declined later during the epoch. In South America medium to large herbivorous mammals belonging to the endemic Notoungulata and Litopterna achieved some diversity during the middle Eocene to early Oligocene (Patterson and Pascual, 1968), somewhat earlier than the main radiation of larger herbivorous mammals in the Northern Hemisphere.

The origin and early radiation of frugivorous bats and birds are two of the most significant changes in herbivore faunas during the Tertiary, but unfortunately they are very poorly known. The first known bats are probable insectivores from the late Paleocene or early Eocene of France (Russell et al., 1973; Godinot, 1981). Although numerous bats are known from the middle Eocene of Germany (Rose, 1984), there is no fossil record for frugivorous bats older than Pleistocene (Smith, 1976).

Frugivorous birds are unknown from the Cretaceous, but appear to have radiated during the early Eocene (Tiffney, 1984; Olson, 1985). The highly frugivorous Steatornithidae (oil birds) are known from the early Eocene of North America, and show strong resemblance to the living species that feeds on large-seeded Lauraceae (Olson, in press). Generally speaking, frugivorous birds probably radiated contemporaneously with arboreal, frugivorous mammals.

Post-Eocene

Oligocene and later herbivore faunas from North America were increasingly dominated by larger, longer-limbed terrestrial herbivores with hypsodont or lophiodont molars (Stucky and Krishtalka, 1985). Primarily arboreal groups such as primates decreased in diversity (Gingerich, 1984).

During the Miocene and Pliocene true grazing faunas developed in North America and other parts of the world (Webb, 1977, 1984). These faunas were the first to have many species with open-rooted, hypsodont molars and long distal limb segments adapted for running (Janis, 1985).

Angiosperm diaspore size

The earliest reports of clearly angiospermous diaspores are of isolated fruits and seeds; the fruits are either tiny (1.0–3.0 mm) endocarps or are larger follicles, often containing tiny seeds (Fig.3; Tiffney, 1984). The earliest angiosperm fruit and seed floras are reported from the Santonian–Campanian sediments in Sweden (Friis, 1984; pers. comm., 1984) and Massachusetts, U.S.A. (Tiffney, 1977; unpublished data). Both floras contain about 50 entities, none of which exceed 3.0–4.0 mm in diameter. The same pattern of tiny diaspores is present in less well dated floras from the Late Cretaceous of Czechoslovakia (Knobloch, 1975, 1977; Knobloch and Mai, 1984). Larger reproductive structures are occasionally reported from Late Cretaceous sediments, but in many cases either their botanical affinity to the angiosperms is uncertain, or they are large fruits containing small seeds. This apparent dominance of small diaspores in the Cretaceous is consonant with the hypothesis that early angiosperms were opportunistic early successional plants (Doyle and Hickey, 1976), and suggests that this ecological style was dominant in the group through the end of the Cretaceous.

Larger, apparently non-dehiscent, fruits increased in frequency in the latest Cretaceous

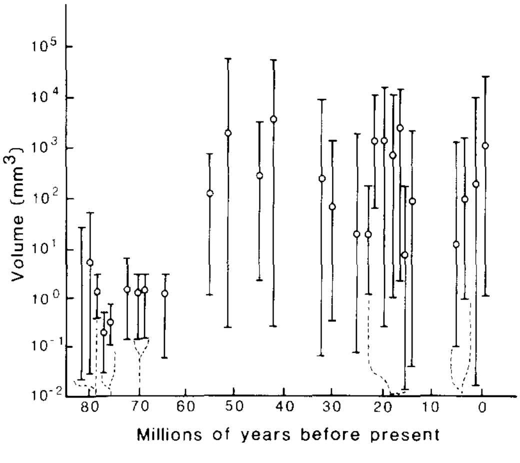


Fig.3. Distribution of angiosperm seed sizes in Cretaceous and Tertiary floras. Open circles are mean values for assemblages, horizontal lines are maxima and minima. Note the dominance of very small seeds in the Cretaceous and the great increase in range of seed size beginning in the Paleocene. Data from Tiffney (1984; fig.2).

(e.g. Chesters, 1955; Monteillet and Lappartient, 1981) and Paleocene (e.g. Brown, 1962). By the late Paleocene and early Eocene, fruit and seed floras generally possessed a variety of sizes of diaspores, including seeds or nondehiscent fruits ranging from very small through quite large (1.0–4.0 cm) in size (e.g. Reid and Chandler, 1933). Tiffney (1984) hypothesized that this increase in diaspore size was associated with increased biotic dispersal of angiosperms, and with the evolution of increasingly closed, light-poor, forest communities of modern physiognomy.

Post-Eocene floras are increasingly dominated by small diaspores, but generally retain some larger ones. The majority of Tertiary fossil fruit and seed assemblages come from middle northern latitudes, an area that became progressively cooler and more seasonal in the later Tertiary. The post-Eocene shift to smaller diaspores may reflect the increasing importance of small-seeded herbs in the vegetation of this area (Tiffney, 1984).

Angiosperm stature

There are remarkably few reliable reports of Early Cretaceous angiosperm wood. Angiosperm wood has not been reported from angiosperm leaf localities in the Lower Cretaceous Potomac Group, although small and large fragments of conifer wood are present in the same deposits (Hickey and Doyle, 1977). Early Cretaceous wood from England (Stopes, 1912), Madagascar (Fliche, 1905), and Japan (Suzuki and Nishida, 1974) are of questionable age and provenance (Wolfe et al., 1975; Page, 1981). Wood reported by Nishida (1962) may not be angiospermous (Page, 1981), and wood reported by Spackman (1948) may be Late Cretaceous. The oldest well-dated angiosperm woods are small (in the range of 5–10 cm width) fragments of *Paraphyllanthoxylon* and *Icacinoxylon* from the late Albian Cedar Mountain Formation of Utah, U.S.A. (Thayn et al., 1983, 1985). The girth of the axes that produced these fragments is not clear.

Cenomanian–Campanian angiosperm wood is also rare. Bailey (1924) reported *Paraphyllanthoxylon* logs over 30 cm (one foot) in diameter from the Late Cretaceous of Arizona, U.S.A. The largest angiosperm trunks from this interval are one meter in diameter logs of *Paraphyllanthoxylon* that occur abundantly in late Cenomanian or younger channel sands of the Gordo Formation in Alabama, U.S.A. (Cahoon, 1972).

A diverse angiosperm wood flora has been reported from Campanian–Maestrichtian marine deposits of California; 70% of the nearly 200 specimens are between 2.5 and 5 cm in diameter (Page, 1981 and references therein). The small size of these wood fragments may in part reflect water transport of the assemblage, because approximately coeval rocks in Illinois and New Mexico, U.S.A. contain large angiosperm trunks (E. Wheeler, pers. comm., 1986; J. McClammer, pers. comm., 1984).

Throughout the Tertiary large angiosperm trunks are relatively abundant and diverse. Ten species of angiosperm wood were reported from probable lower Paleocene marginal marine sediments in Niger (Koeniguer, 1971), but the oldest diverse flora of large angiosperm trunks is from the early Eocene of Wyoming, U.S.A. (Wheeler et al., 1977, 1978). Among many diverse assemblages of large angiosperm trunks in the later Tertiary are those from the Oligocene of Egypt (Kräusel, 1939; Bown et al., 1982), and the Miocene of the northwestern U.S.A. (Prakash and Barghoorn, 1961).

