A CLIMAX INDEX FOR BROADLEAF FOREST: AN *n*-DIMENSIONAL, ECOMORPHOLOGICAL MODEL OF SUCCESSION

Philip V. Wells

University of Kansas
Lawrence, Kansas

INTRODUCTION

Ecological succession from pioneer to climax has been a central stage on which major features of Angiosperm evolution have taken place. The *n*-dimensional, seral gradients of invasibility, canopy closure, interference with light penetration, root competition for water and nutrients, soil development, etc. are obviously powerful selective forces affecting both vegetative and reproductive aspects of plant evolution. Recent studies have focused on the successional relations of reproductive versus vegetative effort (*r*-selection vs *K*-selection) in herbaceous plants (Gadgil and Solbrig 1972; Abrahamson and Gadgil 1973; Gaines *et al*. 1974); however, dry weights of plant parts yield only very general data. The multivariate, ecomorphological model developed here for woody plants offers detailed insights into the mechanisms of forest succession. Because of the important role of herbaceous plants in succession, it would be useful to construct an *n*-dimensional, functional model of their physiognomy along similar lines.

Of course, these methods have well known antecedents in plant geography and numerical taxonomy (cf. Sokal and Sneath 1963). The life-form spectra of Raunkiaer (1934), based simply on positions of the perennating bud, reflect convergent evolution on these vegetative traits by diverse plant families subjected to natural selection under similar climatic conditions in the same or different parts of the world. Analogous spectra, to be based on arrays of reproductive (rather than vegetative) characters, were advocated by Baker (1966). It is a logical step to organize multifaceted vegetative and reproductive spectra into a coherent system (cf. Knight and Loucks 1969) by multivariate analysis, and to extend the method from synecological phytogeography to an autecological model of plant succession by using a different suite of ecomorphological characters. The resultant, *n*-dimensional model of forest succession is a composite of partial (seral) mirror images of the fundamental niches (Hutchinson 1957) of the species. The model provides a numerical basis for assessment of the seral autecology of each species that can be independent of any field knowledge of its actual role, or of its association with other species. The vector of character-values defines the successional ecomorphology of a species; and the sum of the values serves as an index of its position on the scale from pioneer to climax, *i.e.*, its climax index.

Furthermore, it should be feasible to analyze the seral ecomorphology of a stand of trees in a synecological sense by combining the climax index values of the component species, weighted as to their importance values. Inferences about the successional status of the whole stand may be drawn from its composite climax index. Indeed, it may be possible to carry out the ecomorphological analysis of a stand without naming the species, as is commonly done by plant geographers in physiognomic analysis of regional plant formations (Küchler 1949; Beard 1955). This approach would be useful for analyzing succession in poorly known vegetation of high species diversity, as in the tropics.

The concept of plant succession as an invasion sequence beginning with the early-arriving, fast growing "pioneers" and culminating with the tardy, slow-growing, but ultimately dominant, "climax" species, not undergoing further replacement, has been well established on an empirical basis. The phenomenon has been observed in a wide array of vegetation throughout the world, ranging from rainforest to tundra, grassland, and even deserts (Clements 1916, 1920; Richards 1952; Churchill and Hanson 1958; Oosting 1942; Daubenmire 1968; Wells 1961). The traditional approach to succession in plant ecology has been to describe and to arrange in chronosequence as many "stages" as can be discerned in the essentially continuous process. Furthermore, numerous local, ad hoc successions have been painstakingly elaborated in this manner even within one major vegetational formation.

However, the successional process has not been well defined in terms of functional, morphological differences among plant species playing pioneer, climax or intermediate roles. If suites of morphological and physiological characters vary with position on the successional gradient, it should be possible to devise a model of plant succession based upon these intrinsic features of the vegetation itself, and independent of established time sequences. From the seral ecomorphology of a stand, the history of vegetational disturbance and succession could be deduced where historical evidence is lacking, or even where the species composition is difficult to ascertain. Of course, the predictive power of the model has practical value, for example in forestry. Moreover, catastrophic disturbance and subsequent changes in composition of vegetation in all parts of the world are increasingly dominant themes imposed by the onslaught of humanity. Hence, elucidation of the mechanisms of plant succession in terms of the roles played by the component species is becoming ever more important for interpreting the recent history and present stability, or for predicting the future composition, of plant communities. Indeed, these insights are essential for proper management and conservation of world vegetation.

FORM AND FUNCTION IN FOREST SUCCESSION

The most structurally elaborate plant successions have evolved under forest climates, where diverse growth forms are dispersed along a gradient

of canopy closure and environmental control by the dominant trees. The parallel gradient in light intensity, ranging from full sun in openings to extremely low levels on the floor of a multisynusial forest, has been one of the most powerful selective forces in plant evolution. Comparatively few species have attained a dominant position in the exacting environment of dense, shady, climax forests. Much of the flora of forested regions is engaged in the earlier stages of succession, occupying seral niches on the same ground for sequential or overlapping tenures of variable duration.

The familiar sequence of colonization on unvegetated sites begins with an ephemeral stage of cryptogams and weedy annual herbs, which is joined by a following wave of perennial herbs and shrubs, usually in the second year. During the variable period of dominance by these pioneering, nonarboreal forms, saplings of the more invasive species of trees become established at increasing densities. The final upsurge toward canopy closure causes the demise of the physiognomically diverse, heliophile species in the shrub and ground layers, but marks only the beginning of a much more protracted arboreal phase of succession.

