

OPPORTUNISTIC EVOLUTION: ABIOTIC ENVIRONMENTAL STRESS AND THE FOSSIL RECORD OF PLANTS

WILLIAM A. DIMICHELE¹, TOM L. PHILLIPS² and RICHARD G. OLMSTEAD³

¹*Department of Paleobiology, (N.M.N.H.) Smithsonian Institution, Washington, D.C. 20560 (U.S.A.)*

²*Department of Plant Biology, University of Illinois, Urbana, IL 61801 (U.S.A.)*

³*Department of Botany, University of Washington, Seattle, WA 98195 (U.S.A.)*

(Received March 1, 1986; revised and accepted August 19, 1986)

Abstract

DiMichele, W.A., Phillips, T.L. and Olmstead, R.G., 1987. Opportunistic evolution: abiotic environmental stress and the fossil record of plants. *Rev. Palaeobot. Palynol.*, 50: 151–178.

Abiotic stress has played a major role in the evolution of vascular plants by creating or delimiting habitats with low interspecific competition. These are, in effect, opportunities for survival of divergent phenotypes through non-adaptive evolution. The patterns and processes associated with stress-related evolution lend support to concepts of evolution as a process with a distinct hierarchy of levels.

There are two fundamental forms of abiotic stress. Extrinsic stress is induced by an external agent(s) that impinges on ecosystems, altering conditions and leading to selection against indigenous forms; these are aperiodic or have long return times and are thus beyond the limits of adaptation. Intrinsic stress is caused by physical, usually edaphic conditions of certain kinds of habitats that select against almost all plants. These kinds of stress are fundamentally different from "stress" induced by competition or intracommunity, short-period disturbance.

Extrinsic stress induces differential migration and extirpation/extinction as proximate effects. Evolution is a by-product of disrupted communities in which momentary opportunities for divergence are created. The fossil record provides most of the critical sequences recording the effects of extrinsic stress. Evolution in stressed ecosystems is a "sweepstakes", with colonizers/dispersers and preadapted forms speciating the most and gaining the greatest ecological advantage during these episodes. Extrinsic stress has been of extreme importance in shaping the phylogenetic tree of vascular plants by progressively and sequentially pruning clades from the role of ecological codominance.

Intrinsically stressful environments are bounded by asymmetrical ecotones. Entry to these habitats is made possible by preadaptation. They generally are low diversity "species sinks" with highly specialized floras, rarely sites of evolutionary innovations that subsequently spread into non-stressful habitats. Due to limited species exchange with surrounding environments, these kinds of habitats tend to become progressively more archaic through time, preserving a flora that changes little for long periods. They are very susceptible to mass extinction and vegetational reorganization, at which point the cycle of increasing archaicism is reset. They appear to be good analogs for the initial phases of "adaptive" breakthroughs in general, and strongly suggest a highly stochastic process.

Competition-mediated adaptive evolution may hone morphologies created during periods of non-adaptive cladogenesis. The fossil record provides primary data and permits testing of theories by evaluation of predicted patterns versus empirically-determined patterns.

Introduction

The earth has both a phylogenetic and ecological organization. These are presumed to

be related through evolutionary processes, the rules of which most biologists see as embodied by modern neo-Darwinian theory. This theory and the principles of ecology describing ecosys-

tem organization, the framework for natural selection, are drawn almost exclusively from studies of extant organisms. They reflect an underlying uniformitarianism. That is the conviction that the processes observable in the human time-frame, the effects or results of these processes, and the modern world in which they have been observed, can be extrapolated to the past and serve to explain the biological organization of the world at any time in geological history.

The patterns in the fossil record have long been recognized as conforming poorly to the predictions of Darwinian theory. For the most part this lack of correspondence has been attributed to an imperfect record, although minor modifications have been made in the central theory to accommodate it (Simpson, 1944, 1953). Recently, the fossil record again has been raised as a potential test of neo-Darwinian theory primarily through the impetus of punctuated equilibria (Eldredge and Gould, 1972) and the enormous amount of empirical and theoretical research this has engendered. The focus of this research has been mostly on phylogenetic pattern, attempting to derive means to explain stasis and the rarity of continuous transformation series between species by studying organismal architecture and development (e.g.: Gould, 1977; Gould and Lewontin, 1979; Alberch, 1982) or by modifying more general population-level approaches (e.g.: Slatkin, 1981; Lande, 1985).

An additional element to be considered is the role of changing global ecosystems through time. The dominant morphologies and life histories of plants and animals, and the communities that these organisms form define the "selective landscape", the conditions under which biological diversification will occur. Evaluation of ecosystems and their dynamics over geological time suggests that the predominant evolutionary processes and resultant patterns could and did differ in past times from those of today (Valentine, 1980; Arthur, 1984). Furthermore, events outside the scope of adaptive evolution, such as periodic, widespread perturbations of the earth, may have

played a major part in shaping the history of life (Valentine, 1980; Gould, 1985; Jablonski, 1986). These raise the possibility that non-adaptive processes may play a significant role in the origin of plant diversity.

Abiotic stress is one of the major elements of ecosystem dynamics, either as extrinsic factors that impinge on ecosystems, or as intrinsic elements of specific habitats. Studies of modern stressful ecosystems, cited subsequently in this paper, indicate that abiotic stress *creates opportunities* for the establishment and survival of new forms, acting as an agent of selection against individuals intolerant of the stress. Furthermore, the fossil record of plants suggests that abiotic stress has been an important modifier of terrestrial ecology, and hence evolutionary pattern, since plants colonized the land. While this is a fragment of the entire evolutionary picture, it brings nonadaptive evolution into relatively sharp focus.

Arthur (1984) has defined two kinds of selection, which are relevant to our discussion. The first, *w*-selection, leads to adaptation, *sensu* Gould and Vrba (1982), and is the core of neo-Darwinism. The second, *n*-selection, occurs under conditions of very reduced or no competition where a population growth rate > 1 (at low densities) is the only necessary condition for establishment of a mutant lineage. These are hierarchically related in that *n*-selection permits establishment of new forms and involves, in essence, non-adaptive evolution. *W*-selection, driven by competition, hones these forms as population size increases, and also can lead to anagenic evolution of new low-rank taxa. In Arthur's terms, abiotic stress creates opportunities for the manifestation of *n*-selection, which is followed by variable amounts of *w*-selection, depending upon specific conditions.

The fossil record of plants provides us with an unusual opportunity to evaluate these phenomena and to search for generalities because of the enormous changes in flora and vegetation that have occurred since the Silurian. In effect, the plant fossil record presents a test case in which we can analyze the predic-

tions of theory based on modern organisms and ecosystems in worlds that are vastly different from that of today. This provides both a test and a means to enhance and expand general concepts of how life evolves and is organized into complex landscapes.

Stress characterization

In a general sense, stress can be characterized as "any environmental factor potentially injurious to living organisms" (Levitt, 1980, p.3). However, this includes several distinct classes of "stress" with very different relationships to evolution. Biotically-induced stress is that resulting from competition among members of the same or different species. It is manifest primarily through natural selection acting upon differences in relative fitness within populations. It is believed to be the major driving force of adaptation.

Abiotic stress includes at least two distinct forms, extrinsic and intrinsic. Extrinsic stress includes stresses with short return times and local effects, i.e. disturbances (*sensu* Pickett and White, 1985), and stresses with regional to global impact that are unique or have long return times. Disturbances that occur regularly within the span of plant life-histories have "predictable" effects and return time; they are ecological time phenomena, as are biotically-induced "stresses", and thus are driving forces of adaptive evolution. There are numerous examples of organisms, such as weeds, dependent for their continued existence upon regular disturbance. In contrast, extrinsic stresses that occur infrequently, causing widespread ecosystem change or destruction, create opportunities for evolution in a changed landscape. These also modify evolutionary opportunities by changing/reducing genetic variability by large scale destruction of populations.

Intrinsic stress, resulting from physical, usually edaphic attributes of a habitat, has been dealt with in detail by Grime (1977, 1979). Intrinsic stress excludes most organisms from potential resources, often creating low-competi-

tion, target-of-opportunity sites for plants that possess, a priori, a stress-tolerant phenotype.

Our discussion is confined to abiotic intrinsic and extrinsic (widespread, long-period) stress and how they affect plant evolution.

Temporal hierarchy

The effects of extrinsic and intrinsic stress on organisms can be studied both with regard to immediate, proximate effects and effects on a geological time scale. Geological time also permits evaluation of stress effects in different "selective landscapes", revealing generalities about process and how past events place constraints on later events. Things could and did happen in the past that can not and do not happen today, and vice versa, because of changes in organisms and kinds of ecosystems they create.

Intrinsically stressful habitats in any single slice of time can be separated from habitats in which competition or disturbance are the dominant factors structuring communities (Grime, 1977, 1979). The evolutionary dynamics of intrinsic abiotic stress can be understood almost completely on an ecological time scale. Intrinsically stressful habitats can be recognized in the fossil record by analogy to modern stressful habitats, e.g.: swamps, saline coastal or inland regions, etc., assuming such habitats can be indentified in the past.

Extrinsic abiotic stress, because it *impinges on* ecosystems regardless of the factors structuring them, is fundamentally distinct from intrinsic abiotic stress. Extrinsic stress has proximate effects on an ecological time scale, but much of the ecological and evolutionary consequences of natural extrinsic stress must be studied on a geological time scale. Opportunities to study extrinsic stress in extant systems are rare because of the time required to observe the effects.

Empirical studies of the plant-fossil record indicate a broadening spectrum of morphological complexity of plants through time (e.g. Hickey and Doyle, 1977; Banks, 1980; Niklas et al., 1980), contributing directly to changes in

ecosystems (e.g. Knoll et al., 1979, 1984; Beerbower, 1985). Consequently, selective landscapes within which we can examine stress change through geological time. Patterns of recovery from a severe extrinsic stress and the phenotypes available to colonize intrinsically stressful habitats, are highly dependent on biologies of organisms of the time. The taxonomic rank (Division, Class, etc.) assigned to new lineages that evolve during reradiation into vacated habitats following an episode of extrinsic stress diminishes through geologic time (Valentine, 1980). Similarly, the spectrum of intrinsically-stressful habitats has narrowed through time as groups evolved that could exploit such environments. Some environments have specialized floras adapted to the stresses, in the proximate sense (Gould and Vrba, 1982), and remain stressful to most other plants, e.g., deserts. In the Devonian much of the land surface would have presented an almost insurmountable ecological barrier to plant migration. As a consequence, most of the earth's surface probably was "stressful" to early land plants (Beerbower, 1985). Today, environments that remain stressful to most vascular plants include, for example, swamps and bogs, terrestrial habitats high in salinity or heavy metals, and brackish to saline coastal regions.

Extrinsic abiotic stress

Extrinsic abiotic stress is caused by external agents that alter prevailing conditions locally to globally, causing strong selection against indigenous species, alteration of ecosystem structure and, thus, changes in interactions among plants and animals. To differentiate severe extrinsic stress from intra-ecosystem disturbance a geological time axis and/or evidence of short-term irreversibility of effects is necessary. This concept is that of Rapport et al. (1985) and differs, in part, from usage of Vogl (1980) and Seyle (1973); they consider extrinsic disturbance to be ecosystem "stress" that is repetitive and to which many species have adapted. We consider such disturbances

to be fundamentally different from extrinsic stress with long return times.

Extrinsic stress may result from severe, short-term events, such as the purported bolide impact at the end of the Cretaceous (Alvarez et al., 1980). More commonly the stress agents are climatic changes, glaciation, and many eustatic sea-level fluctuations — physical processes, unidirectional in ecological time. These stresses may be imposed as increase in frequency of freezing conditions or ground-water salinity, or change in moisture availability. Physiological responses to such factors (Levitt, 1980) have disturbance-type effects in ecological time. However, extension of these effects through time results in permanently changed ecosystems.

Effects on plants and plant communities

Plant populations generally respond to extrinsic stress by changes in distribution within an ecosystem. On an ecological time scale it is often difficult to distinguish between short-term fluctuations and directional trends. Much of the "noise" of fluctuation is lost in the fossil record. Consequently, stratigraphic documentation of the changes in relative abundance and paleogeographic distribution provide a basis for distinguishing longer-term effects.

Plant populations may undergo the following kinds of changes when subjected to extrinsic stress. They may migrate, tracking favorable conditions by differential death and dispersal of individuals. This can occur only if onset rate of extrinsic stress does not exceed migration rate, and if areal extent of the stress does not exceed the dispersal capability of the population (Knoll, 1984). Favorable conditions must persist somewhere and migration routes must be available or the population will be extirpated or the species may become extinct. This is most likely to occur if the onset of the stress is rapid.

The population may evolve toward stress tolerance or stress avoidance. This usually translates as an adaptive transformation of a non-tolerant population into a tolerant one. We argue that this is unlikely and may be

largely a stochastic process. Extrinsic stress, acting through differential migration and extirpation or extinction, creates opportunities for the survival of derived forms (populations and species), a highly opportunistic process.

In modern ecosystems

The study of extrinsic stress in modern ecosystems has focused mostly on the effects of human activities (e.g. Barrett et al., 1976; Rapport et al., 1985; Schindler et al., 1985). Although the time spans involved are short, these kinds of investigations can document many of the responses of ecosystems to extrinsic stress.

Rapport et al. (1985) describe the changes in ecosystems under extrinsic stress, and find these to be relatively uniform in terrestrial and aquatic systems. Stress affects five major attributes of ecosystems: (1) nutrient cycling, mainly by losses; (2) primary productivity; (3) species diversity; (4) retrogression ("pushing" the community succession to earlier seral stages); (5) size distribution of species. If stress were continued long enough, the effect would be irreversible. These responses to extrinsic stress result in changed community structure. However, most of these ecological parameters can not be recognized in the fossil record.

What can be detected on a geological time scale is general pattern of change from one community organization to another, allowing inferences about the specific mechanisms of change. Analyses of climatic and other physical factors may permit correlation of community change with identifiable extrinsic stresses.