Summary of floristic and vegetational change

Early Cretaceous

Angiosperm macrofossils first occur abundantly in the Barremian–Albian Potomac Group of eastern North America. These leaves display a restricted array of physiognomies, the predominant types being low-rank simple leaves (probably understory plants), peltate (floating aquatics), and pinnatifid, pinnately compound, or palmate (presumably from early successional riparian plants) (Doyle and Hickey, 1976; Hickey and Doyle, 1977). The sedimentary environment of these early angiosperms, along with their foliar physiognomy, the absence of large angiosperm wood (large fragments of gymnosperm wood are present in the same deposits) and the absence of moderate to large sized angiosperm seeds are all consistent with the hypothesis that early angiosperms were relatively *r*-selected plants of small stature (Hickey and Doyle, 1977).

During this time vegetation in many areas may have been dominated by cheirolepidiaceous, taxodiaceous and araucarian conifers (e.g. Pierce, 1961; Jefferson, 1982; LaPasha and Miller, 1984), and angiosperms may have played a subordinate role in vegetation. For example, floodplain swamp vegetation preserved in the Kootenai Formation (Aptian of Montana, U.S.A.) had an overstory of conifers, a middle layer of *Coniopteris* species, and an understory of ferns; angiosperms were lacking (LaPasha and Miller, 1984).

Late Cretaceous

Many Cenomanian and later megafloras are dominated by angiosperm leaf remains, among which are a diversity of platanoids in coarser sediment and magnoliids in finer grained settings. Pollen studies suggest that gymnosperms were still abundant in many areas at some times (Pierce, 1961; Wolfe, 1976). Late Cretaceous forests may have borne some structural similarities to those of present day New Caledonia, with a scattering of emergent araucarians and a low canopy of small angiosperm trees (L.J. Hickey, pers. comm., 1982). The appearance of wind-dispersed angiosperm pollen in the Cenomanian has been taken as evidence that angiosperms had attained canopy status by this time (Doyle and Hickey, 1976), although many living early successional angiosperms are wind-pollinated (e.g. *Betula, Alnus, Platycarya*). Angiosperm leaf physiognomy was more varied in Cenomanian than in Early Cretaceous floras, but some of the most common types were still palmately veined or pinnately compound, suggesting that many angiosperms continued to occupy early successional positions.

Based on a paleobotanical and sedimentological study, Parker (1976) reconstructed the swamp and "bottomland" vegetation of the Campanian Blackhawk Formation (Utah, U.S.A.). Swamp vegetation was dominated by the conifers *"Sequoia" cuneata, Protophyllocladus polymorpha, Brachyphyllum macrocarpum, Moriconia cyclotoxon*, and the dicotyledon *Rhamnites eminens*; subdominants in the swamp floras included various ferns, a palm, and cycadophytes. In contrast, the "bottomland" assemblages (those from siltier, less organic sediment presumably deposited more proximal to a channel) were dominated by dicots such as *"Cercidiphyllum", Platanus* spp., and *Dryophyllum subfalcatum*; many of the living relatives of these forms require high light levels for germination and growth, or are small understory trees and shrubs. Collections from "bottomland" sites also included an additional 10–15 species of dicotyledons and one species of *Protophyllocladus*. Araucarian fossils were reported only in presumably transported channel assemblages. The moderately high abundance and diversity of conifers in swamp assemblages, and the relative importance of possibly *r*-selected dicots in siltier, less organic sediments, seems to be typical of Campanian floras from many areas of North America.

By the late Maestrichtian the Taxodiaceae seem to have been more common than broadleaved conifers in many swamp floras, although the diversity and abundance of Taxodiaceae are reported to have dropped in the late Maestrichtian of New Mexico, U.S.A. and Sakhalin, U.S.S.R. (Krassilov, 1978; J.U. McClammer, pers. comm., 1984). Late Maestrichtian angiosperm floras from western North America were physiognomically similar to those from the Campanian (Wolfe and Upchurch, 1986).

Paleocene

Palynofloras and megafloras from immediately above the K/T boundary are now known from several parts of western North America (Orth et al., 1981; Tschudy et al., 1984; Nichols et al., 1986; Wolfe and Upchurch, in press).

Most of the basal Paleocene palynofloras are fern-dominated (although see Lerbekmo and St. Louis, 1986), and the lowest megafloras are low diversity assemblages of lobed or stenophyllous leaves (Wolfe and Upchurch, in press). These data suggest that earliest Paleocene vegetation (within 10–1000 yr following the boundary?) had an early successional character.

Taxodiaceous conifers (*Glyptostrobus* and *Metasequoia*) continued to be dominant or important members of swamp vegetation in most Paleocene floras from the northern Rocky Mountain region, but conifer diversity (2 or 3 genera by the mid-Paleocene) was considerably lower than in the Late Cretaceous (7 or 8 genera) and some later Paleocene swamp floras are dominated by dicotyledons (Hickey, 1980). Siltier substrates ("bottomland" of Parker, 1976) continued to support a moderately diverse flora of angiosperms, many of them members of the same higher taxa that were common in Late Cretaceous near-channel assemblages.

Eocene

In some earliest Eocene swamp megafloras *Metasequoia* and *Glyptostrobus* were co-dominant with angiosperms, but by the end of the early Eocene — at least in the basins east of the North American Continental Divide — dicot species were numerically dominant in both swamp and near-channel settings (Wing, 1984). In all facies, Eocene floras typically had a higher diversity of angiosperms than those of the Paleocene. There was also an increase in the percentage of thick-textured, entire-margined leaves, and an increase in diversity of species in Lauraceae, Leguminosae, Menispermaceae, Theaceae, Juglandaceae, Palmae, Icacinaceae, and other presently tropical to subtropical families (Wing, 1981).

The middle and late Eocene brought increasing provinciality to floras of North America, probably as a result of increased uplift of some areas of the western interior. Floras east of the uplift began to include many taxa characteristic of seasonally dry climates (MacGinitie and Leopold, 1972). Floras west of the uplift retained more lineages from earlier times. Volcanic highlands in western North America may also have been centers of diversification for modern groups of Pinaceae, and for cold-tolerant members of several angiosperm families (Wolfe and Wehr, 1986).

Post-Eocene

Pinaceous conifers and "microthermal" groups of angiosperms (e.g. Betulaceae, Salicaceae, *Acer*) continued to diversify and came to dominate many Northern Hemisphere floras, although broad-leaved, evergreen types were still present in small numbers in many areas. Savanna and grassland vegetation appears to have spread early in the Miocene of the Neotropics (Germeraad et al., 1968), but not until the late Miocene in mid-northern latitudes (MacGinitie, 1962; Wolfe, 1985).

Summary

Based on the five characteristics we have surveyed: herbivore body size, herbivore locomotion, herbivore diet, angiosperm diaspore size, and angiosperm stature, we can divide the post-Jurassic history of terrestrial biotas into four stages (Table I). From the Early Cretaceous to the Campanian (Stage 1) diversity was relatively high among large, terrestrial, bulk-feeding herbivores. Small specialized herbivores were not diverse, and most angiosperms were probably small, woody plants with small diaspores. From the late Campanian to the end of the Cretaceous (Stage 2) small, trophically specialized herbivores became more diverse, and a few large angiosperms with larger diaspores began to appear. During the Paleocene and much of the Eocene (Stage 3) herbivore faunas were dominated by small species, some of which had dental specializations for eating fruits and seeds and/or postcranial specializations for arboreality or flight; angiosperms of this interval had increasingly large diaspores and were of large size. During the post-Eocene (Stage 4) some (though not all) herbivore faunas became dominated by larger