Attention is restricted here to broadleaf, dicotyledonous trees of the eastern deciduous forest of North America, which exhibit a wide diversity of morphology and physiology connected with seral behavior, and therefore should yield insights applicable to broadleaf forests in general. The ecomorphological diversity of trees along the successional gradient forms a structural and functional continuum, a synoptic view of which may be obtained by contrasting the end-member ecological roles: the early-successional "pioneer" and the late-successional "climax".

Pioneer Strategy

The pioneering way of life is characterized by rapid, opportunistic invasion of ephemerally open, sunny sites, free of dense vegetation, and hence at first with reduced levels of competition or interference among species for light, soil-water and mineral nutrients. Seedlings of pioneers are usually very intolerant of shade because of low photosynthetic efficiency at low light intensities, and because of reduced energy reserves in the seed correlative with reduced seed weight, which in turn is correlative with greatly augmented numbers of seeds produced. Pioneers follow a mobility ("r") strategy of precocious, profligate reproduction with enormous annual crops of light, dispersible seeds that enhance the probability of reaching transiently open sites at some distance from the parent tree. Correlative with the high level of seed production and gregarious abundance of pioneer trees is an option for dioecious sex structure in the population, whereby obligate outcrossing is achieved at the expense of seed production by half the population (the seedless, male individuals).

Potential canopy trees of pioneer character have very rapid, excurrent growth, the strong apical dominance ensuring enough height to

maintain the crown in full sunlight, but at the expense of crown breadth and richness of branching orders, thereby favoring light penetration. Rapidity of growth also results in a correlative shortage in thickness and strength of xylem cell walls, in reduced lignification and hardness, and often in lessened impregnation with other antibiotic substances that confer resistance to herbivores and decomposers. Thus, the wood of pioneer trees tends to be weak, soft, light, subject to infestation by insects or fungi, and lacking in durability. These deficiencies shorten the longevity and, hence, the tenure of pioneers in the canopy. Because of their high light requirements, pioneer trees have a diversity of foliage deployment tactics, that combine with the sparsely branched, excurrent growth habit to bring about a sharing of light and heat load among leaves at different levels in the canopy. The leaves tend to be arranged in spirals on the branches; they are usually small, or deeply lobed, or compound with small leaflets, often pendulous and sometimes oscillating with the slightest air movements; the leaf surfaces are lustrous with waxy cutin that reflects abundant light and heat, and reduces cuticular transpiration. Consequently, the light intensity on the forest floor under a canopy dominated by pioneer species is relatively high, thus permitting the reproduction of potential competitors. However, the heliophil pioneer trees are usually unable to reproduce even in their own light shade, and therefore yield the ground to species of higher seral rank in a single generation.

Climax Strategy

The dominant themes of the climax way of life are interference with light penetration, and competition for other resources, among closely spaced and often superposed individuals. Although the forest microclimate is much more mesic and equable than that of an opening exposed to the full impact of wind and radiation exchange, forest competition can make soil-water and mineral nutrients limiting factors, especially in the shallow root zone penetrated by seedlings. As a consequence of these selection pressures, climax, broadleaf trees tend to have large energy and nutrient reserves in the cotyledons or endosperm of their seeds, which provide a heterotrophic head-start for the seedling, enabling it to put down deeper, more competitive roots ("K" strategy). The increased seed weight carries with it a conservative, short-range dispersal capacity, because of the correlative reduction in seed numbers and because of their lack of mobility, which usually causes them to fall in the shade of the forest canopy or in nearby openings. The extremely low light intensity under a closed canopy has evidently selected for photosynthetic efficiency in the most climax forest species, which are very tolerant of shade at the seedling and sapling stage. Indeed, shade tolerance has been suggested as the principal criterion of climaxness in forest vegetation (MacArthur and Connell 1966).

Climax trees of broadleaf forest tend to have slow, deliquescent growth with weak apical dominance resulting in broad, spreading crowns with numerous branching orders and intricately arranged ultimate twigs

and leaves that cast deep shade. Reproductive maturity is delayed in favor of sound vegetative establishment. The slow growth is usually correlated with a large investment in the production of strong, thick-walled xylem cells that become heavily lignified and impregnated with antibiotic substances. Hence, wood of climax character tends to be mechanically strong, hard, heavy, durable, and resistant to decay. These qualities confer on climax trees great longevity and persistent maintenance of a broad, unbroken crown in the canopy. Tolerance of shade by climax tree species favors the deployment of intricate leaf mosaics that are highly efficient at absorbing light. Under low light intensities, there is a strong tendency for all the leaf blades of a branch to be arranged in a single, thin, horizontal plane with closely fitted or annectant leaf margins that reduce interstitial gaps to a minimum. The planar arrangement is most efficient on trees with numerous branching orders, with a two-ranked or opposite phyllotaxy, and with undivided, broad, horizontally disposed blades. Light absorption is further enhanced in climax species by dull, thin, cuticles on the leaf surfaces. Moreover, trees of climax character are shade tolerant enough to maintain a number of vertically stacked, planar leaf layers in their persistent, broad and deep canopies, which successively reduce the light intensity to an extremely low level. On the climax forest floor only the few most shade tolerant, climax species can reproduce successfully, and a host of potential competitors (usually, the bulk of tree species in the flora) are effectively excluded.