Paleobotanical record

Extrinsic stress has been a major modifier of terrestrial vegetation since plants colonized the land. We have tentatively indentified some time intervals in which extrinsic abiotic stress apparently had major effects on the world's vegetation (Fig. 1). The patterns point out how the fossil record contributes to our understanding of abiotic stress in plant evolution. The

examples will focus on Tertiary–Quaternary and Carboniferous–Permian plant responses to climatic change, and consequences of a short-term disruption at the Cretaceous/Tertiary boundary.

Climatic change in the Quarternary and Tertiary

Major fluctuations in global climate since the beginning of the Tertiary have had a major impact in the northern hemisphere, particularly in the modern temperate zone. Vegetation has ranged from tropical and paratropical to cool-temperate and even boreal. These climatic changes were driven by tectonics, glaciation, and global energy budget affecting patterns of atmospheric circulation (Parrish and Curtis, 1982; Parrish et al., 1982), and possibly by fluctuations in atmospheric CO₂ and Milankovich cycles (Wolfe, 1978; Berger et al., 1984). The time scales over which the vegetational changes can be observed are highly resolved, and the sampling base is excellent. Complications arise in sorting out evolutionary patterns from migration (a persistent problem in the fossil record), particularly during the Paleogene, due to asynchronicity of effects globally and because the woody angiosperms were undergoing extensive phylogenetic radiations during this time.

Pleistocene. The Pleistocene was a time of extensive quasi-periodic changes in climate. During the last 10,000–15,000 years the response of vegetation to warming climate has been almost exclusively migration. Extinction of pre-existing taxa and the evolution of new taxa appear to be insubstantial among woody plants. Palynological data clearly indicate individualistic species responses resulting in changed associations within certain vegetational limits (e.g. Davis, 1976; Tsukada, 1982a,b, 1983). Plant macrofossils from desert fossil pack-rat middens in the western United States indicate the importance of migration (Van Devender and Spaulding, 1979; Spaulding et al., 1983; Spaulding, 1983, 1985; Cole, 1985). Cole (1985) documented this migration as

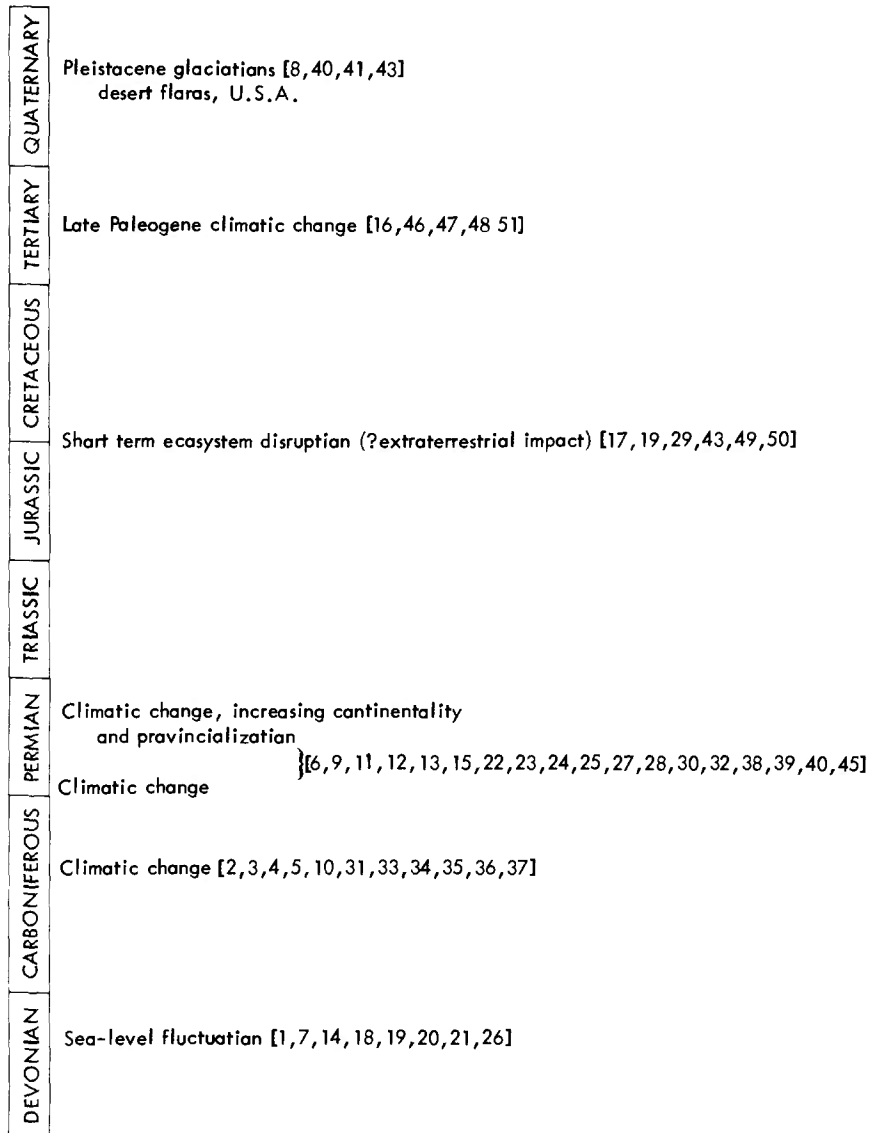


Fig.1. Intervals of extrinsic abiotic stress in the fossil record. This sample of extrinsic-stress events is drawn from the following literature: 1. Banks, 1980; 2. Broadhurst et al., 1980; 3. Caputo and Crowell, 1985; 4. Cecil et al., 1985; 5. Chaloner and Lacey, 1973; 6. Chaloner and Meyen, 1973; 7. Chaloner and Sheerin, 1979; 8. Cole, 1985; 9. Cross, 1975; 10. DiMichele et al., 1985; 11. Foster, 1982; 12. Fredericksen, 1972; 13. Galtier and Phillips, 1985; 14. Gensel and Andrews, 1984; 15. Gillespie et al., 1975; 16. Hickey, 1980; 17. Hickey, 1981; 18. Johnson et al., 1985; 19. Knoll, 1984; 20. Knoll et al., 1979; 21. Knoll et al., 1984; 22. Mamay, 1967; 23. Mamay, 1968; 24. Mamay, 1975; 25. Mamay, 1976; 26. McLaren, 1983; 27. Meyen, 1982; 28. Milner and Panchen, 1973; 29. Nichols et al., 1986; 30. Olson, 1979; 31. Parrish, 1982; 32. Parrish et al., in press; 33. Peppers, 1979; 34. Pfefferkorn and Thomson, 1982; 35. Phillips and Peppers, 1984; 36. Phillips et al., 1974; 37. Phillips et al., 1985; 38. Read and Mamay, 1964; 39. Remy, 1975; 40. Romer, 1973; 41. Spaulding, 1985; 42. Spaulding et al., 1983; 43. Tschudy et al., 1984; 44. Van Devender and Spaulding, 1979; 45. Winston, 1983; 46. Wolfe, 1977; 47. Wolfe, 1978; 48. Wolfe, 1980; 49. Wolfe and Upchurch, 1986; 50. Wolfe and Upchurch, in press; 51. Wolfe and Wehr, 1986.

glacial-age woodland gave way to desert scrub. He discovered apparent response lags of some dominant taxa to changing climate. As new species immigrated, they gradually displaced a depauperate remnant of earlier vegetation, resulting in a period of locally reduced diversity between dynamically stable species associations; however, the generality of this phenomenon, which Cole (1985) called "vegetational inertia", has yet to be demonstrated in other desert areas.

W.G. Spaulding (pers. comm. 1986; Paillet, 1982; Spaulding et al., 1983) has suggested the following scenario linking extrinsic stress and evolution in the Pleistocene. Pleistocene glaciations have had predictable return times ($7-10 \times 10^4$ yr) and upper limits (maximum sea level change of approximately 120 m, maximum southerly extent of continental glaciations to approximately 40°N latitude, maximum temperature change of $\sim 6^\circ\text{C}$ worldwide). These cyclical, relatively closely spaced climatic fluctuations are extreme and may have forced similar repeated changes in terrestrial floras. Pleistocene glaciations may have represented a single stressful interval for plant species. During such an interval the most severe conditions will be those with the greatest selective effect. So, although the return time of glaciations is beyond the limits of adaptive response, regular return of the severe conditions will periodically eliminate marginal forms or excess variation that evolves during interglacials. The greatest period of extinction should have occurred at the beginning of the first glacial cycle, declining subsequently as the proportion of species in the flora capable of tolerating or escaping the peak glaciations increased.

Tertiary. Tertiary climatic changes were relatively frequent, although they do not appear to have had the quasi-periodicity of the Pleistocene. Tertiary woody vegetation was complex, and the dynamic processes regulating it during periods of stable climate dictate caution if the effects of directional climate change are to be differentiated from effects of local disturbance

regime (Cross and Taggart, 1982). In western North America considerable change in vegetation has been documented during the Paleogene (Wolfe, 1977, 1978, 1980; Hickey, 1980; Wing, 1981). Migration seems to be the principal plant response to climate change resulting in quantitative changes in species associations. Species appear to respond individualistically within larger qualitative limits. This is emphasized by latitudinal zonation of floras during periods with steep climatic gradients, and reduction in zonation with homogenization during periods of high climatic equability (Wolfe, 1977). A Tertiary parallel to Cole's "vegetational inertia" may be the low in diversity reached during the Eocene/Oligocene climatic deterioration in the Pacific northwest region; paratropical forest species were replaced gradually by cool-temperate species (Wolfe, 1978).

Changing climate, by causing differential migration and extinction of the plants and animals, alters plant communities and the patterns of resource use. Evolution is not a direct "response" to climate change, but a consequence of opportunistic exploitation of resources made accessible by differential migration and extinction. The probability of survival of new phenotypes is higher during these episodes of environmental disturbance because chances of encountering a momentarily unexploited resource ("empty" niche) are higher. The climatic cooling that began in the Late Eocene may have created conditions that permitted radiations of plants from ancestral stock living in temperate or cool upland regions. During earlier periods of warmer global temperatures these ancestral forms may have persisted in spatially disconnected, peripheral areas. Evidence of this pattern is found in the diversification of the Pinaceae, Salicaceae, Betulaceae and Rosaceae beginning in temperate and upland areas during the Eocene and progressing rapidly during the Oligocene (Wolfe, 1977; Wolfe and Wehr, 1986). This pattern illustrates a *possible* relationship between extrinsic stress and evolution — the opportunistic expansion of tolerant

forms rather than the transformation of non-tolerant forms into stress-tolerators by a directional extrinsic stress.

Woody forest vegetation of the Paleogene and early Neogene was evolving and diversifying and opportunities for phenotypic radiations may have existed. In contrast, during post-glacial times, immigration of well-established existing forms has effectively eliminated the possibility for establishment of new major phenotypes in many environments because of the high levels of resource overlap that have evolved among angiosperms. These differences in pattern may reflect the "time-dependence" of evolutionary events.

Effects of climatic change in the Late Paleozoic

During the Pennsylvanian and Permian Periods plant communities were subject to repeated extrinsic abiotic stress (Fig.2). The floral and vegetational changes induced by climatic fluctuations are best documented for the Euramerican floral province. Climatic changes are deduced from indicators of continental glaciations (Caputo and Crowell, 1985), models of atmospheric circulation and climate (Parrish, 1982; Parrish et al., in press), patterns of coal quality (Cecil et al., 1985) and distribution (Phillips and Peppers, 1984), not all of which suggest the same interpretation. The most detailed data relating community structure and appearance of new taxa come from coal-swamp deposits (Phillips et al., 1985); complementary data from non-swamp, clastic-compression floras suggest similar patterns and present a refined picture (Read and Mamay, 1964; Gillespie and Pfefferkorn, 1979; Pfefferkorn and Thomson, 1982).

Dominance and diversity patterns in swamps, particularly, and in lowland vegetation, in general, changed slowly, and in some cases not at all between major extrinsic stress events. During and immediately following a change in prevailing climatic conditions dominance-diversity structure changed within identifiable kinds of habitats. This usually was

associated with some floral migration and, if rapid, with elevated levels of extinction.

Pennsylvanian Period. New species that appear in association with extrinsic stress are most often from clades in one of two major categories: those with greatest colonizing or dispersal abilities, and those preadapted for growth under the changed climatic regime. *Psaronius* tree ferns were colonizers/dispersers. These plants with small, light homospores, could establish a breeding population from one or few colonizing gametophytes. Trees had cheap construction and rapid growth, probably with tolerance of nutrient stress. These attributes allowed them to preempt vacated habitat space quickly, and favored speciation by the establishment of peripheral isolates. Tree-fern spores first appear in significant numbers in the Westphalian B, during the first drier interval of the Pennsylvanian (Peppers, 1979; Phillips and Peppers, 1984), and increase in diversity and abundance in a step-wise manner, expanding at the expense of lycopods and pteridosperms (Fig.3), after each subsequent climatic change (Pfefferkorn and Thomson, 1982; Phillips et al., 1985). The displaced groups lacked such colonizing potential and probably were narrower in ecological tolerances (Phillips and DiMichele, 1981; DiMichele and Phillips, 1985).

Preadaptation probably was the key to the increasing success of conifers and associated gymnosperms during the Late Pennsylvanian and Early Permian. Conifers are detected first in the early Middle Pennsylvanian (Westphalian B) (Scott and Chaloner, 1983), but did not appear in abundance until the second drier interval of the Pennsylvanian, when they became a major element of lowland, non-swamp floras previously dominated by medullosan pteridosperms (Cross, 1975; Winston, 1983; Galtier and Phillips, 1985). Conifers radiated extensively in the Permian as climatic fluctuations increased in magnitude.

