

dence that chrysotile may be relatively harmless as compared to some types of amphibole asbestos (14). The sub-microscopic chrysotile that occurs within altered chain silicates probably does not pose a major health hazard to the general population. However, possible detrimental effects for miners working in the vicinity of deposits containing abundant altered pyroxene should not be overlooked. In particular, it is possible that significant amounts of chrysotile dust could be generated during mining operations in skarn deposits, such as the one from which the urallite specimen was taken. In view of the intimate geometry of the intergrowths, individual chrysotile fibers may not even be liberated during mining, but dusts produced during such operations should, at least, be monitored for chrysotile content.

DAVID R. VEBLER
PETER R. BUSECK

Departments of Geology and
Chemistry, Arizona State
University, Tempe 85281

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19 March 1979; revised 7 May 1979

Phanerozoic Land-Plant Diversity in North America

Abstract. A strong correlation exists between the outcrop area of nonmarine rocks deposited during a given geologic period and the observed vascular plant diversity for the same period; however, diversity residuals characteristic of certain periods may have underlying biological causes. Within-flora diversity changes through time indicate that stepwise increases in community species packing have accompanied major tracheophyte evolutionary innovations. Total and within-flora data suggest that the track of North American land-plant diversity has been similar in nature, but not in timing, to that inferred for marine invertebrates.

Changes in diversity can provide substantial insight into the tempo and mode of evolution of vascular land plants (1) and, in addition, can furnish an "out-group" comparison for models of biotic diversity change based on the fossil record of marine invertebrates (2-4). We now present a preliminary survey of vascular plant diversity, drawn from a compilation of more than 7500 Silurian to Tertiary plant species, predominantly from North America.

Many of the arguments proposed for the interpretation of the marine invertebrate record apply to the analysis of vascular plant diversity; it is important, however, to recognize that land plants are subject to unique biases (5). (i) Vascular plants show indeterminate growth and significant intraspecific or even intraorganismal morphologic variation. (ii) Vascular plants are rarely preserved in toto; thus organ and form genera cause over- and underestimates of diversity, respectively. (iii) Most land plants inhabit areas of net sediment erosion rather than areas of net sediment accumulation.

If these paleobotanical limitations are borne in mind, the plant fossil record provides an independent and reliable data bank of taxa for interpreting evolutionary phenomena. Figure 1A illustrates the time-standardized diversity of 7500 species plotted by geologic age. The data suggest that species diversity of land plants in North America rose to a relative maximum in the Carboniferous, dropped during the later Permian, and, after a Mesozoic period of low values, rose sharply during the Cretaceous and Tertiary. Figure 1B shows the time-standardized outcrop area of nonmarine sedimentary rocks in each geologic period for the United States and Canada. (The contribution of Mexican and Central American fossil species is negligible.) The linear regression of diversity versus outcrop area can be described by the equation: number of species per million years = 0.0034 km^2 per million years + 15.5. In this case, $r = .868$; if only the period from the Permian to the Jurassic is considered, $r = .995$. Thus,

Raup's (2) admonition that the availability of unmetamorphosed sedimentary rock influences the number of reported fossil taxa is applicable to the paleobotanical record. The correlation for plant data is by no means perfect. Residual diversity values exist for the Devonian, Cretaceous-Tertiary, and, to a lesser extent, the Carboniferous. These periods are associated with major evolutionary innovations in the plant kingdom—the origin and initial radiation of vascular land plants (Devonian), the evolution of heterospory and the seed (Devonian-Carboniferous), and angiospermy (Cretaceous-Tertiary). Various geologic factors may also have contributed to residuals indirectly by providing physical stimuli for speciation and via time-variable biases of preservation: (i) differences in continental sedimentary rocks characteristic for each geologic period, (ii) influence of tectonic modes on species turnover rates, (iii) environmental heterogeneity and climate alteration due to orogenesis, and (iv) variations in provinciality.