CHARACTER ANALYSIS OF SERAL ECOMORPHOLOGY

A wide diversity of morphological characters are correlated with the successional position of forest trees, as briefly outlined above. In the present study, a character analysis of the principal broadleaf trees of the deciduous forest of eastern North America (75 species) yielded 26 readily measured parameters for which I was able to obtain data. Many of the characters probably have wide application to other broadleaf forests of the world, although ring porosity, for example is largely restricted to temperate dicotyledons. The rather heterogeneous array of characters can be grouped in three principal suites: light absorption factors; reproduction factors; and growth, maintenance, and longevity factors. The ecomorphological character analysis is explained as follows:

Light Absorption Factors

The central ecophysiological theme of green plants is, of course, photosynthesis; and there are a number of growth-form attributes that are connected with the interception of light by trees. These include apical dominance (excurrence), branch orders, phyllotaxy, leaf division, area of unit blade, leaf orientation, stomatal distribution, leaf oscillation, cuticle luster, and pigmentation.

1. Apical dominance can be expressed as a range from a single main axis or leader with suppressed lateral branching (excurrent growth habit) to a number of principal axes and a greater development of lateral branching (deliquescent habit). Apical dominance channels energy into rapid vertical growth at the correlative expense of lateral branching and canopy spread. It is an important option in the pioneering way of life because trees of high light requirement can attain a position in the canopy by strongly vertical, excurrent growth, thus diminishing the possibility of being overtopped and shaded. Excurrence is prominent in the sapling and pole stages of heliophile species (e.g. sweet gum, *Liquidambar styraciflua* L.; tulip tree, *Liriodendron tulipifera* L.), but may persist to maturity especially in trees engaged in a race to fill a gap in the canopy (Horn 1971). A related phenomenon is a phototropic response on the part of shade-intolerant species that require a place in the sun. In gap-phase succession, heliophile trees not actually in the opening often grow toward illuminated gaps in the canopy at an angle from the perpendicular, producing slender, excurrent, leaning trees. Shade tolerant, climax species at an early age develop broad, deliquescent crowns that eventually command a large sector of the canopy and cast deep shade over the subtended area, thus adversely affecting the growth and reproduction of all potential competitors with greater light requirements.

It may be noted that the excurrent growth habit is a family trait of the *Pinaceae* and other conifers, including both pioneer and climax species. The trait has a very different adaptive fitness in the snowy, evergreen spire forests of the taiga and the subalpine zone of mountains, where the narrowly conical tops of spruce and fir shed snow much more effectively than hypothetically broad-crowned evergreens. The parallel in architecture is the steeply pitched roof, as in alpine chalets and the modern A-frame.

2. Branch orders are the number of sequential branchings produced along the path from the main axis or trunk to the ultimately distal twig of a main branch (DuMond 1922). Numerically, branch orders range from 2 to 3 in pioneers to 5 or more in climax species. Degree of branching controls the geometry of leaf arrangement and density of canopy. Richly branched trees produce interlocking leaf mosaics that result in maximally dense crowns and canopy closure, as in beech (*Fagus grandifolia* Ehrh.), while poorly branched trees tend to have sparser foliage, more diffuse crowns and open canopies, as in poplar (*Populus*) and Kentucky coffee tree (*Gymnocladus dioica* (L.) Koch). Efficient interception of light by species with many branch orders greatly disadvantages species growing in subjacent layers. However, sparsely branched trees transmit sufficient light to favor the growth of a host of competitors in the understory, including species that can eventually displace the canopy trees. Moreover, the shade-tolerant transgressives may interfere with the reproduction of the heliophile, pioneer canopy species by forming a richly branched subcanopy layer that further reduces the light intensity on the forest floor, even where breaks in the top canopy develop.

3. Phyllotaxy is the mode of leaf arrangement on the branch. The many, diverse phyllotaxies of plants are relevant to the mechanism of succession insofar as they relate to the formation of leaf mosaics efficient in light interception. Under shady, climax, forest conditions, leaves tend to stratify in thin, horizontal planes (cf. Horn 1971). The planar geometry develops most efficiently with a two-ranked phyllotaxy and leaves alternate as in basswood (Tilia americana L.) and beech, or if opposite and decussate as in maple (Acer), than with petioles turned to array successive pairs within the same plane. Species with spiral (e.g. poplar, cherry (Prunus)) or whorled (catalpa (Catalpa speciosa Warder)) phyllotaxy are poorly fitted to the planar strategy, and tend to occur in open, sunny habitats in the earlier phases of succession, where the several ranks of leaves receive illumination from different directions. The climax arrangement of leaves in planar sprays permits maximum reduction of interstitial gaps between the margins of closely spaced or annectant blades. Some features of leaf shape, notably the asymmetric, oblique leaf base of basswood (Tilia) and elm (Ulmus), are connected with this packing strategy (Lubbock 1886). Maximal interception of light by efficiently arranged leaf mosaics, besides being photosynthetically advantageous to shade tolerant canopy species, also interferes adversely with the light regime of potential competitors in subjacent layers.

4. Leaf division into leaflets or lobes permits greater penetration of light through the upper foliage layers, thus increasing the illumination of subjacent layers within the same tree. A quantitative expression of this phenomenon is seen in lobed-leaved oaks, which consistently have deeper, larger sinuses and narrower lobes on leaves developing in full sun, as in the crown of the tree. Shade leaves of lower branches on the same individual oak have shallower lobing, or may be unlobed (Hanson 1917; Talbert and Holch 1957; Horn 1971). A parallel phenomenon occurs among different species of the red oak group (Quercus; subgenus Erythrobalanus) that are restricted to different light environments. Species of open habitats, whether dry or wet, have consistently deeper lobing than species of shady forest habitats. For example, some light-requiring red oaks of wetlands (pin oak, Q. palustris Muench; Nuttall oak, Q. nuttallii E. J. Palmer), or dry uplands (Hill's oak, Q. ellipsoidalis E. J. Hill; scarlet oak, Q. coccinea Muenchh.; black oak, Q. velutina Lam.) have much more deeply cut lobes than the relatively shade tolerant northern red oak (Q. rubra L.) of mesic upland forests.