Permian Period. During the Permian Period terrestrial floras underwent a major transformation. Arborescent lower vascular plants and

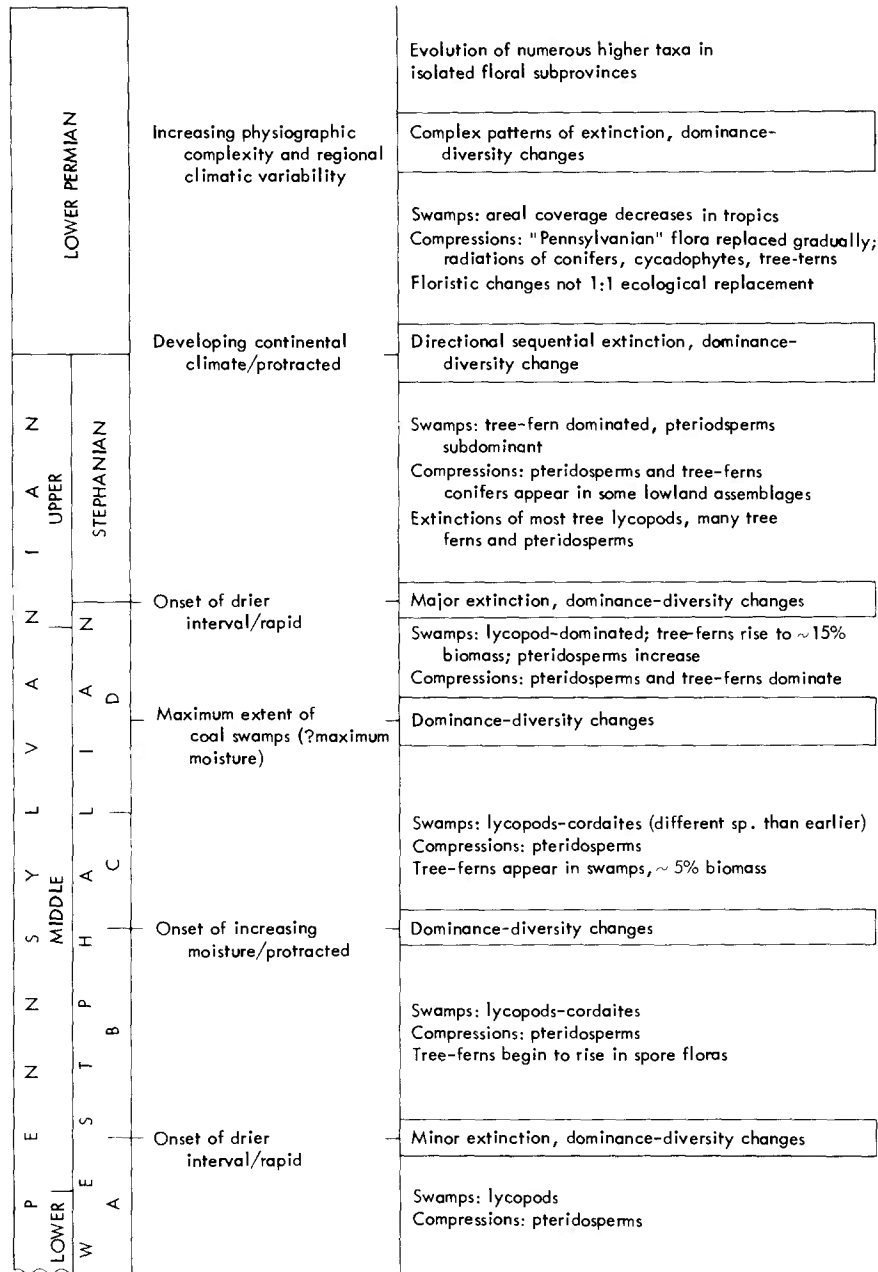


Fig.2. Carboniferous and Permian extrinsic stress events and the general consequences of these events on terrestrial plants and ecosystems. Nature of the extrinsic stress is shown to immediate right of geologic column. On far right, the immediate effects of the stress are shown in the rectangles, the specific effects on swamp and non-swamp floras, with other general comments, are shown in areas above the respective rectangles.

primitive seed plants, such as the medullosan pteridosperms, declined in diversity and ecological importance, except perhaps for the marattialean tree ferns. Coniferophytes (conifers and

cordaites), and a diversity of cycadophytic seed-plant groups formed regionally heterogeneous vegetation. These floral and vegetational changes were globally asynchronous (Knoll,

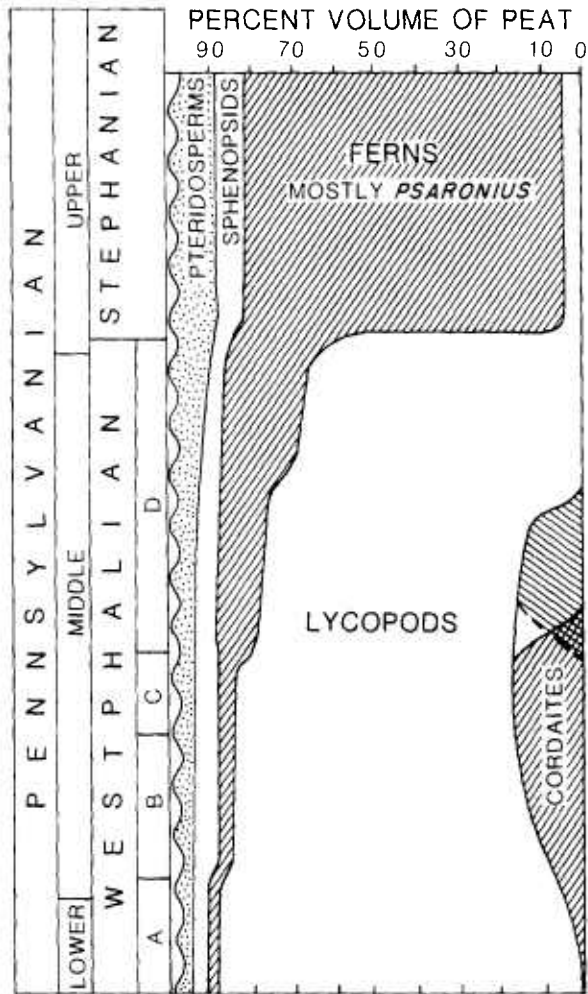


Fig.3. Changes in the relative abundance of major plant groups in Pennsylvanian coal swamp assemblages. Inflections in the *Fern* curve correspond to time periods of change in extrinsic conditions, inferred from other sources of data. Modified from Phillips and Peppers (1984).

1984). For example, coal swamps persisted in France until the Early Permian (Galtier and Phillips, 1985), after their decline in North America. In China, lycopod–tree fern–cordaite coal swamps persisted until the end of the Permian.

These patterns reflect an increasing provincialization of the world's floras during the Permian (Read and Mamay, 1964; Chaloner and Lacey, 1973; Chaloner and Meyen, 1973), a pattern also reflected by vertebrate distribu-

tions (Milner and Panchen, 1973; Romer, 1973; Olsen, 1979; Parrish et al., in press).

The formation of Pangaea is generally believed to have been the impetus for these changes. Changing atmospheric circulation patterns by increasing continentality altered rainfall patterns. This constituted severe, protracted, extrinsic stress, manifested at different times and to different degrees throughout the globe. The general patterns of floral change reflect ultimately major changes in the reproductive and growth strategies of the dominant plants (Niklas et al., 1983; Knoll et al., 1984). Vegetational change in the Carboniferous–Permian transition was gradual. This has been documented in the Dunkard Group of the Appalachians (Cross, 1975; Gillespie et al., 1975; Remy, 1975), in several areas of the Soviet Union (Meyen, 1982), and in Australia (Foster, 1982). These areas were floristically distinct at the time, but the same general trend is suggested in all of them. Despite an essentially gradational change, the declining flora is ecologically different from the expanding flora. Therefore, this does not appear to involve extensive competitive displacement of the older flora by the younger flora.

Gradual climatic and physiographic changes during the Permian had effects at two levels. The most direct effects were within floral provinces where communities were disrupted and changed as radiations occurred in previously marginal or newly established clades. Less direct, but of great importance, was increase in the number of floral provinces within which discrete evolutionary events occurred. Mamay (1976) noted that the earliest Permian radiations had little "morphological significance"; the affinities of the expanding groups usually are very clear. However, by the later Early Permian many novel forms began to appear among seed plants, often of unknown ancestry and with relatively narrow geographical distribution. In summary, the Pennsylvanian vegetational changes in Euramerica illustrate the proximate effects of extrinsic stress and the relationship of these phenomena to evolution. The Permian vegetational

changes are much more complex and demonstrate a hierarchy of effects within floristic provinces and among them.

Cretaceous/Tertiary boundary

There is now extensive evidence of a major environmental catastrophe at the Cretaceous/Tertiary (K/T) boundary. Coincident extinctions in many groups of terrestrial and marine organisms, evidence of large quantities of atmospheric dust and soot, and iridium enrichment of a clay layer derived from the particulates, suggest impact of an extraterrestrial body (Alvarez et al., 1980) or massive volcanism (Officer and Drake, 1985) as the proximate cause. It appears that all or part of the earth was blanketed with a dense cloud that reduced insolation and caused a short, but pronounced climatic cooling — a geologically instantaneous, global extrinsic stress.

The immediate ecological effects of this event on terrestrial plant communities are reasonably clear. The standing biomass in many parts of the northern hemisphere may have been killed, followed by extensive fires (Tschudy et al., 1984; Wolbach et al., 1985). As recovery ensued, colonizing species, in particular ferns, moved rapidly into vacated areas, persisting for a short time before being replaced by typically woody, early successional angiosperms (Tschudy et al., 1984; Nichols et al., 1986; Wolfe and Upchurch, 1986). Ecological effects over the long-term are less clear. Large herbivores, in particular dinosaurs, were eliminated by the boundary event. As a consequence, recovering plant communities had a major modifier of ecosystem structure removed (Wing and Tiffney, this issue). Furthermore, there appear to have been some significant plant extinctions selectively affecting broad-leaved, evergreen species, especially at higher latitudes (Hickey, 1981, 1984; Wolfe and Upchurch, in press).

It seems likely that this event, through the ecological changes it engendered, would have had a major, long-term impact on plant evolution during the Early Tertiary. Regional extirpation or extinction of many plant and animal

species and massive, widespread disruption of communities altered the ecological conditions under which evolution was occurring, that is the "selective landscapes" of the time, were radically altered. The subsequent diversification resulted in a flora/vegetation very different than that existing prior to the perturbation. The land surface of the earliest Paleocene may have been a mosaic of terrestrial "islands" in which resources were abundant and competition low, permitting the establishment of stem species in many clades that later radiated extensively. These events may have been much like those that occurred in plant groups of the Hawaiian Islands, where extensive morphological divergences from small founder populations have occurred (Helenurm and Ganders, 1985; Lowrey and Crawford, 1985).

The plant fossil record is not particularly revealing on this issue, at least at our present level of resolution. Hickey (1981) concluded that extinctions across the K/T boundary were gradual and induced by gradually changing climate and continuing angiosperm radiation. This analysis has been extended by Knoll (1984), implicating competition as a major driving force of Paleocene angiosperm evolution. In contrast, Wolfe and Upchurch (1986, in press) argue for significant extinction, focused primarily on broad-leaved, evergreen taxa, leaving a depauperate flora in which deciduous species were most abundant. They estimate that vegetation required much of the Paleocene to recover from this disequilibrating event. It is clear that much greater resolution, both stratigraphic and geographic, is needed if a clear picture of events is to be constructed, and if we are to be able to distinguish competitively driven from opportunistic patterns of diversification.

Extrinsic stress: summary

Study of life histories, biogeography and ecology of extant plants lead to a general hypothesis of how plants should respond to extrinsic stress. Migration and extinction are the most likely immediate consequences. Evolution is a considerably different phenomenon

because it involves genomic change. During and immediately following the onset of severe extrinsic, abiotic stress, communities are disrupted. Differential rates of migration and extinction lead to change in community structure and, hence, to altered patterns of resource use. Fragmentation of populations magnifies the consequences of vacated resources by creating lowered diversity in many areas. Fragmentation also provides the potential for divergence as effective population sizes are diminished (Wright, 1931; Levin and Wilson, 1978), and gene exchange is reduced or eliminated (Carson, 1982, 1985; Arthur, 1984). These factors create *opportunities* for the differentiation of divergent populations, ultimately the stem populations of new species. This is a highly opportunistic process. The probability of establishment of a new phenotype is increased in an environment in which previously occupied resources are vacated and surviving species are fragmented into isolated populations.

Extrinsic stress acts primarily in opening up resources, permitting the occasional survival of a new phenotype. Thus, its role in evolution is an indirect one. Evolution of stress tolerance in a pre-existing phenotype is no more likely than the appearance and establishment of any new set of traits. This contrasts with expectations of adaptive evolutionary response to extrinsic stress, i.e., in situ gradual change due to a particular "selective pressure". This is supported by modern quantitative genetic studies, which suggest that existing additive genetic variance in populations usually is exhausted or greatly diminished in relatively few generations causing a plateau in the rate of adaptive change (Falconer, 1981). Strong extrinsic stress, directionally changing conditions, should quickly override the ability of local populations to adjust, particularly if population size has been diminished.

Fossil evidence

The fossil record provides critical evidence on the response of species and vegetation to extrinsic stress (long-term effects). Migration is the principal response to climatic change.

Responses of species are individualistic. This results in continuously changing species associations during times of directional extrinsic stress, or during recovery from an event like that at the K/T boundary. Evolutionary radiations appear to occur as ecosystems are disrupted. Evidence for this comes from Pennsylvanian (Phillips et al., 1974, 1985; Pfefferkorn and Thomson, 1982), Permian (Remy, 1975; Meyen, 1982), and Eocene (Wolfe, 1977; Wolfe and Wehr, 1986) data sets. This implies that release from competitive constraints underlies most of these radiations. This is particularly significant because plants of very different phylogenetic lineages diversify nearly simultaneously as resource space is temporarily opened. The most successful species in any one of these events are those with life histories conferring colonizing ability and/or preadaptive tolerance of the stress (xeromorphs or cold-tolerant taxa, for example). Radiations may occur because populations of the stem species can diverge quickly and independently in a large variety of phenotypic "directions" given an opportunity (the colonizers), or because populations have special access to the newly vacated resources due to the traits evolved in previously marginal areas (the preadapted forms). Not all evolutionary radiations occur under these conditions.