Carbonaceous sedimentary rocks are not equally represented in all periods (6); Carboniferous, Cretaceous, and Tertiary continental rocks contain relatively large amounts of coal per unit of outcrop area: 1.13, 0.56, and 0.69 million short tons of coal per square kilometer of outcrop. Sediment quality is not the sole factor in explaining diversity residuals, however; the Devonian residual is not associated with an abundance of organic-rich sediments. The floral biostratigraphic zonation of Pennsylvanian cyclothems illustrates the apparent correlation of turnover rates with tectonic events (7). Similarly, environmental heterogeneity resulting from tectonic uplift may influence Tertiary diversity data. The Laramide orogeny and the climatic deterioration beginning in the early Oligocene (8) may have increased diversity by increasing the number of available niches. Additionally, the superimposition of western North American Tertiary volcanism on this environmental pattern may have increased the number of habitats from which plants were preserved. Volcanic-

ally preserved floras represent the only substantial departure from a lowland floodplain depositional mode in the history of North American plants. Because our data document the floral evolution of a single continent, provinciality effects are negligible. For instance, the Late Devonian–Carboniferous and the Cretaceous diversity increases are not related to paleolatitudinal changes. North America remained in the same position from the early Middle Devonian to Late Carboniferous, and has been within 10° of its present position since the Middle Jurassic.

An examination of within-habitat species diversity patterns through time provides a measure of species packing within a given community—an important determinant of the total number of species in a given realm. Jackson (9) observed that these separate scales of diversity complement each other, a comparison between them being prerequisite to a clear understanding of general diversity trends. Species packing in a fossil flora can be estimated by tallying the number of included paleospecies. These data may be influenced by several specific biases. The remains of perennial plants with seasonally shed structures, such as leaves, will be more common than those of shorter-lived, more herbaceous plants such as ferns and angiosperm herbs. The differential preservability of various vascular plant organs further complicates this influence. Postmortem transport must also be taken into account, but it is unlikely that many of the megafossils included in our analyses were transported so far that extensive intercommunity mixing occurred. It could be argued that observed variations in community diversity are a function of ecological circumstance rather than evolution; however, sedimentary biases preclude the preservation of many plant assemblages and ensure that those that do become fossilized have a certain degree of environmental uniformity. The great majority of the assemblages sampled here represent lowland floodplain or lakeshore communities existing under mesic or warm climatic conditions. Therefore, broad quantitative comparisons among the floras of different periods can be made. Community diversity may also be influenced by the species concept of the individual investigator—"lumpers" find fewer species than "splitters." In general, however, species counts are consistent within the floras of one period from one author to another (10), but vary between periods. [Carboniferous assemblages appear to be consistently oversplit (11), Devonian ones undersplit.]

Table 1. Species diversity of fossil vascular plant floras.

Age	Floras (No.)	Species per flora	
		Maximum	Mean
Late Silurian	1	1	1
Early Devonian	7	11	5
Middle Devonian	4	9	5.3
Upper Devonian	9	17	8.2
Early Mississippian	7	14	10
Late Mississippian	2	26	22.5
Pennsylvanian	24	57	35
Permian			
Triassic	11	48	19
Jurassic	10	50	27.5
Early Cretaceous	15	46	21.5
Late Cretaceous	7	67	43
Tertiary	22	123	51

Bearing these factors in mind, we tabulated species numbers (Table 1). It is possible to infer a pattern of gradually increasing community complexity through the Devonian and Early Mississippian. The Late Mississippian diversity jump reflects an increased packing density that remains broadly constant until the Late Cretaceous, when another sharp increase occurs. [Species diversity for individual localities seems to corroborate the floral picture. Early and Middle Devonian localities average 2.9 species; Pennsylvanian localities, 13; Triassic, 12.2; Jurassic, 11.1; and the Tertiary, 34 species per locality.]