Gaps in the leaf mosaic due to lobing or compounding appear to have selective advantage for species of high light requirement by allowing a more equitable distribution of light among superposed foliage layers. Thus, a larger proportion of lower branches can be retained because of the light-sharing arrangement. Shade tolerant trees, when grown under the same light conditions as heliophiles, may develop even deeper, more multilayered canopies without sacrifice of leaf blade tissue, as in species with simple, broad leaves. The climax strategy of undivided leaves maximizes light absorption and total photosynthesis in the upper canopy of a tree, and minimizes penetration of light to the lower canopy and, of course, to potential competitors in subjacent layers.

5. Area of unit blade (leaf or leaflet) tends to be smaller (1.0 to 50.0 cm^2) in species of relatively open, sunny habitats. Microphylly is an option followed, for example, by hawthorn (Crataegus), honeylocust (Gleditsia triacanthos L.) and black locust (Robinia pseudoacacia L.), and willow (Salix); but it is rare among relatively climax species of shady forests, where broader leaves (>90 cm^2) predominate. There is a parallel plasticity in size of leaves on individual trees, sun leaves usually being smaller in area than shade leaves on the same tree (Hanson 1917; Talbert and Holch 1957). Shade tolerant species with broad leaves form the most efficient planar leaf mosaics characteristic of climax forests dominated by Angiosperms.

6. Leaf orientation is predominantly horizontal in species of shady, climax forest habitats, which dispose their leaves in planar mosaics most efficient in the interception of light. Vertically oriented leaves, whether pendulous or erect, are options of shade intolerant, pioneer trees that permit light penetration deep into the canopy, because of the very open leaf mosaic produced. The vertical option is followed by some extreme heliophiles of wet habitats, as in cottonwood (Populus deltoides Bartr.) and willow, but is more widely distributed among trees of mesic or dry uplands, for example, tulip tree, sweet gum, black cherry (Prunus serotina Ehrh.), American chestnut (Castanea dentata (Marsh.) Borkh.), chinkapin oak (Q. muehlenbergii Engelm.), sourwood (Oxydendrum arboreum (L.) DC.). Vertical orientation of the leaves also reduces the heat load per leaf, and may be an important compensation in sunny, xeric habitats, especially for evergreen trees or shrubs exposed to seasonal drought, as in many species of manzanita (Arctostaphylos) and Eucalyptus of Mediterranean isoclimes (cf. Wells 1962, 1968).

7. Stomatal distribution in woody dicotyledons is invariably of the bifacial mode, with stomata restricted to the shaded, less cutinized, lower surface of the leaf blade. Absence of stomata on the strongly irradiated upper surface of leaves in most species is probably connected with the relatively harsh microenvironment, especially the high heat load, and the potentially high transpiration rate. However, some heliophile species with vertically oriented leaves have isofacial symmetry with stomata equally numerous on upper and lower surfaces of the blades. This arrangement doubles the exits and shortens the diffusion path for gases between the external atmosphere and the photosynthetic mesophyll cells inside the leaf, and thereby enhances the rates of carbon dioxide ingress and oxygen egress. Because of the low natural level of carbon dioxide in the atmosphere (about 0.03%) and the high levels of dangerously reactive oxygen produced internally in the leaf, the concentrations of these gases are limiting factors governing the rate of photosynthesis and growth over a wide range of other environmental parameters.

Photorespiration in C_3 species (i.e., most woody plants) is greatly accelerated by high levels of O_2 (released as gas in the chloroplast by the very rapid photolysis of H_2O), and by low levels of CO_2. Both gases compete for the ribulose diphosphate CO_2 acceptor of the Calvin cycle,

which can react with both carboxylase and oxygenase (Chollet and Ogren 1975). Thus, the necessity of shunting off the highly reactive O_2 on the glycolate pathway of photorespiration under high light intensity and high temperature causes an anomalous decline in the efficiency of CO_2 fixation in C_3 plants. Under these hot, sunny conditions, which are favorable for rapid photosynthesis, free oxygen is a dangerous photo-oxidant. Therefore, the depletion of O_2 in the chloroplast by ribulose diphosphate oxygenase (an expensive pathway), or by enhanced diffusion outward through the stomata, is obviously advantageous. Hence, a more efficient gas exchange (both O_2 and CO_2) with the external atmosphere, associated with isofacial stomatal distribution, may compensate for deficiencies related to photorespiration in pioneer species with high light requirements.

The expected, detrimental enhancement of the concurrent transpiration may be offset by xeromorphic traits (e.g. sunken stomata, thick, waxy cuticle), but it is apparently outweighed by the photosynthetic advantages because isofacial stomatal distribution is a feature of extremely xerophytic broad sclerophyll vegetation, as in Australia and California with many heliophile species of Eucalyptus and Arctostaphylos, respectively (Wells 1962, 1968, 1972). However, in the deciduous forest of North America, isofacial stomatal distribution is found only in Populus and Salix, which are also extremely heliophile, but are trees of wet or mesic habitats where water is obviously less limiting.