Extremely severe, short-term stresses (the K/T boundary, Middle/Late Pennsylvanian or Eocene/Oligocene transitions) that cause widespread extinction, dislocation or destruction of existing species associations often trigger long-term evolutionary changes by resetting all or part of the vegetation far from a global ecological equilibrium. Increased provincialization of the vegetation by widespread climatic change should result in increase of higher taxa, even if global diversity remains stable.

The fossil record of plants indicates that the evolutionary importance of extrinsic stress has varied greatly depending on its timing in geological history. This is due to changes in the plant groups dominating the earth's terrestrial ecosystems, the biologies of the dominant taxa, and the structure and areal extent of the

communities formed; all of these change directionally through time due to the strongly Markovian, historical nature of the evolutionary process. The major effect of extrinsic stress over geological time has been periodic severe selection, mainly against those plant groups comprised of species with similar, relatively narrow ecological amplitudes, particularly arborescent species. In an evolutionary sense this selection has been "nonconstructive", as suggested by Raup (1986) for periodic severe extinctions. Its effect has been to remove species and disrupt ecosystems creating opportunities for evolution rather than directing evolution in a constructive sense.

During the Carboniferous and Early Permian most wetland lowland ecosystems were dominated by varying proportions of arborescent lycopods, tree ferns and sphenopsids, as well as by seed plants. In many cases plants of these groups were co-dominant in lowland forests, giving that particular type of landscape a taxonomic complexity unmatched since. Toward the end of the Paleozoic most of the major arborescent, lower vascular plants disappeared during climatic oscillations of increasing magnitude, which apparently selected most strongly against plants in the most hydric and mesic environments. These extinctions were asynchronous and affected the most strongly swamp-centered species first, the arborescent lycopods (Phillips et al., 1974). Ultimately, after the temporary or permanent return of pre-stress conditions, tree ferns and seed plants gained ascendancy as they moved into vacated habitats. Although all major groups continued to be represented into the Mesozoic, seed plants, in considerable diversity, were the only major clade to dominate most terrestrial ecosystems. They appear to have been the most resistant to extrinsic stress, with some species always able to persist through physically unfavorable periods, providing the stem groups for further diversification. Ultimately, the angiosperms rose within this clade and have expanded and diversified enormously since their appearance.

This pattern illustrates the progressive nar-

rowing of the phylogenetic affinity of the dominant vegetation of the earth. Essentially all post-Devonian groups (Classes) "leave the gate" together. These groups are selectively reduced in dominance and diversity during intervals of major extrinsic stress, but they are seldom eliminated completely. During geological intervals in which climate is equable for long periods of time the flora will diversify, and regional variability in vegetation will develop. This taxonomic and vegetational variability is severely reduced during relatively brief intervals of extrinsic stress, during which selection reaches its maximum intensity, pruning the marginal clades, a process suggested by Waddington (1975). It is during these periods of most stringent selection that the phylogenetic tree is reshaped most profoundly. With each decimation, the more resistant groups persist and move opportunistically into the available resource space. This does not appear to represent competitive displacement because the groups that disappear during this time were quite effective at maintaining their ecological positions in stable ecosystems. Arborescent lower vascular plants and seed plants had coexisted since the Late Devonian; this global equilibrium was not changed until major ecosystem disruptions and sequential, protracted extinctions of the late Paleozoic. This pattern reflects the hierarchy of natural events in which extrinsic environmental catastrophes play a major part in modifying the specifics of phylogenetic history (Gould, 1985).

Intrinsic abiotic stress

Describing stress as intrinsic indicates that it is confined to specific habitats and is due to physical attributes of those habitats. The effect is strong selection against plants not tolerant of the stress agents. Some plants are able to grow under the adverse conditions because of a greater threshold of tolerance and because severe interspecific competition is lacking in such sites (Bradshaw and McNeilly, 1981). Their presence in these habitats represents the fortuitous intersection of habitat and pre-

adapted, marginally tolerant phenotype. There are, of course, gray areas in the concept when scrutinized in detail, but generalities applying to most cases can be discovered, and it is these generalities we wish to address.

Grime (1977, 1979) defined intrinsic stress as the external constraints that limit the rate of dry matter production of all or part of the vegetation. This definition has three major parts. First, by referring to external conditions, Grime attempts to exclude "stress" induced by interspecific competition among organisms. None the less, in his examples of such sites he includes shaded habitats, which overextends the concept and blurs it with biotic competition. The definition could be made more explicit by limiting external constraints to abiotic external conditions, particularly edaphic factors. Second, stress is recognized by limitations it imposes on dry-matter production. This has been criticized as circular (Van der Steen and Scholten, 1985) because it relies on the plants rather than specific physical characteristics of the environment to identify habitats in which stress is intrinsic. However, the concept of stress is relative and meaningless without reference to organisms. Hence, organisms must be included in the recognition of stress at some level. This should be tempered by recognizing that some organisms may adapt evolutionarily to stressful conditions so effectively that their rate of dry matter production becomes maximized in stressful habitats and actually depressed in typically non-stressful habitats. Third, Grime's definition requires that stress affect all or a significant part of the vegetation. This is important because it requires unrelated organisms to suffer similar negative effects in stressful habitats. It makes stress a general phenomenon, recognizing that it selects against basic attributes of most terrestrial plants. It partially addresses the problem that through evolution some species or populations may have adapted to a particular stress and hence no longer respond negatively to it. Grime separates disturbance from intrinsic stress by couching stress in terms of vegetation

rather than limiting it to specific effects on individuals or populations. In so doing he delimits entire habitats, rather than local patches created by disturbance in otherwise non-stressful settings.

In Grime's scheme terrestrial plants exhibit three primary strategies, with intermediates, described in terms of stress and disturbance (Fig.4). Competitors grow in stable environments with low intrinsic stress and low disturbance. Ruderals also occur in areas of low intrinsic stress but favor recently disturbed sites or environments with frequent disturbance, resulting in low levels of competition. Stress tolerators grow in environments of high abiotic stress and low disturbance. The low competition (intra- and interspecific) aspect of highly stressful environments is important evolutionarily because this permits marginally preadapted plants to colonize stressful sites and establish breeding populations. Correlation of high stress and low competition has been identified empirically in swamps (Schlesinger, 1978), mine-tailing sites (Bradshaw and McNeilly, 1981), and subalpine fell fields (Del Moral et al., 1985), among others. When intrinsic stress is not strictly edaphic in

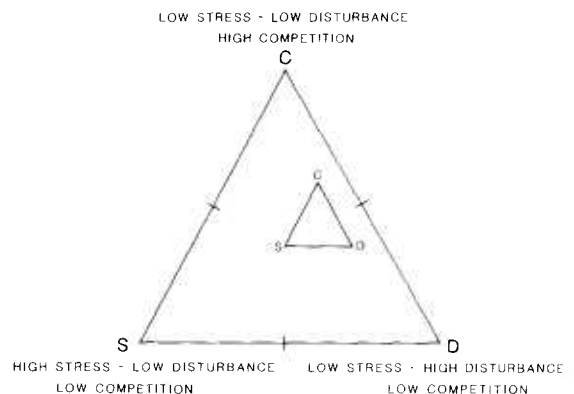


Fig.4. Model illustrating relationship between intrinsic abiotic stress, abiotic disturbance, and competition. Large triangle represents the universe of possibilities. Small triangle represents the local site, community or region being considered; its size may vary from a point to the size of large triangle, and its position may vary. Modified from Grime (1979).

origin, the differentiation of stress-structured and competition-structured communities becomes more difficult (Welden and Slauson, 1986).

A hierarchical expansion of Grime's triangle (Fig.4) (David Chapin, pers. comm. 1986) may resolve some of these difficulties. Any particular vegetational region can be viewed as a small triangle within the larger one. For example, the "alpine" includes a range of environments, all of which are modified by the indigenous temperature and seasonal patterns; within this setting the small triangle is skewed to the stress-disturbance part of the larger triangle. Most intrinsically stressful environments are edaphically distinct from others within their general geographic region, strongly ecotonally bounded, and confined to the narrower high stress part of Grime's scheme.

Recognition of stressful environments

Most stressful habitats are recognized by their edaphic characteristics: swamps and bogs, serpentines or sites enriched in specific heavy metals or toxins, highly saline environments, low-nutrient environments, and, in some cases, moisture-limited areas. Attempts to formulate a definition of stress either aim to include the unifying aspects of these kinds of habitats (Grime, 1977, 1979), or attempt to delimit stress by its effect on individual organisms (Levitt, 1980; Welden and Slauson, 1986). The latter concept usually makes stress indistinguishable from disturbance or local environmental fluctuation. Preferring the approach of Grime, we describe the common attributes of most intrinsically stressful habitats, based largely on those in which stress is edaphic in origin.

The characteristics of stressful environments must be deduced almost entirely from modern ecosystems. Analogy with the present allows recognition of intrinsically stressful habitats in the fossil record. The ecological and evolutionary behavior of stressful systems through geologic time can not be determined empirically from studies of extant systems, but

can be predicted from their structure and dynamics. The fossil record can serve as a test of these predictions because it preserves such information. The following description is divided into ecological aspects of intrinsically stressful habitats, determinable in a single slice of ecological time, and the evolutionary consequences.

Ecology of habitats

Habitats recognized as intrinsically stressful usually are ecological islands with physical conditions, and hence floras, markedly different from those of surrounding areas. Physical conditions of the habitat strongly select against most plants. Those plants capable of growth under a particular kind of stress must be preadapted to the stress, having evolved tolerance mechanisms fortuitously in non-stressful habitats.

These kinds of habitats often are bounded by very sharp ecotones (Fig.5). If stress is induced by factors such as chemical composition of the substrate, the contact between the stress-tolerant vegetation and vegetation in adjacent non-stressful sites may be abrupt and non-

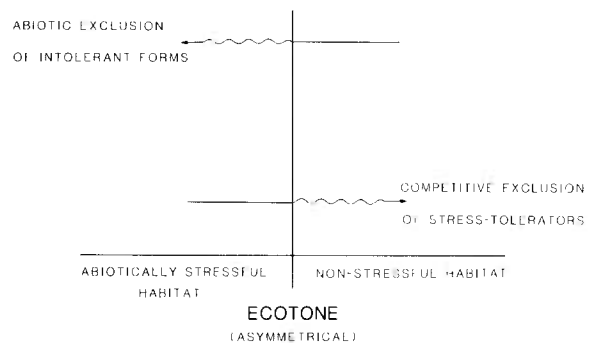


Fig.5. Physical and evolutionary relationship between intrinsically stressful and non-stressful habitats. Ecotone separating such habitats can be described as asymmetrical: most plants are excluded from intrinsically stressful habitats by inability to tolerate the stressful conditions; stress-tolerators are confined to intrinsically-stressful habitats by inability to compete effectively outside of these low-competition sites. To enter an intrinsically-stressful habitat a plant must be preadapted for stress tolerance. These sites become species sinks, enclosing a low-diversity, specialized flora.

gradational. Only occasionally will there be clinal contact between stressful and non-stressful sites. Examples of sharp contacts are found between serpentine and adjacent non-serpentine vegetation (Mason, 1946; Kruckeberg, 1969, 1984), *Taxodium-Nyssa* swamps and surrounding vegetation in non-flooded areas (Hall and Penfound, 1943; Penfound, 1952; Monk, 1966; Schlesinger, 1978), between plants of peat bogs and adjacent mineral soils in Malaysia (Anderson, 1983), mangrove vegetation in areas of contact with dry-land forest (Barbour, 1970; Semeniuk, 1985), and the contact between tailing soils of metal mines and adjacent "normal" soils (Bradshaw and McNeilly, 1981).

These ecotones can be described as asymmetrical. Individual plants are restricted from growth in intrinsically stressful sites by their inability to tolerate the physical conditions of the habitat. In contrast, plants that are characteristic of stressful habitats rarely are successful in non-stressful habitats because they are inferior competitors, perhaps due to lowered growth rates or changes in resource allocation from reproduction to stress-tolerance mechanisms (Parsons, 1968). Where it has been investigated, plants of serpentine substrates (Kruckeberg, 1984), mangrove or other saline habitats (Barbour, 1970), heavy metal substrates (Bradshaw and McNeilly, 1981, and papers cited therein), or swamps (Grime, 1979), grow better in normal soils than in those characteristic of the intrinsically stressful sites they normally occupy. The species or ecotypes largely confined to the stressful habitats are capable of tolerating the conditions; they do better under non-stressful conditions, if competitors are removed, but otherwise are excluded from non-stressful sites by competition with non-tolerant forms.

Because of the high levels of selection against most plants in these habitats, biomass and taxonomic diversity often are low. The result is considerable open physical space or limited niche partitioning. Competition has been difficult to document, although the majority of ecologists appear to believe it exists and

is important in structuring some communities. Grime's assertion that competition is low in highly stressful sites has been corroborated for the Okefenokee Swamp (Schlesinger, 1978) and subalpine fell fields (Del Moral et al., 1985), and suggested by studies of saline habitats (Barbour, 1970) and metal mine tailings sites (Bradshaw and McNeilly, 1981). From their observations, Del Moral et al. (1985) suggest that plants in intrinsically stressful habitats actually facilitate each others growth by creating protected sites where nutrient accumulation is increased and harshness of the physical environment reduced. This contrasts with high competition sites where expropriation of resources is the rule.

Plants of intrinsically stressful habitats have reduced rates of biomass accumulation (Grime, 1979). Corroboration comes from comparative studies, such as those cited previously, that show stress-tolerant plants to have higher rates of biomass accumulation in "normal" soils than in soils from stressful sites, if competitors are excluded. These studies do not utilize Grime's standardized methods but suggest that his conclusions are largely correct.