Species packing within a given habitat is related to the stature, dispersal mechanisms, and other adaptations of the constituent plants. Major diversity changes (Table 1) coincide with the appearance of major evolutionary innovations within the vascular plants. For example, early

land plants used spores to colonize new areas, but most reproduction appears to have been vegetative: single species would, then, "turf in" sizable areas, forming patchy communities of low diversity. Devonian bedding surfaces commonly show dense clusters of a single taxon. Heterospory and the seed habit opened the way to the success of larger and more scattered plants, leading to arborescence in some lineages. The ensuing multilayered community underwent an initial period of diversification resulting in the establishment of a stable level of within-habitat diversity extending from the Pennsylvanian to the Upper Cretaceous. Whereas the taxonomic composition of communities changed throughout this time, turnover apparently had no great effect on species packing and attendant diversity; however, a marked increase in species packing is seen in Upper Cretaceous and Tertiary floras. This occurred presumably in response to the evolutionary refinement of several angiospermous characteristics, including evolutionary mechanisms for pollen and seed dispersal, and great vegetative plasticity, which permitted the high packing densities observed in modern angiosperm communities.

Patterns in the within-habitat and total diversity data reinforce each other. During the Silurian and Devonian periods, species diversity substantially increased; the change was partially analogous to the Late Precambrian–Cambrian diversity rise of marine invertebrates. [Comparisons with the sigmoidal pattern described for the invertebrate curve are premature (4).] Both the total and within-habitat data are consistent with the hypothesis of a relatively stable total diver-

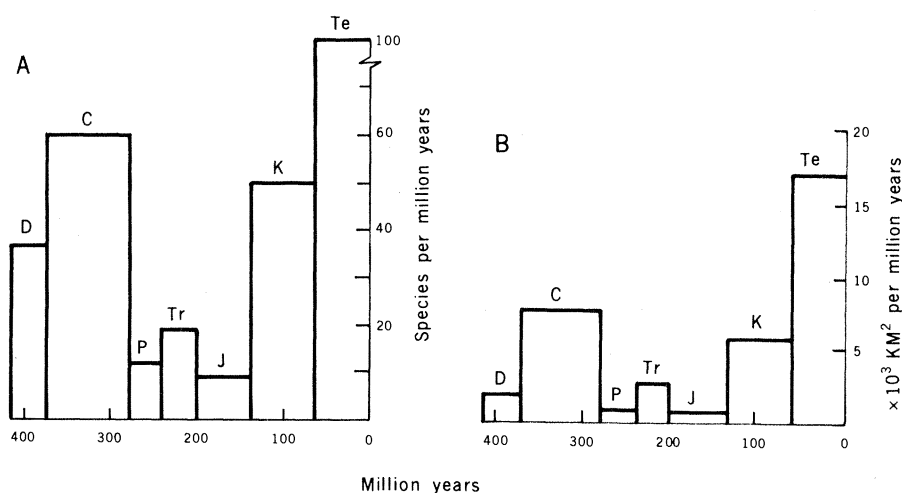


Fig. 1. (A) Species per million years plotted by geologic period through the Phanerozoic. (B) Outcrop area of nonmarine sedimentary rock (per million years) also plotted by geologic period. Abbreviations of periods: D, Devonian; C, Carboniferous; P, Permian; Tr, Triassic; J, Jurassic; K, Cretaceous; and Te, Tertiary.

sity from the Mississippian until the expansion of the angiosperms, when species numbers increased significantly. A parallel can be drawn with the expansion of diversity in the marine record associated with the Ordovician radiation of sessile suspension feeders. While the observed Cretaceous-Tertiary rise may be influenced in part by some of the biases previously discussed, we believe that it is nonetheless a real phenomenon associated with the biology of the angiosperms.