8. Leaf oscillation is another uncommon trait peculiar to a few extremely heliophile species. In some cottonwoods (Populus) and in quaking aspen (P. tremuloides Michx.) it is enhanced by petioles flattened in a plane perpendicular to that of the leaf blade. The slightest air movement induces an oscillating motion about the central axis (midrib) of the leaf. The almost constant motion of the leaves permits light to penetrate deeply into the canopy, so that even the lowermost leaves may be illuminated by flecks of direct sunlight. Because trees possessing the trait are extremely intolerant of shade, the quaking habit may be highly adaptive as a means of sharing high-intensity light among many vertically stacked layers of leaves.

9. Cuticle luster is due to an outer layer of clear, waxy material (cutin) which causes the leaf to reflect part of the incident sunlight, with a resultant loss of light and heat energy. Pioneer species of sunny, xeric habitats tend to have thick, lustrous cuticles that are effective in reducing both heat load and cuticular transpiration. However, the concomitant increase of albedo within the action spectrum of chlorophyll drastically reduces their photosynthetic efficiency under lower light intensities. On the other hand, leaves with dull, thinly-cutinized surfaces are the most efficient absorbers of light (low albedo), a strategy strongly correlated with shady, mesic, climax conditions.

10. Pigmentation of leaves during the verdant season varies qualitatively between two extremes in the trees considered here: light, yellowish-green in pioneer species growing in open, sunny situations,

and dark, bluish-green in species of shady, climax conditions. Probable differences in concentration of the several chlorophylls and carotenoids invite analysis, and would provide a quantitative basis for scoring the trait.

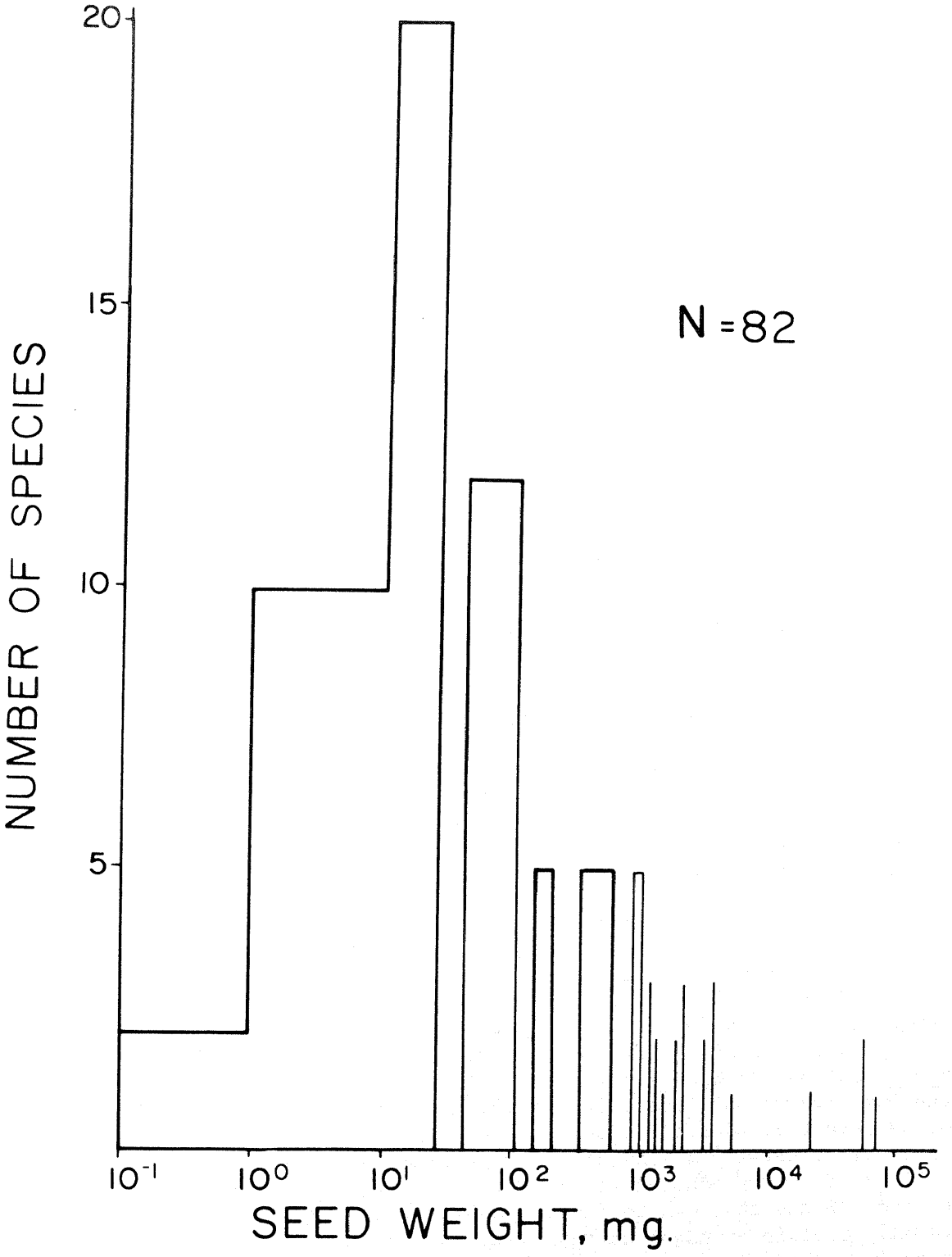
Reproduction factors

The reproductive ecology of plants has been receiving much attention in recent years. The concepts of *r* and *K*-selection are directly applicable to plant succession. Indeed, the concepts are beautifully illustrated by the wealth of reproductive versus vegetative, ecomorphological traits of plants vis-a-vis successional position. Assignment of positions on the continuum between *r* and *K* may be less interesting than the evolutionary insights to be gained from functional analysis of the traits. These include shade tolerance of seedlings, seed weight, dispersal mechanisms, periodicity of mast years, age at first fruiting, and sex structure.