As a result of these ecological characteristics, intrinsically stressful environments can be considered species "sinks". Many species or ecotypes capable of exploiting these sites are confined to them by the inability to compete under more favorable conditions. The stressful environments tend to accumulate a low-diversity, specialized flora of stress-tolerant species. The local distinctiveness of the flora from an intrinsically stressful habitat is highly modified by two major factors. The severity of the stress relative to conditions in surrounding habitats strongly influences the number of marginally-tolerant individuals from adjacent populations that can exploit the stressful habitat. The areal extent of the intrinsically stressful habitat and proximity to similar sites control, in part, the amount of migration among sites. In extensive stressful settings, such as deserts or brackish coastal regions, the flora may be cosmopolitan but restricted to the stressful areas. In areas

where stressful conditions occur in isolated patches of small areal extent, such as many of the serpentine areas of the western U.S., many narrow endemics occur (Mason 1946).

Evolutionary consequences

The key evolutionary feature of intrinsically stressful habitats is the strong selection exerted by physical factors *against* intolerant forms. Under these conditions stress-tolerance does not develop gradually within non-tolerant populations; the critical traits permitting growth in these stressful habitats were not created by selection for stress tolerance, which is adaptation, *sensu* Lewontin (1978). Rather, a phenotypic preadaptation within the ancestral population permits nonadaptive entry of individuals to such sites, from which a new population is founded. This is a major evolutionary consequence of the natural bounding of intrinsically stressful habitats by selective filters. Individuals must possess a preadapted phenotype that confers tolerance to the specific stress before they are dispersed into the habitats; i.e., they must possess nonaptations or exaptations (Gould and Vrba, 1982; Fiedler, 1985).

Experimental studies of the ecology and genetics of these phenomena confirm the interpretations, particularly of stress-tolerant populations on mine-tailing soils enriched in heavy metals and on serpentine substrates (Bradshaw and McNeilly, 1981; Kruckeberg, 1984; Fiedler, 1985). Low interspecific competition in the early phases of population establishment permits survival of stress tolerators that otherwise may be poor competitors. Establishment of a large breeding population depends almost solely on a population growth rate greater than 1, which is *n*-selection. As population size builds, intraspecific fitness effects will result in a rising importance of *w*-selection, but not to levels found in non-stressful sites. These intervals of low competition may be quite protracted in intrinsically stressful habitats and permit fixation of derived traits that may deviate quite significantly from those in the

ancestral taxa. Once a breeding population is established in a stressful environment micro-evolutionary change may increase its threshold of stress tolerance. It also is possible that, if extrinsic conditions remain stable for extended periods, the level of interspecific competition would rise gradually, the extent of this being controlled by the local disturbance regime and nature of the stress agents.

Fossil record of swamps

There is an extensive fossil record of floras from intrinsically stressful environments, particularly deltaic or coastal plain swamps and shoreline habitats (Fig.6). Desert, arctic-alpine, periglacial, or other kinds of vegetation from environments not specific to lowland areas are rarely preserved as fossils. Because intrinsically-stressful habitats often are spatially disjunct they draw much of their flora locally from non-stressful surrounding environments. As a consequence, edaphically similar environments in different parts of the world often contain distinctly different floras (Elsol, 1985). This can be assumed to be true for intrinsically stressful environments of the past. Interpretation requires understanding the nature of the stress, the physical extent of the habitat, and also the taxonomic composition of the surrounding vegetation, which may contain the ancestors of many of the stress-tolerant species. In order to understand the dynamics of intrinsically-stressful ecosystems over long time spans, it is necessary for a particular kind of habitat and flora to have a reasonably dense stratigraphic record.

Freshwater swamps

Swamps are intrinsically-stressful environments due to periodic flooding, resultant reduction of oxygen supplies to plant roots, and associated factors such as low pH and low nutrient availability. Swamp vegetation is common in the fossil record, represented by coals, organic shales, or completely premineralized peat beds, and by non-fossiliferous gleyed clayey soils. In many cases it is possible

| | SWAMP FLORAS | MANGROVE FLORAS |
|---------------|---|--|
| TERTIARY | Taxodiaceous swamps [3,7,9,11,16,17,18,28,29,33,37,38] | Rise of extant angiosperm [15] mangrove families |
| CRETACEOUS | <i>Tempskye</i> coastal swamps [27,35] | <i>Pseudofranelopsis</i> (gymnosperm) [16,26] <i>Walchseia</i> (fern) [2,5] |
| JURASSIC | | <i>Pechydermophyllum</i> (gymnosperm) [10,24] |
| TRIASSIC | <i>Lingulellum</i> coastal [25] swamps (Australia) | <i>Pleuromeia</i> (lycopad) [24,25] |
| PERMIAN | <i>Glossopteris/Gangamopteris</i> [26] swamps (Australia) | |
| CARBONIFEROUS | Pennsylvanian coal and [1,6,19,20,21,22,32] clastic swamps | Cardaite (gymnosperm) [4,23] |
| | Price Farmation (Virginia) [14,30] coal swamps | |
| | <i>Recophyton</i> swamps [31] | |
| DEVONIAN | Rhynie Chert [8,12,13,34] | |

Fig.6. Plant assemblages of intrinsically-stressful environments in the fossil record. Sample is representative, not exhaustive. Data are drawn from the following sources: 1. Batenburg, 1982; 2. Batten, 1975; 3. Christophel, 1976; 4. Cridland, 1964; 5. Daber, 1968; 6. DiMichele et al., 1985; 7. Elsik, 1978; 8. Gensel and Andrews, 1984; 9. Hall and Penfound, 1943; 10. Harris, 1965; 11. Hickey, 1980; 12. Hoeg, 1967; 13. Kidston and Lang, 1921; 14. Kreisa and Bambach, 1973; 15. Muller, 1981; 16. Oldham, 1976; 17. Parker, 1975; 18. Penfound, 1952; 19. Peppers and Pfefferkorn, 1970; 20. Pfefferkorn and Thomson, 1982; 21. Phillips and Peppers, 1984; 22. Phillips et al., 1985; 23. Raymond and Phillips, 1983; 24. Retallack, 1975; 25. Retallack, 1977; 26. Retallack, 1980; 27. Retallack and Dilcher, 1981; 28. Rich and Goodrum, 1982; 29. Saulnier, 1950; 30. Scheckler, 1985; 31. Scheckler, 1986; 32. Scott, 1978; 33. Taggart and Cross, 1980; 34. Tasch, 1957; 35. Tidwell et al., 1976; 36. Upchurch and Doyle, 1981; 37. Wing, 1981; 38. Wolfe, 1980.

to compare swamp floras with those of contemporaneous non-swamp environments, permitting tests of the patterns predicted from studies of modern intrinsically stressful habitats. Taxonomic comparisons often are limited by different forms of preservation (anatomical vs. compression-impression) or different means of assessing the floras (palynology vs. megafos-

sils), but some equivalences have been established at the species level. A general picture emerges for modern and ancient swamps. Swamp floras are of markedly lower diversity than those of adjacent non-stressful sites, they contain species, genera and sometimes higher taxa that are absent or occur infrequently and in low abundances in non-stressful habitats,

and few species and genera abundant in adjacent non-stressful settings occur in swamps. Where taxonomic overlap does occur there often are subtle morphological differences between swamp and non-swamp forms.

Our sample of swamp vegetation covers eight stratigraphic intervals. In each case the swamp floras are of lower diversity and differ substantially or completely in taxonomic composition from contemporaneous non-swamp fossil floras (Fig.6). This pattern is consistent with these being naturally-bounded "ecological islands". Where stratigraphic patterns provide additional information, particularly for the Rhynie Chert, Pennsylvanian coal swamps and Tertiary taxodiaceous swamps, the swamp floras illustrate a much greater conservativeness than the surrounding vegetation. This is illustrated in taxonomic composition and, perhaps more interestingly, also in vegetational structure and in the predominant morphologies of the plants. For example, plants of the Rhynie Chert flora are morphologically simple, reflecting the grades reached by plants in their respective clades earlier in the Devonian. Pennsylvanian coal swamps remained the bastion of lower vascular plants, particularly heterosporous arborescent lycopsids, until the end of the Middle Pennsylvanian, a pattern of dominance established in the Mississippian. Species in these swamps were very long ranging stratigraphically and the clades to which they belonged appear to have included less morphological variation than clades centered in non-swamp, clastic-substrate lowlands. The Tertiary and Recent swamps dominated by *Taxodium*, *Glyptostrobus*, and, in some cases, *Metasequoia*, parallel the Pennsylvanian coal swamps. There is regional and stratigraphic variation in floristic composition but there also is a persistent dominance-diversity structure and conservative composition. This pattern contrasts with the taxonomically distinct, much more variable non-swamp vegetation throughout the Tertiary and Holocene.

Knoll (1985) suggests that swamps may preserve a relictual flora, but in a special

sense. These environments undergo periodic colonization with establishment of a flora drawn mostly from ancestral stock in contemporary non-swamp habitats. Swamp vegetation then persists, semi-isolated from species exchange with non-swamp habitats, and develops its own swamp-centered patterns. Once a lineage is established in swamps the rate of morphological evolution is slowed relative to lineages in non-stressful habitats by environmental stress. This results in a progressively developing relictual character. This "clock" is reset during the next severe disturbance of these environments, at which time they are recolonized by plants drawn from the then-existing, contemporaneous, non-swamp flora, or from surviving swamp taxa. Our analysis lends strong support to this interpretation.

Saline swamps

Vegetation from coastal regions, where intrinsic abiotic stress presumably is induced by salinity and seasonal or long-term flooding, is preserved occasionally in the fossil record. All of the examples (Fig.6) are isolated "time windows". They illustrate low diversity floras comprised of species that occur rarely or not at all in the contemporaneous surrounding vegetation. In the coexisting lowland floras from non-stressful sites, diversity is higher and species are much less confined in their habitat distributions and cooccurrences with other taxa. For example, Harris (1965) encountered *Pachydermophyllum* at only 24 of 235 sites sampled in the Yorkshire Jurassic flora. The *Pachydermophyllum* assemblage has a totally distinct flora, very low diversity compared to the other sites, which may overlap vegetationally, and occurs in a distinct lithofacies (Retallack, 1977, 1983). This appears to be characteristic of most of the purported mangrove vegetation described from the fossil record.

Long-term dynamics of swamp habitats

The fossil record provides a means to assess the long-term dynamics of ecosystems structured by intrinsic abiotic stress. In so doing,

additional characteristics of these environments may be discovered that are not obvious if investigation is restricted to single slices of time. The most continuous record of intrinsically stressful habitats is that of Pennsylvanian-age coal swamps from the Euramerican region. The plants of these deposits are anatomically preserved in coal balls (permineralized structural peat) and their morphology and systematics are known as well, or better, than those of any geological period before the Quaternary. In addition, great strides have been made in recent years in understanding the paleoecology and biostratigraphic distribution of Pennsylvanian plants, and the climatic and tectonic factors that may have affected their distributions (see Phillips and Cecil, 1985). Pennsylvanian coal-swamp vegetation has been characterized quantitatively from 32 coal seams, based on megafossils, and over 150 coal seams, based on palynology (Peppers, 1970, 1979, 1985; Phillips et al., 1974; Phillips et al., 1985).

Coal-swamp vegetation differed greatly from that of non-swamp habitats in taxonomic composition and structure (dominance-diversity patterns, etc.). This difference was greatest during the Early and Middle Pennsylvanian, when lycopods and/or cordaites dominated coal-swamp floras, and pteridosperms, ferns and sphenopsids dominated non-swamp floras (Scott, 1978; Pfefferkorn and Thomson, 1982). The distinction decreased significantly in the Late Pennsylvanian, when both peat swamps and clastic environments were fern and pteridosperm dominated (Fig.3). The difference increased again in the latest Pennsylvanian and earliest Permian as clastic environments became gymnosperm, especially conifer, dominated, and swamps retained their archaic character (Winston, 1983; Galtier and Phillips, 1985).

The taxonomic composition and community structure of coal swamps did not change at a continuous, uniform rate during the Pennsylvanian. Rather, it changed little for relatively long periods of time, then underwent rapid changes in dominance-diversity pattern and

species composition during short intervals (Fig.3) (Phillips et al., 1985).

The rise of tree-fern dominated vegetation is detected palynologically (Peppers, 1979) and in clastic-compression megafossil assemblages (Pfefferkorn and Thomson, 1982) well before it is detected with coal balls. This suggests that the fern radiation began in non-swamp habitats. The pattern is similar for the Late Pennsylvanian rise of the coniferophytes, which appear in clastic environments before they can be detected in coal swamps (Winston, 1983).

The sequential stratigraphic change from one major coal-swamp plant association to the next is correlated with inferred changes in regional climate and/or with changes in regional and global tectonics (Cecil et al., 1985; Phillips et al., 1985). The ultimate demise of Euramerican coal-swamp vegetation in the Permian may reflect continuing cyclical, and increasingly severe climatic changes (Parrish et al., in press).

This suggests a major role for extrinsic abiotic stress in the long-term dynamics of intrinsically stressful habitats. Coal swamps were periodically disrupted and even momentarily eliminated by severe extrinsic stress (Figs. 2 and 3), breaking up internal species associations and the low levels of niche partitioning that may have evolved. It was during and immediately after these times of community disruption that reorganization of the coal-swamp assemblage occurred. With each major disruption there appeared an opportunity for invasion of the swamps by preadapted tolerant forms, or for establishment of new taxa evolved from swamp-centered ancestors.

Swamps dominated by the Taxodiaceae and other conifers during the Tertiary appear to conform to the same basic patterns of organization, invasion resistance, and occasional disruption as Pennsylvanian coal swamps. These swamps are taxonomically heterogeneous in time and space, and their stratigraphic record has not been studied as intensively as that of late Paleozoic swamps. However, the similarity in long-term dynamics is striking, which,

considering the totally different floras of these time periods, suggests that basic ecological controls on swamp dynamics transcend the taxonomic composition of those swamps.

The fossil record confirms the generality of patterns observed in modern intrinsically stressful habitats. The foundation of our understanding of these environments comes from studies of extant plants in which factors controlling colonization of and evolution in intrinsically stressful sites can be evaluated. The fossil record enhances our understanding of the long-term dynamics of these ecosystems and the relationship of these dynamics to evolution.