TABLE I

Post-Jurassic history of terrestrial biotas

	Herbivore fauna size distribution	Herbivore locomotion	Inferred feeding type	Angiosperm diaspore size (mm)^2	Angiosperm stature	Inferences
Stage 4 (Late Eocene–Present)	variable, 70–80% <10 kg in forest; $\sim 50\%$ <10 kg in open vegetation	terrestrial, arboreal, and volant	grazing, browsing, frugivory, granivory	mean, 10–~ 2000 max. $\sim 30{,}000$	broad range of sizes	Relative importance of frugivory/dispersal varies by local vegetation type and climate
Stage 3 Paleocene–mid Eocene)	initially all <10 kg later 70–80% <10 kg	arboreal, volant, terrestrial	frugivory, granivory, folivory	mean, 100–1000 max. $\sim 80{,}000$	broad range including many large species	Frugivory/dispersal dominant. Generalized herbivory/herbivore disturbance levels low. Angiosperms more *K*-selected, animal dispersed, and formed closed forest
Stage 2 (Campanian–Maestrichtian	bimodal 20–50% <10 kg 50–80% >1000 kg	dominantly terrestrial	generalized browsing, some frugivory	mean? max. ~ 1000?	few large, most small	Transitional between Stages 1 and 3. Possibly increased importance of tetrapod dispersal of angiosperms. Local areas of closed angiosperm forest?
Stage 1 (Barremian–Campanian)	almost all >100 kg	terrestrial	generalized browsing	mean <10 max. <100	most species small	High levels of generalized herbivory/herbivore vegetational disturbance. Angiosperms *r*-selected and forming open vegetation.

herbivores; many of these faunas were associated with grassland vegetation in which many (though not all) plants and their diaspores were relatively small.

Changes in plant–herbivore interactions and community structure

In our analysis of the fossil record we will focus on the functional consequences of change in faunas and floras, and thus be concerned with the ecological roles of lineages or taxa. Based on changes in the fossil biotas discussed in the previous section and summarized in Table I, we can make a series of inferences about the nature of angiosperm–herbivore interactions in the past, and the structure of extinct communities.

Stage 1

Many aspects of the diet and feeding behavior of herbivorous dinosaurs were probably similar to those of large living mammalian herbivores, similar physiological, metabolic and mechanical constraints applying to both. The relation between size and diet observed in living mammals (Demment and Van Soest, 1985) implies that most herbivore species in the Late Jurassic and Early Cretaceous were bulk feeders, consuming large amounts of fibrous plant parts such as foliage and branches. Fruits and seeds may have been eaten incidental to general browsing, but apparently fruits and seeds are too spatially dispersed to be efficiently used as a major resource by large herbivores (Dubost, 1979).

The low diversity of small herbivores in Stage 1 assemblages suggests a paucity of obligate frugivore/granivores. Thus a whole guild of herbivores that accounts for much of vertebrate diversity in some living ecosystems (Fleming, 1973; Janson, 1983; Emmons et al., 1983) was nearly absent during Stage 1. This feature is also implied by seed size. While the absence of large angiosperm diaspores during this period does not preclude some animal dispersal (small seeds may be buried in large fruits e.g. *Muntingia* [Fleming et al., 1985]), the absence of larger diaspores does suggest that many of the kinds of dispersal relationships common in modern communities were absent during Stage 1.

The absence of large diaspores of angiosperms from floras of this stage also has strong implications for the range of habits and habitats the flowering plants could have occupied. Among living plants small seeds are usually seen in species that germinate and grow in relatively light-rich vegetation or in light gaps created by treefalls, fire, or other disturbances (Salisbury, 1942; Harper et al., 1970; Fleming et al., 1985). Species that can germinate and grow under a closed canopy almost invariably have seeds longer than one cm (Ng, 1978). Thus, most Stage 1 angiosperms probably could not have colonized closed vegetation types.

Although it is negative evidence, the rarity of large angiosperm axes before the Campanian is consistent with the hypothesis that flowering plants were relatively small. Among living plants some early successional or "fire-adapted" species that produce small seeds may attain large mature size if no fatal disturbance occurs (e.g. *Platanus*), so there is no one-to-one correlation between small seeds and small stature. However, studies of related groups of species have shown that those with larger seeds tend to achieve larger mature sizes (Levin, 1974; Strauss and Ledig, 1985).

Some retardation in the evolution of larger angiosperm trees may also be implied by wood anatomy. Wolfe et al. (1975) commented that wood characters seem to be at a lower grade than reproductive and other vegetative characters of Late Cretaceous angiosperms. Much Cretaceous angiosperm wood also has high "V" values (Wolfe, pers. comm., 1985). These high "V" values (V=mean vessel diameter/mean vessel density; Carlquist, 1977) have been taken to indicate equable climatic conditions. However, since the probability of embolism is in part related to the amount of negative pressure in the vessel, and hence the height of the tree (Carlquist, 1975), the high "V" values of Cretaceous angiosperm woods could also be related to small stature.

Based on our reconstruction of the ecological roles of angiosperms and vertebrate herbivores we infer the dominance of generalized herbivory. Large dinosaurs ate branches, leaves and possibly wood of angiosperms. Small herbivores were rare, low in diversity, and probably relied, at least partly, on animal protein. Angiosperms were primarily abiotically dispersed, although some dispersal incidental to dinosaur browsing might have occurred. Small angiosperm seeds dictated high light levels for germination and seedling growth; the sporophytes were probably small to medium size trees with relatively rapid growth and reproduction. Vegetation formed by angiosperms was relatively open.

Stage 2

Stage 2 (Late Campanian–Maestrichtian) herbivore faunas are characterized by an increase in the diversity of small species, largely as a result of the radiation of multituberculates. Based on size (and therefore on inferred metabolic rate) and dental morphology, it is likely that multituberculates ate fruits and/or seeds. Many living small frugivores and granivores are more seed predators than dispersers, but even voracious vertebrate seed predators may carry out some dispersal (e.g. Janzen, 1983; Howe and Smallwood, 1982). Wherever multituberculates fell on the predator-disperser spectrum they were the first diverse group of herbivores that were of the right size to respond to fruits or seeds as discrete entitities since the angiosperms had appeared.

Although Late Cretaceous hadrosaurs evolved increasingly sophisticated masticatory apparatuses (Weishampel, 1984a) their large size suggests they necessarily would have been generalist browsers in the manner of earlier ornithopods. In North America the continuing reduction in sauropod diversity may have resulted in reduced browsing in upper levels of the vegetation (Coe et al., 1987), but in South America, Africa and India sauropods remained dominant elements of the fauna (Weishampel, pers. comm., 1986). A slight increase in the diversity of small herbivorous dinosaurs (most of them still over 100 kg adult body weight) may have increased the number of species of somewhat selective herbivores in Stage 2.

Although assemblages from Stage 2 still lacked larger angiosperm diaspores (Tiffney, 1984), some reports of possible angiosperm diaspores up to 2 cm in length from compression floras in western North America and in Africa (Monteillet and Lappartient, 1981), suggest that some lines of flowering plants may have been animal dispersed. Presumably these larger seeded angiosperms could also have colonized and formed more closed vegetation. Reports of angiosperm axes up to a meter in diameter from late Campanian and Maestrichtian rocks in several parts of North America (E.A. Wheeler, pers. comm., 1985; J.U. McClammer, pers. comm., 1984) also suggest that large angiosperm trees were more common than during Stage 1.

The angiosperm–herbivore interactions we have inferred for late Campanian–Maestrichtian communities are intermediate between those of the Early Cretaceous and the Early Tertiary. The radiation of small, herbivorous mammals and the scattered reports of larger angiosperm diaspores and axes suggest that dispersal interactions were becoming more important, and possibly that the structure of angiosperm vegetation was beginning to change as well. However, these developments did not change the continued dominance of large generalist herbivores, and presumably, *r*-selected angiosperms.