11. Shade tolerance of seedlings and saplings ranges from very intolerant in extreme pioneer species to very tolerant in climax species. Relative shade tolerances of most species of North American forest trees have been estimated empirically by direct field observations (Baker 1949). Species reproducing under a closed canopy as seedlings, saplings, and transgressives are shade tolerant, and species reproducing only in the open, under full sunlight, are shade intolerant. Shade tolerance is obviously a key climax character, and it should be placed on a more quantitative basis by direct measurement of photosynthetic efficiency under low light intensity, as has been done for some species (*e.g.* oak: Bourdeau 1954).

12. Seed weight has two important adaptive aspects with respect to forest succession: the mobility aspect, and the energy reserve aspect. Mobility of seeds is enhanced by reduction in weight with correlative increase in number of seeds. The lightest seeds in the deciduous forest weigh less than a milligram. Sourwood produces seeds averaging 0.06 mg, and in enormous numbers. Willow at 0.18 mg and cottonwood at 1.3 mg have a similar fecundity. On the other hand, the heaviest seeds, averaging 15,900 mg, are produced by yellow buckeye (*Aesculus octandra* Marsh.) in comparatively parsimonious numbers. The acorns of some species of oak are nearly as heavy. The frequency distribution of mean seed weights for 82 principal species of trees in the eastern deciduous forest of North America is plotted in figure 1. Clearly, most of the species are concentrated in the light-seeded range (<100 mg, or 0.1 gram). Thus, the pioneering *r*-strategy appears to be a much more probable evolutionary pathway for trees than the climax *K*-strategy.

Figure 1. Distribution of seed weights among 82 species of trees from the broadleaf deciduous forest of eastern North America, including the 75 species of the present study. All of the major dominant species are included, and almost all of the genera, with a wide representation of minor species. Weights are expressed on a logarithmic scale to accommodate the extremely wide range (0.08 mg to 15,920 mg). The modal value is in the light-seeded range at 10 mg.



Range : 0.08 - 15,920 mg.

The light-seeded mobility strategy, which is followed by r-selected pioneers, sacrifices energy reserves in favor of reaching a wider range of sites potentially more suitable for germination than the immediate vicinity of the parent tree (cf. Salisbury 1942; Wells 1962; Harper et al. 1970). Seedlings of pioneer trees can succeed only in sunny places where they may become photosynthetically self-sufficient soon after germination. Open sites are often scattered and ephemeral in forest vegetation. Therefore, the advantage of an abundance of lighter seeds with high dispersal capacity, which can rain over a wide area, thus increasing the probability of reaching a photosynthetically favorable, open site, is nicely correlated in pioneers with a lesser requirement for weight-increasing energy reserves (Wells 1959a, 1959b, 1962). Also, on the larger, biogeographic scale, the most rapid rates of migration are predicted for light-seeded heliophiles, which are prone to the vagaries of long-distance dispersal.

The second adaptive aspect of seed weight is the reserve of starch, lipid, proteins and other nutrients that maximizes the chance for establishment of each seed, regardless of where it germinates (Salisbury 1942; Wells 1962; Harper et al. 1970). The cotyledonary or endosperm reserves afford a heterotrophic headstart for root and shoot development in the seedling, which can be critical where photosynthesis is suboptimal because of low light intensity, as under the forest canopy. On the other hand, the correlative link between weight per seed and number of seeds per individual makes for smaller crops of heavier seeds, which, in combination with their generally shorter range of dispersal, can restrict the mobility of the species drastically. However, limited dispersal capacity is not disadvantageous for shade tolerant species of climax forest vegetation, inasmuch as rapid movement to distant sites is not essential for survival of climax species. Slower rates of migration predicted for species with climax dispersal strategy may suffice for a conservative, economical probing of nearby sites that are indeed more likely to be suitable. These K-selected species should migrate by a gradual, lateral encroachment on the periphery of their range, waiting for geographic advancement on the slow maturation of the successional process enacted by more r-selected species.

13. Dispersal mechanisms of forest trees can be divided into three categories with respect to succession: wind-borne pioneers, bird-borne pioneers, and mammal-borne, relatively climax species. Seeds light enough to be wind-borne have too little energy reserve to compete successfully under shady, climax forest conditions, unless there is compensating photosynthetic efficiency or mycorrhizal heterotrophism (cf. Ericaceae, Monotropaceae, Orchidaceae). Wind dispersal is obviously adaptive to the invasive way of life characteristic of extreme pioneers. Also, seeds of baccate fruits, light enough to be dispersed by frugivorous birds or bats, are generally disadvantaged when germinating under dense canopies, but may be better adapted to intermediate light conditions than the anemochores. Seeds that can be dispersed only by mammals, or by gravity, usually contain abundant energy reserves that favor seedling establishment in relatively climax vegetation.

14. Periodicity of mast years varies from a bumper seed crop at irregular intervals of 3 to 4 or more years in relatively climax species to an annual production of uniformly large seed crops in the more invasive pioneer species. The mobility requirement of the pioneers selects for consistently large annual seed production. However, under closed-canopy conditions of relatively climax forests, where opportunities for successful establishment are infrequent, economy in expenditure of energy resources is the dominant strategy. Periodic production of large seed crops may suffice to probe for rare, new canopy-gaps that appear at intervals. The most shade-tolerant species maintain, as it were, standing armies of suppressed saplings and transgressives awaiting release by a break in the dense canopy; under these conditions, sustained annual production of seeds at a high level would be a profligate waste of resources. Where seed predation is critical (cf. Janzen 1970), bumper crops at irregular intervals may outstrip the consuming capacity of the predators. For example, even fast-breeding beetles may be caught at a low point in their population cycle by a sudden, out-of-phase largesse of their favorite seeds, and might be completely satiated by a fraction of the bumper crop in a heavy mast year. The acorn weevil (*Curculio*) and oak play this game.