Once groups have established successfully in intrinsically stressful environments, they appear to undergo little evolutionary change. The reasons for this are not entirely clear. Because of the relative physical homogeneity of intrinsically stressful sites, once a relatively large flora and large population sizes have developed there may be little ecological opportunity for evolutionary divergence. Even low levels of competition, when combined with physical stress, may be sufficient in such settings to preclude establishment of most invaders and to inhibit significant morphological evolution within indigenous clades.

Lastly, the fossil record of swamps suggests that floras of intrinsically stressful habitats are susceptible to extinction of a large proportion of their biota much more readily than the vegetation in non-stressful habitats. This is predictable, although not easily testable, from modern stress-tolerant vegetation. Because of the low competitive ability of the stress tolerators in non-stressful sites, and because intrinsically-stressful habitats often are disjunct spatially, opportunities for migration are limited. Tolerant forms are effectively trapped in local intrinsically stressful sites as external conditions change (see also Knoll and Niklas, this issue).

Summary and discussion

Paleoecology is a central theme in this analysis, providing the means to circumscribe "selective landscapes" of the past. The relationship between abiotic stress and evolution can be understood only when organisms, living or fossil, are studied within their respective ecological spheres. This is the basis of the ability to test, with the fossil record, hypotheses constructed from data on modern plants and animals. There appears to be a fundamental relationship between abiotic stress and evolution, independent of geological time. However, changes, many of enormous scope, in vascular plant taxa and in the ecosystems they created during the Phanerozoic have made many aspects of these patterns very dependent on when in geological time they occurred.

Common ground of extrinsic and intrinsic abiotic stress

Extrinsic stress impinges on ecosystems, disrupting them by causing differential extinction, migration and fragmentation of populations. The fossil record contributes greatly to our understanding of the effects of this kind of stress because these effects are long-term, often on a geological-time scale, or involve catastrophic events that we can infer but not study directly today. Intrinsic abiotic stress creates areas or habitats that are physically inhospitable to almost all plants, selecting strongly against forms not tolerant of the stress agents. Much of the ecological and evolutionary dynamics of intrinsically stressful systems can be constructed from data on extant environments, although the fossil record adds elements not detectable on an ecological-time scale.

These otherwise different phenomena are tied together by a common thread. Abiotic stress either creates (extrinsic) or delimits (intrinsic) habitats that are momentarily in severe disequilibrium, such that a great deal of potential resource is unutilized. In these en-

vironments levels of interspecific competition are reduced, and opportunities for divergent evolution created. Survival of forms capable of locating targets of opportunity is enhanced because they may not be eliminated by local resource competition and can diverge rapidly from ancestral populations.

Evolution and abiotic stress

Intrinsically stressful environments as new adaptive zones

Intrinsically stressful habitats present conditions under which macroevolutionary, saltational phenotypic changes have a greater likelihood of surviving than in non-stressful habitats. The low interspecific competition found in intrinsically stressful sites permits establishment of individuals and populations that deviate significantly from ancestral morphology if the derived forms can tolerate the stress and if reproductive capacity is not compromised. Traits not associated with stress tolerance or reproduction should be able to vary widely particularly during the low-density phases of initial colonization and population establishment. Rapid change may occur through drift (Carson, 1982; Carson and Templeton, 1984) or by truly saltational changes controlled by genes with major phenotypic effect (Hilu, 1983; Gottlieb, 1984) because of reduced (or no) selection.

This argument can be extrapolated, *by analogy*, to certain types of macroevolutionary events that occurred in the geological past. In much of the past, particularly before the late Paleozoic, a great proportion of the land surface may have been unvegetated (Cross, 1975), fundamentally inaccessible to the vascular plants existing at the time due to constraints of their physiology and reproductive biology. Thus, many habitats that we now characterize as non-stressful were intrinsically stressful relative to the earth's vegetation of some past time.

The fundamental modern organizational plans in vascular plants (Classes: Isoetopsida, Selaginellopsida, Lycopodiopsida, Progymnospermopsida, Spermatopsida, Arthrospida,

Filicopsida) all originated during the Late Devonian and Early Mississippian. This represents a series of phenotypic breakthroughs that made accessible to plants resources previously unavailable to their ancestors, due in large part to intrinsic physical stress. The dynamics of these evolutionary events may have been very similar to those that accompany colonization of intrinsically stressful habitats today. Preadaptations permitted the initial "colonization", the fundamental phenotypic breakthrough, into conditions with little or no interspecific competition for resources, while densities remained low. The radiation of these lineages then occurred under little or no selection, permitting diversification to occur limited primarily by the breadth of the new adaptive zone (Simpson, 1953). We do not see events of such morphological/taxonomic magnitude occur today because of changes in the selective landscapes and the spectrum of existing morphologies. Thus, intrinsically stressful habitats constitute a unique analogy for the dynamics of these past events.

The confinement of these major macroevolutionary events to such a narrow spectrum of geological time may be a consequence of two factors. First, ancestral form places progressive architectural and developmental constraints on descendants (Gould and Lewontin, 1979). This results in reduced morphological "distance" between ancestor and descendant with continuing cladogenesis. Therefore, there will be progressively fewer occurrences of highly deviant descendant forms through time, i.e., less raw material. Second, with each colonization and subsequent exploitation of a new adaptive zone the spectrum of major habitats (resources) that remain as sites of low or no competition narrows. There is progressive filling of ecological-adaptive space through time (Valentine, 1980). Consequently, the likelihood that a preadapted deviant morphology will locate such a site declines through time.

This implies that, as a generality, *n*-selection (sensu Arthur, 1984) is the critical element in the origin and establishment of many new

species, particularly if a large ancestor-descendant discontinuity exists. Subsequent *w*-selection and filling of adaptive space combine to slow any one adaptive radiation and to reduce the frequency of major breakthroughs through time. In this context we are not overextending the concepts developed to explain evolutionary events in intrinsically stressful environments. Rather, we believe that the *processes* controlling aspects of evolution in these settings are general ones that have broader explanatory value when considered in specific contexts.

Simpson (1953) argued that adaptive evolution was the process driving exploitation of new adaptive zones. Hence, in his formulation, an "adaptive" breakthrough is simply a rapid, adaptively-driven shift from the old mode of life to the new one. Population genetics suggests that this can occur by a combination of drift and weak selection in small populations (Wright, 1982). Evidence from intrinsically stressful environments suggests that non-adaptive entry to new adaptive zones is at least as likely an explanation of major phenotypic breakthroughs as their attribution to directional selection.

Extrinsic abiotic stress in the evolutionary hierarchy

Extrinsic stress has been a major factor in the evolution of vascular plants. Widespread destruction or alteration of ecosystems give extrinsic stress a very different role than processes described in traditional formulations of adaptive evolution. By periodically disrupting ecosystems through extinction or enforced migration, times of extrinsic stress are qualitatively different from more stable periods. This indicates that simple extrapolation of unbroken, competition-mediated adaptation is probably inadequate to explain phylogenetic patterns. Extrinsic stress is part of a hierarchy of processes that mediate evolution.

The search for this hierarchy of natural processes in evolution has long been a major concern in the formulation of "macroevolution" hypotheses (e.g., Schindewolf, 1950; Stan-

ley, 1975; Gould and Eldredge, 1977; Valentine, 1980). Recently an explicit case has been made (Gould, 1985; Jablonski, 1986) for the role of extrinsic stress in this hierarchy. Gould (1985) described three evolutionary "tiers". The "third tier" is periodic mass extinctions, which can be expanded to include any severe extrinsic stress as we have defined it here. It is the ecological consequences of mass extinction rather than the extinction itself that are important to evolution. Similar consequences can result from mass migration, mixed with extinction. If the scope of this "third tier" is broadened the available evidence from the fossil record of plants lends strong support to the concept.

Knoll (1984) suggested that competition for resources has been a major process causing plant extinction and stimulating the evolution of new form. This relationship of competition to evolution and extinction is essentially the Red-Queen hypothesis of Van Valen (1973), which integrates coevolution and competition. In order to demonstrate competition convincingly as a primary agent of evolution on a geological time scale, it is necessary to hypothesize ecological replacement in kind in a stable physical-climatic setting. Simple correlation of rise in one species or group with decline in another is not sufficient to demonstrate competition. During periods of changing physical conditions, such as the Permian, late Paleogene, or Pleistocene, extrinsic stress will reduce the effectiveness with which indigenous species compete locally. As a consequence, they may be displaced by migrants from other climatic zones, a competitive replacement, but one made possible by extrinsic abiotic stress. This is the essence of the "vegetational inertia" pattern discussed by Cole (1985). At this level and under these conditions, competition is in effect the final blow to species at the edges of their tolerance limits. Competitive displacement has been made possible by changes in the physical environment. Thus, during times of extrinsic stress the relative importance of physical processes and competition in mediating evolution appears to be different from

periods of more stable environmental conditions; the result is visible in different proportions of micro- and macroevolution under these different regimes.

Acknowledgments

W. Geoffrey Spaulding, William Pfitsch and Jeffrey H. Braatne, University of Washington, Scott L. Wing, Smithsonian Institution, Jack A. Wolfe and Garland Upchurch, U.S. Geological Survey, Andrew H. Knoll, Harvard University provided critical comments on the manuscript and valuable discussion. For discussion of ideas we also thank Robyn J. Burnham, University of Washington, Ralph Chapman, John Damuth, Francis M. Hueber, Nicholas Hotton and Sergius H. Mamay, Smithsonian Institution. Any errors of fact, interpretation or omission are ours. Thanks go to Mary Parrish, Smithsonian Institution, for drafting the figures. T.L. Phillips acknowledges partial support of this research by NSF Grant EAR 83-13094 entitled "The Quantitative Analysis of Middle and Upper Pennsylvanian Coal-Swamp Vegetation in Relation to Coal in the United States and China (Stephanian)".

References

- Alberch, P., 1982. Developmental constraints in evolutionary processes. In: J.T. Bonner (Editor), *Evolution and Development*, Dahlem Konferenzen. Springer, New York, N.Y., pp.313-332.
- Alvarez, L.W., Alvarez, W., Asaro, F. and Michael, H.W., 1980. Extraterrestrial causes for the Cretaceous-Tertiary extinctions. *Science*, 208: 1095-1108.
- Anderson, J.A.R., 1983. The tropical peat swamps of western Malesia. In: A.J.P. Gore (Editor), *Mires: Swamp, Bog, Fen and More (Ecosystems of the World, 4B)*. Elsevier, Amsterdam, pp.181-199.
- Arthur, W., 1984. *Mechanisms of Morphological Evolution*. Wiley, New York, N.Y., 275 pp.
- Banks, H.P., 1980. Floral changes in the Siluro-Devonian. In: D.L. Dilcher and T.N. Taylor (Editors), *Biostratigraphy of Fossil Plants*. Dowden, Hutchinson and Ross, Stroudsburg, Pa., pp.1-24.
- Barbour, M.G., 1970. Is any angiosperm an obligate halophyte? *Am. Midl. Nat.*, 84: 105-120.
- Barrett, G.W., Van Dyne, G.M. and Odum, E.P., 1976. Stress ecology. *Bioscience*, 26: 192-194.
- Batenburg, L.H., 1982. "Compression species" and "petrification species" of *Sphenophyllum* compared. *Rev. Palaeobot. Palynol.*, 36: 335-359.
- Batten, D.J., 1975. Wealden paleoecology from the distribution of plant fossils. *Proc. Geol. Assoc.*, 85: 433-458.
- Beerbower, R., 1985. Early development of continental ecosystems. In: B. Tiffney (Editor), *Geological Factors and the Evolution of Plants*. Yale Univ. Press, New Haven, Conn., pp.47-91.
- Berger, A., Imbrie, J., Hays, J., Kukla, G. and Salzman, B. (Editors), 1984. *Milankovich and Climate: Understanding the Response to Astronomic Forcing*. Reidel, Dordrecht, 895 pp.
- Bradshaw, A.D. and McNeilly, T., 1981. *Evolution and Pollution*. (Studies in Biology, 130). Edward Arnold, London, 76 pp.
- Broadhurst, F.M., Simpson, I.M. and Hardy, P.G., 1980. Seasonal sedimentation in the Upper Carboniferous of England. *J. Geol.*, 88: 639-651.
- Caputo, M.V. and Crowell, J.C., 1985. Migration of glacial centers across Gondwana during Paleozoic Era. *Geol. Soc. Am. Bull.*, 96: 1020-1036.
- Carson, H.L., 1982. Speciation as a major reorganization of polygenic balances. In: C. Barigozzi (Editor), *Mechanisms of Speciation*. Liss, New York, N.Y., pp.411-433.
- Carson, H.L., 1985. Unification of speciation theory in plants and animals. *Syst. Bot.*, 10: 380-390.
- Carson, H.L. and Templeton, A.R., 1984. Genetic revolutions in relation to speciation phenomena: the founding of new populations. *Annu. Rev. Ecol. Syst.*, 15: 97-131.
- Cecil, C.B., Stanton, R.W., Neuzil, S.G., Dulong, F.T., Rupert, L.F. and Pierce, B.S., 1985. Paleoclimate controls on Late Paleozoic sedimentation and peat formation in the central Appalachian Basin. *Int. J. Coal Geol.*, 5: 195-230.
- Chaloner, W.G. and Lacey, W.S., 1973. The distribution of Late Paleozoic floras. In: *Organisms and Continents Through Time*. *Spec. Pap. Palaeontol.*, 12: 271-289.
- Chaloner, W.G. and Meyen, S.V., 1973. Carboniferous and Permian floras of the northern continents. In: A. Hallam (Editor), *Atlas of Palaeobiogeography*. Elsevier, Amsterdam, pp.169-186.
- Chaloner, W.G. and Sheerin, A., 1979. Devonian macrofloras. *Spec. Pap. Palaeontol.*, 23: 145-161.
- Christophel, D.C., 1976. Fossil floras of the Smoky Tower locality, Alberta, Canada. *Palaeontographica*, 157 B: 1-43.
- Cole, K., 1985. Past rates of change, species richness, and a model of vegetational inertia in the Grand Canyon, Arizona. *Am. Nat.*, 125: 289-303.
- Cridland, A.A., 1964. *Ameylon* in American coal-balls. *Palaeontology*, 17: 186-209.
- Cross, A.T., 1975. The Dunkard in perspective: geology, sedimentation and life. In: J.A. Barlow (Editor), *The Age of the Dunkard*. W.Va. Geol. Econ. Surv., Morgantown, W.Va., pp.297-299.
- Cross, A.T. and Taggart, R.E., 1982. Causes of short-term