The spatial manifestation of the intermediacy of Stage 2 communities is unclear. One possibility is that rather divergent community types were coeval but geographically separated, much as savanna and tropical forest occur now in different areas depending on rainfall or other factors. Van Valen and Sloan (1977) have suggested that divergent community types coexisted on different parts of a river floodplain system during the late Maestrichtian in Montana, U.S.A., with one community dominated by dinosaurs, the other by mammals (although the separation of faunal "facies" may in part reflect faulty stratigraphic correlation [Fastovsky and Dott, 1986]). Alternatively, small herbivores and larger-seeded angiosperms may have become more common in a variety of ecosystems that were still dominated by dinosaurs and *r*-selected angiosperms.

Stage 3

Stage 3 (Paleocene–late Eocene) began with the extinction of all herbivores over 10 kg, an event that must have had a profound effect on angiosperm–herbivore interactions. Based on herbivore body size, early Tertiary plants would not have experienced the sort of generalized browsing herbivory that dominated during Stages 1 and 2. Through the early Eocene 70% of the herbivorous species were under 10 kg, and many of the larger herbivores were so short that they probably could not have browsed higher than one or two meters. During this same interval radiations of small herbivorous mammals and birds would presumably have greatly increased predation, and potentially dispersal, of fruits and seeds. The Stage 1-to-Stage 2-to-Stage 3 transition records a striking transformation in the nature of vertebrate herbivory, from an almost complete dominance of generalized browsing with incidental dispersal to a near total dominance of specialized herbivory and dispersal.

Earliest Paleocene angiosperm assemblages are only now in the process of being described (Wolfe and Upchurch, 1986, in press), but immediately post K/T boundary vegetation has an early successional appearance (Orth et al., 1981; Nichols et al., 1986). The angiosperms involved may have been dominantly deciduous (Wolfe and Upchurch, in press). The implications of this for vertebrate herbivory and dispersal are unclear. In the absence of large herbivores some of the food resource represented by widespread early successional vegetation might have gone uncropped. By near the end of the Paleocene angiosperms had evolved a range of diaspore sizes almost as great as that of modern floras. This dramatic increase in the range of diaspore sizes from the Late Cretaceous to the late Paleocene is strong evidence for the increased importance of animal dispersal among the angiosperms. Increased diaspore size also implies that angiosperms would have had much greater abilities to colonize and form closed canopy vegetation, and large angiosperm trunks became common in the Eocene (e.g. the diverse Yellowstone wood assemblages from western North America; Wheeler et al., 1977, 1978).

Overall, the ecological characteristics of Stage 3 faunas and floras are reminiscent of present-day dense forests of the tropics: high diversity of small herbivores (some arboreal and frugivorous), low diversity of large herbivores, and a large range of angiosperm diaspore size. The angiosperm–herbivore interactions of more open vegetation during Stage 3 are more difficult to interpret, but open vegetation was probably less extensive than in the later Tertiary (Wolfe, 1985).

Stage 4

Not surprisingly, the post-Eocene took on an increasingly modern appearance. A diversity of large herbivores evolved among mammals, although in forested environments small herbivore diversity remains high even to the present (Fleming, 1973). Many large herbivorous mammals of the Miocene and later were probably grazers living in grassland or open woodland/grassland vegetation (Webb, 1984). Some large Pleistocene herbivores are inferred to have been important dispersers of angiosperms with large diaspores (Janzen and Martin, 1982). This is in contrast to large Cretaceous herbivores which, if they evolved dispersal interactions with angiosperms, would probably have been attracted by foliage rather than diaspore features, as in Janzen's (1984) "foliage as fruit" hypothesis. The evolution of angiosperm dispersal syndromes involving large diaspores and large herbivores, like that seen in "elephant fruits" (Alexandre, 1978), is likely to have been a Middle to Late Tertiary phenomenon. Development of this type of interaction may have required an initial Early Tertiary period of diffuse coevolution between small frugivore/dispersers and angiosperms that resulted in the spread of large seeds and diaspore attractants in many angiosperm lineages. Subsequently, during the later Tertiary, angiosperms already possessing large seeds and disperser "rewards" might have evolved more specialized relationships with diversifying large mammalian herbivores.

Mean diaspore size in temperate latitude angiosperm floras declined in the later Tertiary; although the decline is not statistically significant, it may reflect the increasing diversity of small-seeded herbaceous angiosperms in these floras (Tiffney, 1984). Evidence from fossil pollen (Muller, 1981), leaves (MacGinitie, 1962), and seeds (Chaney and Elias, 1936) also confirm a later Tertiary diversification of herbaceous families and the spread of more open vegetation.

During Stage 4 neither frugivory/dispersal nor generalized herbivory was the overwhelmingly dominant interaction between angiosperms and vertebrate herbivores. If modern communities are a good analog, frugivory/dispersal probably assumed greater importance in forested vegetation, while generalized herbivory was more significant in open vegetation. These different types of vegetation were probably patchily distributed according to climate and topography.

Evolutionary causes and effects

Our purpose in reconstructing the history of interactions between angiosperms and herbivorous tetrapods has been to create a basis for understanding their evolutionary effects on one another. We have divided this history into four stages: Stage 1 (Barremian–Campanian) in which generalized herbivory was much more important than frugivory/dispersal; Stage 2 (Campanian–Maestrichtian) in which generalized herbivory remained the dominant mode of interaction but frugivory/dispersal became more common; Stage 3 (Paleocene–Eocene) during which frugivory/dispersal was the exclusive or dominant type of interaction; and Stage 4 (Oligocene– Recent) during which both frugivory/dispersal and generalized herbivory were common.

This history raises several questions with important implications for ecology and evolution. Our view from the present predisposes us to think that plant–herbivore interactions, particularly those in warm climates, will include both frugivory/dispersal and generalized herbivory, even though their relative importance may vary among communities (e.g. Gentry, 1982; McNaughton, 1984). It is not surprising to find that in the geologic past a given ecological interaction was carried out by different organisms than carry it out today. However, the fossil record indicates that the present may not always be an accurate guide to the past, and that some of the most important ecological interactions of plants and animals in modern communities were limited or nonexistent during geologically long intervals of time.

The very existence of Stages 1 and 3 forces us to account for periods of many millions of years during which generalized herbivory or frugivory/dispersal dominated interactions between vertebrate herbivores and angiosperms. The duration of these stages implies stability in the kinds of interactions that take place in ecosystems. This lack of change in the kinds of ecological roles that plants and animals play is particularly interesting because it is concurrent with continuing change in the taxonomic composition of terrestrial communities. If the taxonomic composition of communities is unstable over relatively short periods of time (e.g. Davis, 1976, 1981), why do the roles that taxa play appear to be stable over much longer periods of time? In the remainder of this section we will be concerned first with explaining the periods of stability in ecological organization represented by Stages 1 and 3, and second with explaining how and why these systems broke down during Stages 2 and 4.

Stability in community structure (Stages 1 and 3)

Stage 1

The evolution of specialized frugivores among Tertiary descendants of Cretaceous birds and mammals, and the independent evolution of bird- and mammal-dispersed diaspores in many lineages of angiosperms strongly suggests that the potential for these developments was present in the Early Cretaceous. Why then did angiosperms, mammals and birds not evolve extensive dispersal/frugivory interactions during the first 40–50 Ma of their coexistence (Barremian–Campanian). We think the lack of "diffuse coevolution" between mammals and birds and the angiosperms during Stage 1 is attributable to the stable structure of Early Cretaceous communities. This, in turn, is explicable in terms of the sequence in which major members of the biota evolved and the ecological interactions that developed between them.

We suggest that the key element in structuring angiosperm–herbivore interactions during Stage 1 was the diverse fauna of large, generalist herbivores. Although the taxonomic composition of this fauna varied significantly through time, large herbivorous dinosaurs were common over much of the world throughout the Jurassic and Cretaceous (Bakker, 1978). When angiosperms radiated in the Early Cretaceous it was into an established community of which large, generalist herbivores were a major component.