15. Age at first fruiting is least in pioneer species (less than 15 years) and greatest in relatively climax species (more than 30 years). The mobility requirement associated with invasion of ephemeral forest openings selects for early reproductive maturity in pioneers. The old-field or gray birch (*Betula populifolia* Marsh.) fruits at 8 years (Fowells 1965). Pioneering *r*-strategists are programmed to be disadvantaged by competition as succession proceeds, and must make the most of favorable reproductive opportunities available to early colonists. Climax species destined for longer tenure follow the *K*-strategy of economy with delayed fruiting, and concentrate their energy expenditures on vegetative growth during the first few decades. For example, beech commonly attains an age of 40 years before fruiting (Fowells 1965).

16. Sex structure in most tree populations is either monoecious (unisexual flowers of both sexes present on the same individual) or hermaphrodite (flowers bisexual), a distinction apparently not correlated with successional rank. On the other hand, the less common dioecious sex structure (sexes segregated on different individuals) is an option strongly correlated with the pioneering way of life. Consider the dioecious trees of the deciduous forest: willow, cottonwood, boxelder (*Acer negundo* L.), corkwood (*Leitneria floridana* Chapm.) and some ashes (*Fraxinus*), all heliophiles of wetlands; and sassafras (*Sassafras albidum* (Nutt.) Nees), sumac (*Rhus*), osage-orange (*Maclura pomifera* (Raf.) Schn.), persimmon (*Diospyros virginiana* L.), prickly ash (*Zanthoxylum*), and several true ashes (*Fraxinus*), of drier or more well-drained habitats. With the dioecious arrangement, self-pollination is ruled out and the genetic advantages of outcrossing are obligate. However, about half the individuals in the population (the pollinating male trees) do not produce seeds. There are some outstanding features possessed by trees of pioneer character that make this strategy feasible. Foremost is the *r*-strategy of channeling a greater proportion of energy resources into the

production of uniformly large annual seed crops, often with enormous numbers of seeds per individual. In dioecious pioneers, the lavish hyperproductivity of seeds by the female trees may compensate for the seedlessness of male trees.

Another critical feature favoring dioecism in pioneer trees is their abundance and gregariousness in appropriate, disturbed or open habitats. Gregariousness ensures that individuals of opposite sex will be in close proximity, thus facilitating cross-pollination by wind (as in poplar, boxelder, and ash) or by insects (as in willow, sassafras, and sumac). A dispersed or diffusely scattered population of unisexual individuals would be a comparatively inefficient arrangement for pollination, and evolutionarily improbable.

The same strategy may be involved on a wider scale in the evolution of wind pollination: like dioecism, it is efficient only with a gregarious population structure. All wind-pollinated trees are diclinous, either monoecious or dioecious, an arrangement which necessitates or favors outcrossing; but it is not efficient unless many individuals of the same species are in close proximity. The correlation between gregariousness and anemophily is nearly complete in the boreal forest (taiga or montane), almost all of the arboreal genera being anemophilous (spruce, Picea; fir, Abies and other conifers; alder, Alnus; birch; poplar). Extreme concentration of dominance in anemophilous species is also seen in cold desert (temperate shrub-steppe), as in the sagebrush (Artemisia tridentata Nutt.) and shadscale (Atriplex confertifolia S. Wats.) zones of western North America. Of course, the same is true of all grasslands and marshlands, which are dominated by the anemophilous families (Gramineae, Cyperaceae, Juncaceae, Typhaceae).

Most of the dominant trees in temperate deciduous forest are wind pollinated, as general observation and available sampling data clearly indicate (Whitehead 1969). On the other hand, because of the extreme concentration of dominance, comparatively few taxa are anemophilous, the great majority being subordinate in biomass and entomophilous. Thus, the deciduous forest of eastern North America has 30 families, 44 genera, and 260 species of trees with entomophilous pollination; but only 12 families, 22 genera, and 87 species of trees in this forest are anemophilous (Wells, original). Moreover, the anemophiles are of diverse seral rank, including poplar, birch, walnut (Juglans), hickory (Carya), mulberry (Morus), elm, boxelder, ash, oak, beech and, of course, pine (Pinus) and juniper (Juniperus). Therefore, mode of pollination is not useful as an index of climaxness in temperate forest.

The other side of the coin is seen in tropical forests of high species diversity, and consequently extremely low gregariousness in the population structure of most species; wind pollination is remarkably rare among tropical trees, which are overwhelmingly entomophilous (Richards 1952). It is significant that there are indeed anomalous examples of anemophilous trees in the tropics, but they are all abundant, gregarious

pioneers of forest margins, openings or clearings. For example, there are the many American species of dioecious Cecropia (Moraceae) and its seral analog in Africa, Musanga cecropioides (Richards 1952), the American Triplaris (Polygonaceae), and the pantropical Trema (Ulmaceae), all possessing the highly specialized floral morphology requisite for wind pollination, and all dominating the early phase of forest succession. Of course, entomophily is either universal or well represented among all phases of tropical forest succession, including the early pioneer phase. Thus, wind pollination, which is prevalent in all stages of succession in monodominant temperate forests, may have evolved as a specialty among gregarious, r-selected invaders of forest openings in the species-rich tropics. Mode of pollination should be a useful trait for a climax index of tropical forests.