- sequential changes in fossil plant assemblages: some considerations based on a Miocene flora from the northeast United States. *Ann. Mo. Bot. Gard.*, 69: 676–734.
- Daber, R., 1968. A *Weichselia*–*Stiehleria*–*Matoniaceae* community within the Quedlinburg Estuary of Lower Cretaceous age. *J. Linn. Soc. Bot.*, 61: 75–85.
- Davis, M.B., 1976. Pleistocene biogeography of temperate deciduous forests. *Geosci. Man*, 13: 13–26.
- Del Moral, R., Clappitt, C.A. and Wood, D.M., 1985. Does interference cause niche differentiation? Evidence from subalpine plant communities. *Am. J. Bot.*, 72: 1891–1901.
- DiMichele, W.A. and Phillips, T.L., 1985. Arborescent lycopod reproduction and paleoecology in a coal-swamp environment of late Middle Pennsylvanian age (Herrin Coal, Illinois, U.S.A.). *Rev. Palaeobot. Palynol.*, 44: 1–26.
- DiMichele, W.A., Phillips, T.L. and Peppers, R.A., 1985. The influence of climate and depositional environment on the distribution and evolution of Pennsylvanian coal-swamp plants. In: B.H. Tiffney (Editor), *Geological Factors and the Evolution of Plants*. Yale Univ. Press, New Haven, Conn., pp.223–256.
- Eldredge, N. and Gould, S.J., 1972. Punctuated equilibria: an alternative to phyletic gradualism. In: T.J.M. Schopf (Editor), *Models in Paleobiology*. Freeman and Cooper, San Francisco, Calif., pp.82–115.
- Elsik, W.C., 1978. Palynology of Gulf coast lignites: the stratigraphic framework and depositional environments. In: W.R. Kaiser (Editor), *Proceedings Gulf Coast Lignite Conference: Geology, Utilization and Environmental Aspects*. Tex. Bur. Econ. Geol., Rep. Invest., 90: 21–32.
- Elsol, J.A., 1985. Illustrations of the use of higher plant taxa in biogeography. *J. Biogeogr.*, 12: 433–444.
- Falconer, D.S., 1981. *Introduction to Quantitative Genetics*. Longman, New York, N.Y., 2nd ed, 340 pp.
- Fiedler, P.L., 1985. Heavy metal accumulation and the nature of edaphic endemism in the genus *Calochortus* (Liliaceae). *Am. J. Bot.*, 72: 1712–1718.
- Foster, C.B., 1982. Spore-pollen assemblages of the Bowen Basin, Queensland (Australia); their relationship to the Permian/Triassic boundary. *Rev. Palaeobot. Palynol.*, 36: 165–183.
- Fredericksen, N.O., 1972. The rise of the Mesophytic flora. *Geosci. Man*, 4: 17–28.
- Galtier, J.L. and Phillips, T.L., 1985. Swamp vegetation from Grand Croix (Stephanian) and Autun (Autunian), France and comparisons with coal-ball peats of the Illinois Basin. C.R. IXth Int. Congr. Carboniferous Stratigr. Geol., 4: 13–24.
- Gensel, P.G. and Andrews, H.N., 1984. *Plant Life in the Devonian*. Praeger, New York, N.Y., 380 pp.
- Gillespie, W.H. and Pfefferkorn, H.W., 1979. Distribution of commonly occurring plant megafossils in the proposed Pennsylvanian System stratotype. In: K.J. Englund et al. (Editors), *Proposed Pennsylvanian System Stratotype, Virginia and West Virginia*. 9th Int. Congr. Carboniferous Stratigr. Geol., Guidebook Field Trip No.1, pp.87–96.
- Gillespie, W.H., Hennen, G.J. and Balasco, C., 1975. Plant megafossils from Dunkard strata in northwestern West Virginia and southwestern Pennsylvania. In: J.A. Barlow (Editor), *The Age of the Dunkard*. W. V. Geol. Econ. Surv., Morgantown, W.Va., pp.223–244.
- Gottlieb, L.D., 1984. Genetics and morphological evolution in plants. *Am. Nat.*, 123: 681–709.
- Gould, S.J., 1977. *Ontogeny and Phylogeny*. Belknap Press, Cambridge, Mass., 501 pp.
- Gould, S.J., 1985. Rates of evolution. *Paleobiology*, 11: 2–12.
- Gould, S.J. and Eldredge, N., 1977. Punctuated equilibria: the tempo and mode of evolution reconsidered. *Paleobiology*, 3: 115–151.
- Gould, S.J. and Lewontin, R.C., 1979. The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme. *Proc. R. Soc. London B*, 205: 581–598.
- Gould, S.J. and Vrba, E.S., 1982. Exaptation — a missing term in the science of form. *Paleobiology*, 8: 4–15.
- Grime, J.P., 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *Am. Nat.*, 111: 1169–1194.
- Grime, J.P., 1979. *Plant Strategies and Vegetation Processes*. Wiley, New York, N.Y., 222 pp.
- Hall, T.F. and Penfound, W.T., 1943. Cypress-gum communities in the Blue Girth Swamp near Selma, Alabama. *Ecology*, 24: 208–217.
- Harris, T.M., 1965. Dispersed cuticles. *Palaeobotanist*, 14: 102–105.
- Helenurm, K. and Ganders, F.R., 1985. Adaptive radiation and genetic differentiation in Hawaiian *Bidens*. *Evolution*, 39: 753–765.
- Hickey, L.J., 1980. Paleocene stratigraphy and flora of the Clark's Fork Basin. In: *Early Cenozoic Paleontology and Stratigraphy of the Bighorn Basin, Wyoming*. Univ. Michigan Pap. Paleontol., 24: 33–49.
- Hickey, L.J., 1981. Land plant evidence compatible with gradual, not catastrophic, change at the end of the Cretaceous. *Nature*, 292: 529–531.
- Hickey, L.J., 1984. Changes in the angiosperm floras across the Cretaceous/Tertiary boundary. In: W.A. Berggren and J.A. Van Couvering (Editors), *Catastrophes in Earth History*. Princeton Univ. Press, Princeton, N.J., pp.279–313.
- Hickey, L.J. and Doyle, J.A., 1977. Early Cretaceous fossil evidence for angiosperm evolution. *Bot. Rev.*, 43: 3–104.
- Hilu, K.W., 1983. The role of single gene mutations in the evolution of flowering plants. *Evol. Biol.*, 16: 47–122.
- Hoeg, O.A., 1967. Psilophyta. In: E. Boureau (Editor), *Traité de Paléobotanique*. Masson, Paris, pp.191–433.
- Jablonski, D., 1986. Background and mass extinctions: the alternation of macroevolutionary regimes. *Science*, 231: 129–133.
- Johnson, J.G., Klapper, G. and Sandberg, C.A., 1985. Devonian eustatic sealevel fluctuations in Euramerica. *Geol. Soc. Am. Bull.*, 96: 567–587.
- Kidston, R. and Lang, W.H., 1921. On Old Red Sandstone

- plants showing structure, from the Rhynie Chert bed, Aberdeenshire. Part V. The Thallophyta occurring in the peat bed; the succession of the plants through the vertical section of the beds, and the conditions of accumulation and preservation of the deposit. *Trans. R. Soc. Edinburgh*, 52: 831-854.
- Knoll, A.H., 1984. Patterns of extinction in the fossil record of vascular plants. In: M. Nitecki (Editor), *Extinctions*. Univ. Chicago Press, Chicago, Ill., pp.21-68.
- Knoll, A.H., 1985. Exceptional preservation of photosynthetic organisms in silicified carbonates and silicified peats. *Philos. Trans. R. Soc. London B*, 311: 111-122.
- Knoll, A.H. and Niklas, K.J., 1987. Adaptation, plant evolution, and the fossil record. *Rev. Palaeobot. Palynol.*, 50: 127-149.
- Knoll, A.H., Niklas, K.J. and Tiffney, B.H., 1979. Phanerozoic landplant diversity in North America. *Science*, 206: 1400-1402.
- Knoll, A.H., Niklas, K.J., Gensel, P.G. and Tiffney, B.H., 1984. Character diversification and patterns of evolution in early vascular plants. *Paleobiology*, 10: 34-47.
- Kreisa, R. and Bambach, R., 1973. Environments of deposition of the Price Formation (Lower Mississippian) in its type area, southwestern Virginia. *Am. J. Sci.*, 273-A: 326-342.
- Kruckeberg, A.R., 1969. Soil diversity and the evolution of plants, with examples from western North America. *Madroño*, 20: 129-154.
- Kruckeberg, A.R., 1984. California serpentines: flora, vegetation, geology, soils, and management problems. *Univ. Calif. Publ. Bot.*, 78: 1-180.
- Lande, R., 1985. Expected time for random genetic drift of a population between stable phenotypic points. *Proc. Natl. Acad. Sci. U.S.A.*, 82: 7641-7645.
- Levin, D.A. and Wilson, J.B., 1978. The genetic implications of ecological adaptations in plants. In: A. Freyseh and J. Woldendorp (Editors), *Structure and Functioning of Plant Populations North Holland*, Amsterdam, pp.75-98.
- Levitt, J., 1980. *Responses of Plants to Environmental Stress, Vol.1: Chilling, Freezing and High Temperature Stresses*. Academic Press, New York, N.Y., 2nd ed.
- Lewontin, R.C., 1978. *Adaptation*. *Sci. Am.*, 239: 156-169.
- Lowrey, T.K. and Crawford, D.J., 1985. Allozyme divergence and evolution in *Tetramolopium* (Compositae: Asteraceae) on the Hawaiian Islands. *Syst. Bot.*, 10: 64-72.
- Mamay, S.H., 1967. Lower Permian plants from the Arroyo Formation in Baylor County, north-central Texas. *U.S. Geol. Surv. Prof. Pap.*, 575-C: 120-126.
- Mamay, S.H., 1968. *Russellites*, new genus, a problematical plant from the Lower Permian of Texas. *U.S. Geol. Surv. Prof. Pap.*, 593-I, 12 pp.
- Mamay, S.H., 1975. *Sandrewia*, n. gen., a problematical plant from the Lower Permian of Texas and Kansas. *Rev. Palaeobot. Palynol.*, 20: 75-83.
- Mamay, S.H., 1976. Paleozoic origin of the Cycads. *U.S. Geol. Surv. Prof. Pap.*, 934, 48 pp.
- Mason, H.L., 1946. The edaphic factor in narrow endemism. I. The nature of environmental influences. *Madroño*, 8: 209-226.
- McLaren, D.J., 1983. Bolides and biostratigraphy. *Bull. Geol. Soc. Am.*, 94: 313-324.
- Meyen, S.V., 1982. The Carboniferous and Permian floras of Angaraland (a synthesis). *Biol. Mem.*, 7, 109 pp.
- Milner, A.R. and Panchen, A.L., 1973. Geographical variation in tetrapod faunas of the Upper Carboniferous and Lower Permian. In: D.H. Tarling and S.K. Runcorn (Editors), *Implications of Continental Drift to the Earth Sciences*, vol.1. Academic Press, New York, N.Y., pp.353-368.
- Monk, C.D., 1966. An ecological study of hardwood swamps in north-central Florida. *Ecology*, 47: 649-654.
- Muller, J., 1981. Fossil pollen records of extant angiosperms. *Bot. Rev.*, 47: 1-142.
- Nichols, D.J., Jarzen, D.M., Orth, C.J. and Oliver, P.Q., 1986. Palynological and iridium anomalies at Cretaceous-Tertiary boundary, south-central Saskatchewan. *Science*, 231: 714-717.
- Niklas, K.J., Tiffney, B.H. and Knoll, A.H., 1980. Apparent changes in the diversity of fossil plants. *Evol. Biol.*, 12: 1-89.
- Niklas, K.J., Tiffney, B.H. and Knoll, A.H., 1983. Patterns in vascular land plant diversification. *Nature*, 303: 614-616.
- Officer, C.B. and Drake, C.L., 1985. Terminal Cretaceous environmental events. *Science*, 227: 1161-1167.
- Oldham, T.C.B., 1976. Flora of the Wealden plant debris beds of England. *Palaeontology*, 19: 437-502.
- Olsen, E.C., 1979. Biological and physical factors in the dispersal of Permo-Carboniferous terrestrial vertebrates. In: J. Gray and A.J. Boucot (Editors), *Historical Biogeography, Plate Tectonics and the Changing Environment*. Oregon State Univ. Press, Corvallis, Oreg., pp.227-238.
- Paillet, F.L., 1982. The ecological significance of American chestnut [*Castanea dentata* (Marsh.) Borkh.] in the Holocene forests of Connecticut. *Bull. Torrey Bot. Club*, 109: 457-473.
- Parker, L.R., 1975. The paleoecology of the fluvial coal-forming swamps and associated floodplain environments in the Blackhawk Formation (Upper Cretaceous) of central Utah. *Brigham Young Univ. Geol. Stud.*, 22: 99-116.
- Parrish, J.M., Parrish, J.T. and Zeigler, A.M., in press. Permian-Triassic paleogeography and paleoclimatology and implications for Therapsid distributions. In: J. Roth, C. Roth and N. Hotton III (Editors), *The Biology and Ecology of Mammal-like Reptiles*. Smithsonian Press, Washington, D.C.
- Parrish, J.T., 1982. Upwelling and petroleum source beds, with reference to the Paleozoic. *Am. Assoc. Petrol. Geol. Bull.*, 66: 750-774.
- Parrish, J.T. and Curtis, R.L., 1982. Atmospheric circulation, upwelling and organic-rich rocks in the Mesozoic