Doyle and Hickey (1976) argued that Aptian–Albian angiosperms possessed a number of *r*-selected life-history traits such as small stature, rapid life cycle, and high colonizing ability. These traits were probably associated with the evolutionary radiation of the early angiosperms on disturbed substrates along river channels, or in areas affected by fire (Doyle and Hickey, 1976; Hickey and Doyle, 1977). This led Bakker (1978) to propose that the diversification of angiosperms during the Cretaceous was, in part, a consequence of their preadaptations to survival under the intense browsing disturbance of Cretaceous ornithopods. While we agree that the inferred life-history traits of these early angiosperms would have been advantageous under heavy browsing, the evolutionary consequences of this interaction have not been fully explored.

Present day large herbivores frequently have a profound effect on vegetation (e.g. Laws, 1970; Wing and Buss, 1970; Croze, 1974; Merton et al., 1976; Sinclair and Norton-Griffiths, 1979). Vertebrate herbivores generally are recognized as having a greater impact on plant succession and community structure than invertebrate herbivores (Crawley, 1983). Given the generality of this observation in living systems, it is likely that dinosaur herbivores had a strong influence on the structure of Cretaceous vegetation.

A variety of mechanisms allow plants to respond to herbivory: secondary compounds, mechanical deterrents, and regrowth among others. Species that are relatively *r*-selected are more likely to respond to herbivory by regrowth than by protective mechanisms (Schultz et al., 1982; Finegan, 1984; Danell and Huss-Danell, 1985). Such *r*-selected forms may produce defensive chemicals, but generally they are metabolically inexpensive compounds that are less effective in deterring herbivory than the tannins and other compounds more typical of evergreen, *K*-selected trees (Coley et al., 1985).

By analogy with living forms, we infer that dinosaur herbivory would have reinforced the *r*-selected traits of early angiosperms through three mechanisms: (1) selection against delayed reproduction; (2) selection against larger diaspores; and (3) maintenance of relatively open vegetation. First, like any disturbance, dinosaur browsing and trampling would have increased the chance of death or damage of individual plants. Individuals that delayed reproduction in favor of continued sporophytic growth would thus be less likely to reproduce before being damaged or killed. The same would apply for plants that invested resources in defense mechanisms, unless those defenses were quite effective. The strength of selection against delayed reproduction would of course depend upon the frequency and severity of herbivore attacks, and the amount of protection conferred by an investment in defense.

These latter parameters are difficult to measure even in living ecosystems, and we can suggest only the roughest qualitative answers based on the fossil record. Frequency of attack must have been related to the energy requirement of herbivore populations, a quantity determined by multiplying the energy requirement of an individual by the number in the population. Such calculations by previous authors suggest that the rate of biomass consumption in dinosaur and modern large herbivore faunas is not radically different (Bakker, 1972; Farlow, 1976; Weaver, 1983). Thus, we presume that frequency of attack was also similar. The consequences of an individual event of dinosaur herbivory for an individual plant must have varied widely, but such large herbivores certainly had the potential to destroy moderately large trees, just as elephants do today (e.g. Laws, 1970). The efficacy of defensive measures would have depended on the kind of defense. The secondary compounds of angiosperms have been cited as a possible cause of the decline of dinosaurs, based on the inability of living lizards and turtles to detect relatively high concentrations of alkaloids (Swain, 1976). This suggestion seems unreasonable because the decline of dinosaurs took place some 60 Ma after the initial radiation of the angiosperms, and because turtles and lizards are not very closely related to dinosaurs. Furthermore, most herbivorous dinosaurs were large, and living large herbivores (particularly ruminants) reduce the effect of plant secondary compounds by bacterial fermentation of the plant matter (Freeland and Janzen, 1974; Janis, 1976; Guthrie, 1984).

To summarize the qualitative estimates made above, it seems probable that early angiosperms would have been attacked frequently by large herbivores, and that the attacks had the potential to be fatal to individual plants. The efficacy of defenses is hard to estimate, but might have been rather low. Under these circumstances, the most fit individuals would have been those that retained the primitive *r*-selected traits of rapid growth to maturity and early reproduction.

While dinosaurs inadvertently may have consumed angiosperm diaspores along with foliage, they probably would not have fed on diaspores specifically. The relationship of herbivorous dinosaurs to angiosperm diaspores likely was analogous to the relationship between living ungulates and grass seeds (Janzen, 1984). Although this sort of seed-eating might lead to dispersal, there are several reasons why it is unlikely to select for diaspores that are attractive to the herbivore. If the consumption of seeds by the large herbivore results in seed death, then clearly there would be no selection for more attractive diaspores. The suitability of dinosaur digestive tracts for passing seeds is an open question, but the presence of gastroliths (in sauropods), and the presumably long passage of time for food in such large herbivores, raise the possibility that dinosaurs were poor dispersers. Even if seed consumption by large herbivores does lead to improved dispersal, Janzen (1984) has suggested that there may be little selection for more attractive fruits because the foliage of the plant is itself acting as the attractant. Lastly, there is the possibility that the damage sustained by the plant during feeding by its potential dinosaur disperser was greater than the benefit it gained by the dispersal. In an environment where larger seed or diaspore size conveyed no advantage for dispersal, and where probability of seed or seedling death due to predation was also high, it may be that greater investment of parental resources in any given offspring (larger diaspores and/or seeds) was actively selected against. As with growth and reproduction, the primary selective forces acting on seed and diaspore size would have encouraged retention of the primitive state.

The third effect of dinosaur herbivory on the evolutionary direction of early angiosperms involves the impact of herbivory on vegetation rather than on individual plants within a species. As mentioned above, large vertebrates, as a result of feeding and trampling, often prevent vegetation from developing a closed structure. They may also reduce the severity of interspecific competition between plants by preferential feeding on more abundant or more desirable species (Crawley, 1983). One result could be that species with inferior competitive abilities would be able to colonize areas from which they would be excluded in the absence of herbivores. The point made by Bakker (1978), and emphasized here, is that by maintaining large areas in a relatively open state, dinosaurs created land surfaces that could be colonized by *r*-selected angiosperms. Herbivorous dinosaurs may have played a key role in forming the environmental context for the mid-Cretaceous radiation of flowering plants. It is important to note that we are not proposing that individual fitness of angiosperms was *increased* by dinosaur herbivory. We are only suggesting that angiosperms were more successful than other groups under conditions of frequent herbivory and disturbance.

The success of angiosperms during Stage 1, both in terms of their taxonomic radiation and of their numerical abundance, had important consequences for the evolution of both large and small herbivores. Several characteristics of *r*-selected plants make them good fodder for large herbivores: they tend to be small statured (Finegan, 1984), to have relatively little wood (Coe, 1983; Demment and Van Soest, 1985), and they grow rapidly (Finegan, 1984; Coley et al., 1985). As a result of these characteristics low-stature vegetation produces more edible plant matter and provides forage with more protein than does forest. Dinosaur herbivory maintained open vegetation and allowed the spread of *r*-selected angiosperms; simultaneously angiosperms provided an expanding resource for large herbivorous dinosaurs. This reciprocal interaction may have been analogous to the coevolution between grazing ungulates and grasses described by McNaughton (1984), and may have led to increased diversity and abundance of low-browsing ornithopod dinosaurs in the mid and Late Cretaceous (Bakker, 1978).

The spread of *r*-selected angiosperms also may have affected the evolution of small herbivores. The primitive diet of both mammals and birds was probably some variant of insectivorous or carnivorous (Crompton and Jenkins, 1979). As angiosperms with small diaspores came to be a larger proportion of the vegetation during the Cretaceous, they would have provided few resources for small herbivores requiring relatively high-energy plant food. Thus, birds or mammals tending toward a more herbivorous diet did not find a large, untapped reservoir of food and did not undergo an evolutionary radiation. Without a coterie of potential small vertebrate dispersers, any angiosperms that did develop larger diaspores would not have derived an advantage from improved dispersal.