The temporal pattern of land-plant diversity in North America resembles that described for marine invertebrates (2-4) in nature, if not in timing. Extrapolation of the present data to a historical interpretation of worldwide vascular plant diversity will require consideration of changing levels of geographic and climatic provinciality through time. Estimates of Phanerozoic phytogeographic provinciality show maximums in the Permian and Tertiary-Quaternary (12). These correspond to times of maximum climatic or geographic heterogeneity, or both. This suggests the likelihood of a pre-angiosperm global diversity peak in the late Paleozoic. The coincidence in the present day of both maximum geographic/climatic provinciality and high levels of species packing in many communities supports the hypothesis of Hughes (13) that the modern flora contains a greater number of vascular plant species than any previous flora in earth history.

ANDREW H. KNOLL

Department of Geology,
Oberlin College,
Oberlin, Ohio 44074

KARL J. NIKLAS

Division of Biological Sciences,
Cornell University,
Ithaca, New York 14853

BRUCE H. TIFFNEY

Department of Biology,
Yale University,
New Haven, Connecticut 06520

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19 June 1979; revised 27 August 1979

The "Little Ice Age": Northern Hemisphere Average Observations and Model Calculations

Abstract. Numerical energy balance climate model calculations of the average surface temperature of the Northern Hemisphere for the past 400 years are compared with a new reconstruction of the past climate. Forcing with volcanic dust produces the best simulation, whereas expressing the solar constant as a function of the envelope of the sunspot number gives very poor results.

The term "Little Ice Age" refers to the period from about 1430 to 1850 during which the Northern Hemisphere climate was alleged to be cooler than the periods before or after (1, p. 151; 2, pp. 185-186). Earlier attempts to describe the hemispheric average temperature variations during this period have been hampered by a lack of uniformly distributed observations around the hemisphere. As a consequence, most curves describing the climatic change during this period are based on European data compiled by Lamb (1, pp. 130 and 152; 2, pp. 228-229). Using two of these curves, Eddy (3) has suggested that the Little Ice Age was caused by variations in the solar constant related to the envelope of the sunspot cycle. In fact, the Maunder sunspot minimum (4) does correspond to a cool period in the winter severity index of Lamb (2, p. 229), particularly at 50°N, 37.5°E. Both a comprehensive hemispheric average temperature curve and

modeling studies, presented below, show this to be a spurious relationship. The hemispheric average temperature is not well represented by an index at one location (5), and volcanic dust produces a much better model simulation of the climatic change during and after this period.

Borzenkova *et al.* (6) have presented the annual average hemispheric surface temperature from 1881 to 1975; their data are taken from instrumental observations distributed over the hemisphere. Although a dense enough network of stations did not exist before this period from which to obtain a representative hemispheric temperature by spatial averaging, many annual average individual station records do exist. These include instrumental observations from Archangel and Irkutsk, U.S.S.R.; Berlin and Regensburg, Germany; Montreal, Canada; and Philadelphia, Pennsylvania; as well as proxy data such as tree ring

Table 1. Correlation coefficients of model results with observations. Significance levels (in percentage) are given in parentheses (29); a dash indicates not significant at the 10 percent level. V = volcanic dust simulation, S = smoothed sunspots, C = carbon dioxide, R = random forcing (natural variability). Autocorrelations of each series are also presented, to be compared with that of the entire data record, .766. The 5-year average correlations are to be compared with the correlation of .93 between this set of observations (24) and those of Mitchell (17).

Model forcing	Correlation with entire record, 1620 to 1975		Correlation with instrumental observations, 1881 to 1969		Autocorrelation (1-year lag)
	Including linear trend	With linear trend removed	Annual average	5-year average	
V	.408 (.2)	.373 (.5)	.823 (.1)	.965 (.1)	.971
S	.297 (2.0)	.037 -	.269 (2.0)	.384 -	.999
V + S	.441 (.1)	.313 (2.0)	.692 (.1)	.829 (.1)	.986
V + C	.430 (.1)	.384 (.5)	.819 (.1)	.958 (.1)	.972
S + C	.322 (1.0)	.070 -	.297 (.5)	.420 -	.999
V + S + C	.451 (.1)	.323 (1.0)	.681 (.1)	.820 (.1)	.987
R	.035 -	.079 -			.530