- and Cenozoic Eras. *Palaeogeogr., Palaeoclimatol., Palaeoecol.*, 40: 31–66.
- Parrish, J.T., Zeigler, A.M. and Scotese, C.R., 1982. Rainfall patterns and the distribution of coals and evaporites in the Mesozoic and Cenozoic. *Palaeogeogr., Palaeoclimatol., Palaeoecol.*, 40: 67–101.
- Parsons, R.F., 1968. The significance of growth-rate comparisons for plant ecology. *Am. Nat.*, 102: 595–597.
- Penfound, W.T., 1952. Southern swamps and marshes. *Bot. Rev.*, 18: 413–446.
- Peppers, R.A., 1970. Correlation and palynology of coals in the Carbonate and Spoon Formations (Pennsylvanian) of the northeastern part of the Illinois Basin. *Ill. State Geol. Surv., Bull.*, 93, 173 pp.
- Peppers, R.A., 1979. Development of coal-forming floras during the early part of the Pennsylvanian in the Illinois Basin. In: *Guidebook to Field Trip 9, 9th Int. Congr. Carboniferous Stratigr. Geol.*, part 2, Invited Papers. *Ill. State Geol. Surv., Urbana, Ill.*, pp.8–14.
- Peppers, R.A., 1985. Comparison of miospore assemblages in the Pennsylvanian System of the Illinois Basin with those in the Upper Carboniferous of western Europe. *C.R. 9th Int. Congr. Carboniferous Stratigr. Geol.*, 2: 483–502.
- Peppers, R.A. and Pfefferkorn, H.W., 1970. A comparison of floras of the Colchester (No.2) Coal and Francis Creek Shale. In: W.H. Smith, R.B. Nance, M.E. Hopkins, R.G. Johnson and C.W. Shabica (Editors), *Depositional Environments in Parts of the Carbonate Formation — Western and Northern Illinois*. *Ill. State Geol. Surv., Guidebook Ser.*, 8: 61–74.
- Pfefferkorn, H.W. and Thomson, M.C., 1982. Changes in dominance patterns in Upper Carboniferous plant-fossil assemblages. *Geology*, 10: 641–644.
- Phillips, T.L. and Cecil, C.B., 1985. Paleoclimatic controls on coal resources of the Pennsylvanian System in North America — Introduction and overview of contributions. *Int. J. Coal Geol.*, 5: 1–6.
- Phillips, T.L. and DiMichele, W.A., 1981. Paleoecology of Middle Pennsylvanian age coal swamps in southern Illinois/Herrin Coal Member at Sahara Mine No.6. In: K.J. Niklas (Editor), *Paleobotany, Paleoecology and Evolution*. Praeger, New York, N.Y., pp.231–284.
- Phillips, T.L. and Peppers, R.A., 1984. Changing patterns of Pennsylvanian coal-swamp vegetation and implications of climatic control on coal occurrence. *Int. J. Coal Geol.*, 3: 205–255.
- Phillips, T.L., Peppers, R.A. and DiMichele, W.A., 1985. Stratigraphic and interregional changes in Pennsylvanian coal-swamp vegetation: environmental inferences. *Int. J. Coal Geology*, 5: 43–109.
- Phillips, T.L., Peppers, R.A., Avcin, M.J. and Laughnan, P.F., 1974. Fossil plants and coal: patterns of change in Pennsylvanian coal swamps of the Illinois Basin. *Science*, 184: 1367–1369.
- Pickett, S.T.A. and White, P.S., 1985. *The Ecology of Natural Disturbance and Patch Dynamics*. Academic Press, New York, N.Y., 472 pp.
- Rapport, D.J., Regier, H.A. and Hutchinson, T.C., 1985. Ecosystem behavior under stress. *Am. Nat.*, 125: 617–640.
- Raup, D.M., 1986. Biological extinction in earth history. *Science*, 231: 1528–1533.
- Raymond, A. and Phillips, T.L., 1983. Evidence for an Upper Carboniferous mangrove community. In: H.J. Teas (Editor), *Tasks for Vegetation Science*, Vol.8. Junk, The Hague, pp.19–30.
- Read, C.B. and Mamay, S.H., 1964. Upper Paleozoic floral zones and floral provinces of the United States. *U.S. Geol. Surv. Prof. Pap.*, 454-K, 35 pp.
- Remy, W., 1975. The floral changes at the Carboniferous — Permian boundary in Europe and North America. In: J.A. Barlow (Editor), *The Age of the Dunkard*. W. Va. Geol. Econ. Surv., Morgantown, W. Va., pp.305–344.
- Retallack, G.J., 1975. The life and times of a Triassic lycopod. *Alcheringa*, 1: 3–29.
- Retallack, G.J., 1977. Reconstructing Triassic vegetation of eastern Australasia: a new approach for the biostratigraphy of Gondwanaland. *Alcheringa*, 1: 247–277.
- Retallack, G.J., 1980. Late Carboniferous to Middle Triassic megafossil floras from the Sydney Basin. In: C. Herbert and R.J. Helby (Editors), *A Guide to the Sydney Basin*. *Geol. Surv. N.S.W. Bull.*, 26: 384–430.
- Retallack, G.J., 1983. Middle Triassic estuarine deposits near Benmore Dam, southern Canterbury and northern Otago, New Zealand. *J.R. Soc. N.Z.*, 13: 107–127.
- Retallack, G.J. and Dilcher, D.L., 1981. A coastal hypothesis for the dispersal and rise to dominance of flowering plants. In: K.J. Niklas (Editor), *Paleobotany, Paleoecology and Evolution*. Praeger, New York, N.Y., pp.27–77.
- Rich, F.J. and Goodrum, C.K., 1982. Paleocology and sedimentology of the Fort Union Formation, Harding County, South Dakota. *Proc. Fifth Rocky Mountain Coal Symp., Utah Geol. Mineral. Surv. Bull.*, 118: 158–162.
- Romer, A.S., 1973. Permian reptiles. In: A. Hallam (Editor), *Atlas of Palaeogeography*. Elsevier, Amsterdam, pp.159–167.
- Saulnier, H.S., 1950. The paleopalynology of the Fort Union coals of Red Lodge, Montana. Thesis. Univ. Massachusetts, Amherst, Mass., 62 pp.
- Scheckler, S.E., 1985. Origins of the coal-swamp biome: evidence from the southern Appalachians. In: *Geol. Soc. Am., Southeast. Sect., Tech. Abstr.*, 1985 Meeting, Knoxville, Tenn.
- Scheckler, S.E., 1986. Geology, floristics, and paleoecology of Late Devonian coal swamps from Appalachian Laurentia (U.S.A.). *Ann. Soc. Géol. Belg.*, 109: 209–222.
- Schindewolf, O.H., 1950. *Grundfragen der Paläontologie*. Schweizerbart, Stuttgart.
- Schindler, D.W., Mills, K.H., Malley, D.F., Findlay, D.L., Shearer, J.A., Davies, I.J., Turner, M.A., Linsey, G.A. and Cruikshank, D.R., 1985. Long-term ecosystem stress: the effects of years of experimental acidification on a small lake. *Science*, 228: 1395–1401.
- Schlesinger, W.H., 1978. Community structure, dynamics

- and nutrient cycling in the Okefenokee cypress swamp forest. *Ecol. Monogr.*, 48: 43–65.
- Scott, A.C., 1978. Sedimentological and ecological control of Westphalian B plant assemblages from west Yorkshire. *Proc. Yorkshire Geol. Soc.*, 41: 461–508.
- Scott, A.C. and Chaloner, W.G., 1983. The earliest fossil conifer from the Westphalian B of Yorkshire. *Proc. R. Soc. London B*, 220: 163–182.
- Semeniuk, V., 1985. Development of mangrove habitats along ria shorelines in north and northwestern tropical Australia. *Vegetatio*, 60: 3–23.
- Seyle, H., 1973. The evolution of the stress concept. *Am. Sci.*, 61: 692–699.
- Simpson, G.G., 1944. *Tempo and Mode in Evolution*. Columbia Univ. Press, New York, N.Y., 237 pp.
- Simpson, G.G., 1953. *The Major Features of Evolution*. Columbia Univ. Press, New York, N.Y. 434 pp.
- Slatkin, M., 1981. A diffusion model of species selection. *Paleobiology*, 7: 421–425.
- Spaulding, W.G., 1983. Late Wisconsin macrofossil records of desert vegetation in the American southwest. *Quat. Res.*, 19: 256–264.
- Spaulding, W.G., 1985. Vegetation and climates of the last 45,000 years in the vicinity of the Nevada Test Site, south-central Nevada. *U.S. Geol. Surv. Prof. Pap.*, 1329, 55 pp.
- Spaulding, W.G., Leopold, E.B. and Van Devender, T.R., 1983. Late Wisconsin paleoecology of the American southwest. In: S.C. Porter (Editor), *The Late Pleistocene*. Univ. Minnesota Press, Minneapolis, Minn., pp.259–293.
- Stanley, S.M., 1975. A theory of evolution above the species level. *Proc. Natl. Acad. Sci. U.S.A.*, 72: 646–650.
- Taggart, R.E. and Cross, A.T., 1980. Vegetation change in the Miocene Succor Creek flora of Oregon and Idaho: a case study in paleosuccession. In: D.L. Dilcher and T.N. Taylor (Editors), *Biostratigraphy of Fossil Plants*. Dowden, Hutchinson and Ross, Stroudsburg, Pa., pp.153–170.
- Tasch, P., 1957. Flora and fauna of the rhynie chert: a paleoecological reevaluation of published evidence. *Univ. Wichita Bull.*, 36, 24 pp.
- Tidwell, W.D., Thayne, G.F. and Roth, J.L., 1976. Cretaceous and Tertiary floras of the intermountain area. *Geol. Stud. Brigham Young Univ.*, 22: 77–98.
- Tschudy, R.H., Pillmore, C.L., Orth, C.J., Gilmore, J.S. and Knight, J.D., 1984. Disruption of the terrestrial plant ecosystem at the Cretaceous–Tertiary boundary, western interior. *Science*, 225: 1030–1032.
- Tsukada, M., 1982a. *Cryptomeria japonica*: glacial refugia and late-glacial and post-glacial migration. *Ecology*, 63: 1091–1105.
- Tsukada, M., 1982b. Late Quaternary shift of *Fagus* distribution. *Bot. Mag. (Tokyo)*, 95: 203–217.
- Tsukada, M., 1983. Vegetation and climate during the last glacial maximum in Japan. *Quat. Res.*, 19: 212–235.
- Upchurch, G.R. and Doyle, J.A., 1981. Paleoecology of the conifers *Frenelopsis* and *Pseudofrenelopsis* (Cheirolepidiaceae) from the Cretaceous Potomac Group of Maryland and Virginia. In: R.C. Romans (Editor), *Geobotany II*. Plenum, New York, N.Y., pp.167–202.
- Valentine, J.W., 1980. Determinants of diversity in higher taxonomic categories. *Paleobiology*, 6: 444–450.
- Van der Steen, W.J. and Scholten, M., 1985. Methodological problems in evolutionary biology. IV. Stress and stress tolerance, an exercise in definitions, *Acta Biotheor.*, 34: 81–90.
- Van Devender, T.R. and Spaulding, W.G., 1979. Development of vegetation and climate in the southwestern United States. *Science*, 204: 701–710.
- Van Valen, L., 1973. A new evolutionary law. *Evol. Theory*, 1: 1–30.
- Vogl, R.J., 1980. The ecological factors that produce perturbation-dependent ecosystems. In: J. Cairns (Editor), *The Recovery Process in Damaged Ecosystems*. Ann Arbor Science Publishers, Ann Arbor, Mich. pp.63–94.
- Waddington, C.H., 1975. Colonizing species. In: *Evolution of an Evolutionist*. Mackay, Chatham. pp.192–197.
- Weldon, C.W. and Slauson, W.L., 1986. The intensity of competition versus its importance: an overlooked distinction and some implications. *Q. Rev. Biol.*, 61: 23–44.
- Wing, S.L., 1981. A study of paleoecology and paleobotany in the Willwood Formation (Early Eocene, Wyoming). Thesis. Yale Univ., New Haven, Conn., 391 pp.
- Wing, S.L. and Tiffney, B.H., 1987. The reciprocal interaction of tetrapod herbivory and angiosperm evolution. *Rev. Palaeobot. Palynol.*, 50: 179–210.
- Winston, R.B., 1983. A Late Pennsylvanian upland flora in Kansas: systematics and environmental interpretations. *Rev. Palaeobot. Palynol.*, 40: 5–31.
- Wolbach, W.S., Lewis, R.S. and Anders, E., 1985. Cretaceous extinctions: evidence for wildfires and search for meteoritic material. *Science*, 230: 167–170.
- Wolfe, J.A., 1977. Palaeogene floras from the Gulf of Alaska region. *U. S. Geol. Surv. Prof. Pap.*, 997, 108 pp.
- Wolfe, J.A., 1978. A paleobotanical interpretation of Tertiary climates in the Northern Hemisphere. *Am. Sci.*, 66: 694–703.
- Wolfe, J.A., 1980. Tertiary climates and floristic relationships at high latitudes in the Northern Hemisphere. *Palaeogeogr., Palaeoclimatol., Palaeoecol.*, 30: 313–323.
- Wolfe, J.A. and Upchurch, G.R., 1986. Vegetation, climatic and floral changes at the Cretaceous — Tertiary boundary. *Nature*, 324:148–152.
- Wolfe, J.A. and Upchurch, G.R. submitted. Leaf assemblages across the Cretaceous — Tertiary boundary in the Raton Basin, New Mexico and Colorado. *Proc. Natl. Acad. Sci. (U.S.A.)*.
- Wolfe, J.A. and Wehr, W., 1986. Middle Eocene dicotyledonous plants from Republic, northeastern Washington. *U.S. Geol. Surv. Bull.*, 1597.
- Wright, S., 1931. Evolution in mendelian populations. *Genetics*, 16: 97–159.
- Wright, S., 1982. The shifting balance theory and macroevolution. *Annu. Rev. Genet.*, 16: 1–19.