In the foregoing discussion we have tried to evaluate the kind of selective pressures that the members of Stage 1 communities would have placed on one another, based on our reconstruction of their ecological interactions. The most important aspect of these inferred selective pressures (Fig.4) is that they would have formed a positive feedback loop reinforcing the initial ecological roles of each of the participants in the system. For example, large herbivore browsing and disturbance maintained the *r*-selected life histories of early angiosperms; the angiosperms, in turn, provided a resource that reinforced the dominance of large herbivores and provided few opportunities for frugivores/dispersers. We suggest that this resulted in near stasis in the ecological roles of angiosperms, dinosaurs and mammals during the 40–50 Ma of Stage 1.

Stage 3

Although the angiosperm–herbivore interactions we have inferred for Stage 3 are very different from those inferred for Stage 1, the two stages are similar in representing periods of stasis in aspects of community organization. For the first 20–30 Ma of the Tertiary mammalian herbivores were largely confined to small body sizes. Following the early Paleocene, angiosperm diversification involved the ap-

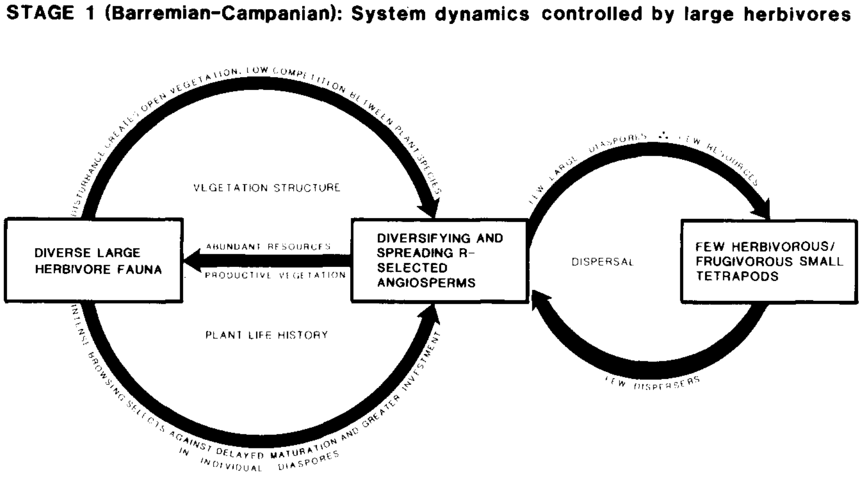


Fig.4. Diagram of the hypothesized forces acting to stabilize ecological interactions between angiosperms and herbivorous tetrapods during Stage 1. See text for detailed discussion.

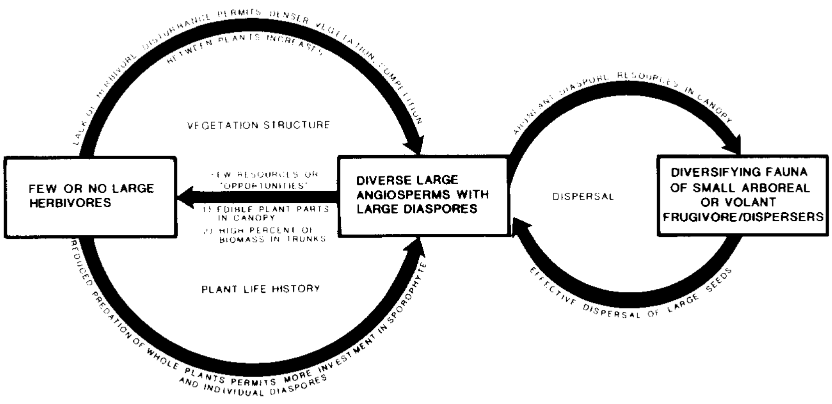
pearance of larger diaspores, which are inferred to have come from dense forest vegetation. Following the same approach used in analyzing Stage 1, what selective forces can we infer from the ecological roles played by angiosperms and herbivorous tetrapods?

The extinction of all large herbivores at the end of the Cretaceous, dramatically altered the selective landscape in which angiosperms were evolving. Gone was large scale vegetational disturbance created by herbivores. The chance that individual plants would be greatly damaged or killed during a single episode of herbivory must have been reduced. Most Stage 3 herbivores could not have fed on whole plants because of their small size and associated physiological limitations (Peters, 1983; Demment and Van Soest, 1985). Small herbivores would have required relatively high energy diets consisting in large part of fruits and seeds, perhaps supplemented with insect or other animal prey. Only a very few early Tertiary herbivores were large enough to have been generalist bulk-feeders. Many of these forms were short-statured and terrestrial, precluding access to vegetation higher than one to two meters.

This decrease in disturbance and generalized herbivory would have removed at least three pressures that had helped maintain *r*-selected features in the angiosperms. First, decreased disturbance of vegetation presumably would have allowed plants to grow more densely; denser growth would have decreased the amount of light reaching the ground and thus favored success of seeds with greater stored reserves. Second, decreased herbivory might have increased the importance of interspecific competition between plants because of decreased mortality unrelated to competition. Third, the decreased probability of death or major loss of resources due to herbivory would have reduced the necessity of rapid reproduction and low investment of reserves in individual seeds. This last factor, particularly if it were in combination with denser vegetation and increased plant competition, could have resulted in the rapid evolution of angiosperms with extended sporophytic growth, larger stature, and larger seeds.

At the same time that generalized herbivory had been eliminated, predation on angiosperm diaspores was probably increasing because of the diversification of small herbivores. Increased diaspore predation probably would have favored angiosperms with mechanically or chemically protected seeds. However, even efficient predation on seeds may lead to some beneficial dispersal. When denser vegetation and perhaps increased seedling competition created an environment favoring larger seeds that could not be effectively dispersed by the wind, animal dispersal might have been especially advantageous. If so, then the evolution of a reward or attractant to dispersers would have resulted in a lineage that was both highly competitive in the seedling stage and widely distributed. This situation could have led to a coevolutionary spiral in which increasing numbers of animal dispersed diaspores provided greater resources for frugivore/dispersers, leading to greater abundance (and eventually diversity) of frugivore/dispersers. The rate of development of this coevolutionary spiral would have been accelerated if a few dispersal interactions between tetrapods (presumably multituberculates) and plants survived the K/T boundary. In any case the diversification of frugivorous mammals (and presumably birds) in the early Paleocene to early Eocene, and the increasing abundance of large angiosperm diaspores in the late Paleocene, indicate that the development of modern types of tetrapod/angiosperm dispersal interactions was concentrated in a 10 Ma interval from the latest Cretaceous to the earliest Eocene. The evolution of larger seeds in many lines of angiosperms, in conjunction with the coevolution of a mechanism allowing their dispersal, were probably two of the key developments that permitted angiosperms to form closed-canopy vegetation of the type found in many parts of the world today. Paleoclimatic and paleobotanical evidence indicates that this dense forest vegetation was much more widely spread in the Early Tertiary than in the present day (Savin, 1977; Wolfe, 1985).

The low diversity of large herbivores in tall and dense vegetation is also seen in comparisons of living communities (Fleming, 1973; Andrews et al., 1979; Andrews and Evans, 1979; Coe, 1983; Fig.2). The reasons for this pattern probably include some of the following. Large herbivores may find it difficult to maneuver in closed vegetation (Dubost, 1979), and thus choose to stay in more open areas. Large, terrestrial herbivores may also find comparatively little to eat in vegetation where most of the edible plant tissue (leaves, small branches, fruits, flowers) is high above the ground; it would be mechanically difficult to be a large, arboreal or volant herbivore. Furthermore, fruits and seeds, two of the primary food sources for arboreal and volant herbivores, tend to be spatially dispersed, making them an energetically inefficient diet for large herbivores. Finally, much of the standing biomass of some forest ecosystems is devoted to tree trunks (Coe, 1983), consequently there is less edible plant food in the forest for earth-bound herbivores. As a result, distribution of limited resources in the forest may favor smaller body size. The spatial distribution of food resources in the developing and spreading closed-canopy forests of the Paleocene would have favored the radiation of small herbivorous/frugivorous mammals while limiting the diversification of large terrestrial herbivores. Recognizing that a relatively warm, wet climate was a prerequisite, we argue that the absence or low diversity of large herbivores at the beginning of the Tertiary was a major factor in establishing a stable ecological system that continued to suppress the evolution of large herbivores for some 20–30 Ma. The selective pressures that maintained these ecological relationships are summarized in Fig.5. As with Stage 1, these selective pressures formed a self-reinforcing system that could have held the chief participants in these interactions to the same basic ecological roles for geologically long periods of time. Reduced disturbance and browsing because of an absence of large herbivores would have allowed competitive interactions to favor increased sporophytic growth and increased investment in individual seeds. These changes in angiosperm life history would have permitted the development of coevolutionary dispersal relationships with small herbivores, and could eventually have resulted in the development of dense angiosperm forests. Dense forests provided many opportunities for small arboreal or volant herbivores but few opportunities for large terrestrial herbivores. As a



STAGE 3 (Paleocene - late Eocene): System dynamics controlled by large angiosperms

Fig.5. Diagram of the hypothesized forces acting to stabilize ecological interactions between angiosperms and herbivorous tetrapods during Stage 3. See text for detailed discussion.

result small frugivore/dispersers continued to radiate, but large herbivores remained low in diversity and perhaps uncommon, yielding continued low levels of generalized herbivory and herbivore disturbance.

Rearrangements in community structure (Stages 2 and 4)

In the preceding section we have discussed stages 1 and 3 of the history of angiosperm–tetrapod interaction. Although the dominant interactions during these stages were very different, both systems of interaction apparently were stable for many Ma as a result of the positive feedback loops formed by selective pressures. In both cases we argue that the cycle of selection pressures was determined by the ecological roles of the major biotic components of the system *and* by the order in which these evolved. Having offered an explanation for stasis in community structure, how do we explain the breakdown of Stage 1 and Stage 3 systems?

Breakdown of Stage 1 community structure

Although the sharpest change in the entire history of angiosperm– herbivore interactions occurred at the end of the Cretaceous, there is some evidence of change beginning in the Campanian. These last 10 Ma of the Cretaceous, designated Stage 2, saw increased diversity of smaller herbivores, a probable increase in the number of large angiosperms and large angiosperm diaspores, and in the last 5 Ma a possible decrease in the diversity of dinosaurs. These events may represent an increase in dispersal/frugivory, an increase in range of tree habits displayed by angiosperms, and possibly a decrease in generalized browsing. Stage 2 also corresponds to a time of major taxonomic radiation at the familial and ordinal level in angiosperms as reflected by pollen (Muller, 1981), and may have been the period during which many of the more advanced insect pollination syndromes evolved (Crepet and Friis, 1987).

In terms of the ecological roles of angiosperms and herbivorous tetrapods, Stage 2 seems to foreshadow conditions that came to dominate in the Early Tertiary. How and why did these changes occur under the self-reinforcing selective regime we have hypothesized for Stage 1? Whatever the ultimate cause of these initial changes in Stage 1 community structure, the proximate cause presumably involved a shift in selective pressures that allowed some angiosperms to evolve more *K*-selected traits. This shift could have been initiated by physical separation of dinosaurs from angiosperms, or by an evolutionary innovation in angiosperms that decreased generalized herbivory and disturbance by dinosaurs.

Physical separation of angiosperms and dinosaurs could have occurred globally or locally. Evidence for a global decline in species diversity of dinosaurs during the last 10 Ma of the Cretaceous is equivocal (Colbert, 1962; Russell, 1984). Our evaluation of the data is that they do not support a long-term decline beginning in the Campanian, but they may indicate a late Maestrichtian decrease in diversity. Because the changes that define Stage 2 began in the Campanian, the putative global decline in dinosaur diversity is too late to be a primary factor in the ecological and evolutionary "release" of angiosperms. This leaves open the possibility that some angiosperms could have been freed from dinosaur herbivory earlier in Stage 2 by local extinction of dinosaurs, dispersal to areas not inhabited by dinosaurs, or by occupying topographic or edaphic sites not favorable to dinosaurs. The lack of geographic and stratigraphic resolution in the fossil data make it difficult to evaluate these possibilities, although it should be noted that such local geographic or topographic isolation would have had to persist for a long enough period to allow evolutionary change to take place.

The evolutionary development in angiosperms of an effective defense mechanism could have decreased herbivory and permitted the subsequent evolution of prolonged sporophytic growth and larger seeds. However, we have no evidence of such a development. Regardless of the route by which angiosperms began to evolve more *K*-selected traits, if dense forest became established during Stage 2 the plant species that formed this vegetation probably would have been freed from many of the effects of large herbivores, simply because large herbivores do not frequent dense vegetation. This raises the possibility that Maestrichtian landscapes may have been mosaics with interspersed patches of dense forest and open vegetation. The dynamics of the open patches would have been basically unaltered from Stage 1, whereas in the forested patches angiosperms and small herbivores would have evolved interactions similar to those seen in Stage 3.

Major climatic changes took place in the latest Cretaceous and may have been the ultimate cause for the ecological/evolutionary changes discussed above. Kauffman (1984) attributed some of the major changes in marine life during the late Campanian and Maestrichtian to large sea-level fluctuations that, in turn, caused severe changes in ocean area, circulation and chemistry. Boersma (1984) reported a major decrease in ocean temperature from the late Campanian to the Maestrichtian based on isotopic analysis of foraminiferal tests. Such large changes in the oceans would doubtless have affected terrestrial climate, but we see no obvious causal link between climatic changes and the observed shift in angiosperm–herbivore interactions.

These post-Campanian changes presumably were independent of the terminal Cretaceous event. The hypothesis that an extraterrestrial body struck the earth's surface about 65 Ma before the present (Alvarez et al., 1980, 1984; Bohor et al., 1984) is now widely accepted, although the data could be explained by intense volcanism (Officer and Drake, 1985). Whatever its cause, the terminal Cretaceous event had a major effect on the vegetation of a large part of North America. Floras from the few cm just above the boundary are dominated by ferns (Orth et al., 1981; Tschudy et al., 1984; Nichols et al., 1986; although see Lerbekmo and St. Louis, 1986); in Colorado, U.S.A., the subsequent few meters of sediment preserve dispersed cuticle and megafossils that indicate early successional angiosperms (Wolfe and Upchurch, 1986, in press). Wolfe and Upchurch (1986, in press) suggest this records vegetational succession following regional devastation of Maestrichtian plant communities. Among terrestrial animals the K/T boundary is roughly synchronous with the extinction of all large herbivores and some small tetrapods as well.

We suggest that the brief, but apparently severe and geographically widespread, disturbance at the K/T boundary also administered the *coup de grace* to Stage 1 style communities. Following the total extinction of large herbivores, angiosperms and small herbivores would rapidly have begun to form the interactions that characterize Stage 3. Whether or not Stage 2 would have eventually given way to Stage 3 without the extrinsically caused disturbance is a difficult, but perhaps futile question. It may be that the organization of Stage 1 communities was stable enough that both long-term deterioration and catastrophic change were required to generate the conditions leading to the development of Stage 3.

Breakdown of Stage 3 community structure

The change from Stage 3 to Stage 4 appears to have been gradual, and probably proceeded at different rates in different parts of the world. Indeed, on the basis of the functional and ecological criteria that we have used, there is little difference between the Stage 3 communities of the early Tertiary and some extant, tropical forest communities. Although the fossil record is not temporally and geographically complete, it seems probable that communities with diverse small frugivore/dispersers, few large herbivores, and diverse large angiosperm trees with a large range of diaspore sizes have been continually present since the early Tertiary, even if no one area supported such a community continually.

The development of more open grassland and herbaceous vegetation during the Tertiary is probably related to climatic deterioration and local orographic effects. There is evidence for seasonally dry climates in the early Eocene in parts of western North America (Bown and Kraus, 1981), and middle Eocene vegetation of the same region has been reconstructed as open woodland, as opposed to the dense forests of the early Eocene (MacGinitie, 1969). Dry tropical forests may also have been present in the Mississippi Embayment region in the middle Eocene (Wolfe, 1978). However, the most profound climatic change of the Tertiary was probably the marked drop in mean annual temperature and increase in mean annual range of temperature that coincided with the end of the Eocene (Wolfe, 1978). Although this temperature decline may not have been precisely synchronous in all parts of the world, evidence from the marine realm indicates global cooling during the late Eocene–Oligocene interval (e.g. Savin, 1977; Moore et al., 1982; Wolfe and Poore, 1982).

Increasing seasonality and decreasing temperature over much of the earth during the Middle Tertiary gave an advantage to plant lineages with perennating structures or short life cycles (Tiffney, 1984). In environments where growth was limited by seasonal lack of water or warmth, dense forest was replaced by more open vegetation composed of shrubs, grasses, and herbaceous dicots. Extensive low, open vegetation would have removed the blocks to radiations of large herbivorous mammals. Within these mammals sexual selection, greater efficiency of movement, predator defense, or other factors could rapidly have led to the evolution of large size in many lineages. Once large herbivores were diverse and abundant, the effect of their herbivory would have been to favor the maintenance of relatively open vegetation. Areas that retained closed, Stage 3-style vegetation would not have been subject to the same degree of generalized herbivory as neighboring regions of open vegetation, because of the difficulties encountered by large herbivores in dense forest. In sum, we suggest that the breakdown of Stage 3 organization was a consequence of climatic deterioration, and subsequent spread of open vegetation, especially grassland. Angiosperm–herbivore dynamics established in those areas would have been similar to those of Stage 1 communities, and would have helped to maintain open vegetation. In areas less affected by climatic change angiosperm–herbivore interactions would have remained similar to those seen in Stage 3.

Conclusions

Predictions

As an aid to the future evaluation of the conclusions drawn in this paper, we offer some predictions about the fossil record. If the conclusions we have drawn are largely correct, then most of these predictions should also be correct. However, these are probabilistic predictions, not falsifiable hypotheses, and therefore any of them could be proven partly incorrect.

(1) As Cretaceous mammal faunas become better known the diversity of small herbivores generally will be lower in those of pre-Campanian age and higher in those of Campanian–Maestrichtian age.

(2) The diversification of frugivorous birds began in the Campanian–Maestrichtian interval, and accelerated in the Paleocene.

(3a) As Campanian–Maestrichtian angiosperm diaspore floras become better known they generally will show larger mean size and larger size range than those of the pre-Campanian, although small diaspores will remain dominant.

(3b) The time of diversification for most groups of angiosperms that primitively have large, vertebrate dispersed seeds will prove to be Maestrichtian or Tertiary. Many of the higher rank taxa (e.g. subfamilies and families) probably diversified in the Maestrichtian–Eocene interval.

(4a) With better knowledge of fossil-wood floras mean and range of angiosperm axis size will also be found to increase from the Campanian–Maestrichtian into the early Tertiary.

(4b) The time of diversification for most groups of angiosperms that primitively are large trees will prove to be Maestrichtian or Tertiary. Many of the higher rank taxa probably diversified in the Maestrichtian–Eocene interval.

Implications

We think several aspects of this reconstructed history of angiosperm–herbivore interactions have broad implications for how terrestrial ecosystems are organized and how evolution occurs within them. These implications are discussed in relation to the following points: (1) the long periods of stasis in patterns of angiosperm–herbivore interactions; (2) the disruption of these periods of stasis; (3) the influence of the sequence of evolution of plants and herbivores on the dynamics of the ecosystems they form; and (4) the effect of this sequence of evolution on the subsequent evolutionary history of major groups of angiosperms and herbivorous vertebrates.

The geologically long periods of stasis in angiosperm–herbivore interactions (Stages 1 and 3) are interesting (although we suspect not rare), especially in the context of recent ecological views that communities are not "real", and that combinations of species have little temporal stability (e.g. Davis, 1976, 1981; Finegan, 1984 and references therein). One reason for this discrepancy is that ecologists (and paleoecologists as well) have tended to define communities by their taxonomic composition, whereas we have tried to define communities by the functional groups that compose them. These functional groups are similar to the "guilds" of Root (1967, 1973). If, over periods of time long enough to permit evolution, change in taxonomic composition does not yield change in functional relationships, then this implies that some force(s) is acting to maintain the integrity of ecological roles even though the kinds of organisms that fill the roles may change. In the case of angiosperm–tetrapod communities we have suggested that this force is a cycle of selective pressures generated by the interaction of guilds of organisms. These selective pressures exert a stabilizing force that, though perhaps intermittent, favors the retention of established ecological relationships over evolutionary time. We predict that studies of other kinds of ecosystems will also show long periods of stasis in the organization of communities.

The mechanisms by which long-standing patterns of community organization are disrupted or eliminated is also a question of broad significance. If ecological interactions have a stability conferred by selective pressures operating over evolutionary periods of time, how does the nature of ecological interactions change? Based on major changes in the nature of angiosperm–herbivore relationships, it appears that exogenous forces like severe climatic change and bolide impacts may be the chief mechanisms for drastic reorganization in community structure. However, Stage 2 of our inferred history raises the possibility that over long periods of time evolutionary change in lineages may create major new kinds of ecological interaction, even within the confines of pre-existing communities.

The sequence in which major components of an ecosystem evolve has important effects on the kinds of ecological relationships that characterize the system. The fact that angiosperms radiated after large herbivorous dinosaurs was a major factor in determining the dominance of generalized herbivory in late Mesozoic terrestrial ecosystems. The evolution of dense angiosperm forests before the evolution of a diverse fauna of large herbivorous mammals was a controlling factor in the organization of early Tertiary ecosystems. Thus, the interactions that take place among species at any point in time cannot be fully understood in the absence of an historical context, implications to the contrary (Howe, 1985; p.861) notwithstanding.

The reciprocal observation to the one just made is that the structure of an ecosystem can have a strong effect on the evolutionary path taken by a group that evolves into it. The range of ecological roles occupied by angiosperms between their initial radiation and the end of the Cretaceous appears to have been far more limited than might be expected based on their taxonomic radiation, their abundance in later Cretaceous floras, or their rapid increase in ecological scope during the early Tertiary. A similar point might be made concerning the evolutionary history of mammals and birds. We predict that, in general, diversifications of higher level taxa that take place during periods of stasis in ecosystem organization should produce taxonomic diversification within a relatively narrowly defined adaptive zone. Diversifications taking place following major ecosystem disruptions should yield higher taxa with broader adaptive zones, perhaps in addition to taxonomic diversity. Angiosperms may be one of the best examples of a group that has undergone both kinds of radiation.

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