Growth, Maintenance and Longevity Factors

The relatively long life span of trees has numerous facets shaped by evolution in relation to succession. Assembled under one heading is a seemingly heterogeneous but interrelated array of traits, including growth rate, longevity, and maximum height; the various wood characters, viz. wood density, modulus of rupture, tyloses, decay resistance, ray volume, and ring porosity; and spiny armament.

17. Growth rate is very rapid in opportunistic trees (as much as 2.5 cm in diameter/yr for cottonwoods under optimal conditions), but very slow in relatively climax species (as little as 0.2 cm in diameter/yr for beech, even in young or early mature forest; cf. Fowells 1965). Rapid growth in height is essential for light-demanding, pioneer trees that cannot survive if overtopped and shaded in the race to the canopy level. On the other hand, species following the climax strategy usually can tolerate shade, and can afford to grow at slower rates, investing a larger proportion of their energy budget in maintenance and longevity factors, such as density, strength and decay resistance of wood.

18. Longevity in deciduous forest trees ranges from less than 100 years for many pioneers to more than 250 years for relatively climax species. For example, willow attain 85 years or less, compared to 600 years for some oak species (Fowells 1965). Pioneering species occupying sites only ephemerally open (such as canopy gaps) or sites subject to catastrophic disturbance (such as river banks) are at a selective advantage with rapid growth and early maturity. Structural or biochemical investments fostering longevity are sacrificed for quick success in the race for sunlight, and for precocious, profligate seed dispersal to increase the probability of colonizing new, ephemeral sites before the old ones are eliminated. Trees of greater longevity have the potential advantage of attaining and holding favored positions in the canopy from which they can rain dispersal units over long time periods. Even if they produce relatively small seed crops, long life-spans provide extended opportunities for enough reproduction to saturate all available sites in the vicinity. When coupled with extreme tolerance of shade, this

strategy may lead to dominance of both canopy and understory layers by a single species; the culmination of the 'monoclimax' concept of Clements (1916).

19. Maximum height varies widely in all phases of the successional gradient; both pioneer and climax trees vary at maturity from relatively short (10 m or less) to very tall (35-60 m or more). Nevertheless, at any given stage of succession, the taller species exert environmental control over subjacent layers, particularly with respect to light intensity, and hence have a relative advantage over shorter species. When coupled with longevity (as in oaks), great height compensates for a lack of shade tolerance, and prolongs tenure into the climax phase of succession.

20. Wood density, expressed as specific gravity, tends to increase along the seral gradient from pioneer to climax. Pioneers of rapid growth, profligate reproduction, and short life-span, constantly dispersing to new sites where they are soon engaged in a growth race for temporary places in the sun, tend to have lighter wood; they do not expend more than minimal energy on thickening and hardening of cell walls with polysaccharides and lignin. Relatively climax species, growing at slower rates and with a different longevity and dispersal strategy, invest more heavily in strength and durability of wood, for example, with thicker, more lignified xylem (vessel and fiber) cell walls, which confer a greater density to the wood.

The lightest woods (specific gravity 0.2-0.4) of temperate deciduous forests are found in the most opportunistic, invasive species: cottonwood, willow, corkwood, boxelder, silver maple (A. saccharinum L.), tulip tree, and Hercules club (Zanthoxylum clava-herculis L.). Species in the middle to upper ranges of the seral spectrum have some of the heaviest (and hardest) woods (specific gravity 0.5-0.7), for example, many oaks, beech and sugar maple (Hough 1898; Record 1914; Brown and Panshin 1940).

In the tropics, a parallel pattern is seen (Richards 1952). Extremely light-wooded trees pioneer in openings, clearings or margins of the tropical rain forest. Most ubiquitous are the many species of Cecropia in America, and their analog in Africa, Musanga cecropioides. Balsa (Ochroma) and kapok (Ceiba) trees, well-known for their extraordinarily light wood (specific gravity 0.23 in Ochroma) and seed fiber, typify the entire pantropical family of Bombacaceae, which has specialized in the pioneering way of life in much the same way as the temperate family Salicaceae, but often in more upland or xeric habitats. They are mostly fast-growing, flimsy-wooded trees, widely invasive in open sites by virtue of enormous crops of wind-dispersed, cottony-fibered seeds. At the other extreme of the seral gradient, there are families represented in well established, tropical forests by trees with some of the heaviest, hardest woods in the world. Economically valuable examples are American, African, and Philippine mahogany (Swietenia, Khayia, and Toona), ebony (Diospyros), teak (Tectona), and lignum vitae (Guaiacum). It may be noted that slow

growth and dense, heavy wood are also characteristic features of some trees of arid regions.

21. Modulus of rupture (kg/cm^2) is a more direct measure of the mechanical strength of wood (Hough 1898; Record 1914; Meyer 1922). Again, pioneer species tend to have weaker wood than relatively climax species, for the correlative reasons cited above. The pioneering life-style sacrifices strength of wood for extremely rapid growth, and this weakness is probably the limiting factor determining the short life-span of pioneer trees. Not only are pioneers subject to total loss from early breakage of the main trunk, but they also tend to lose position in the canopy as a result of wind damage to branches, especially when laden with wet foliage, or when glazed with ice or decked with wet snow. Willow and cottonwood (modulus of rupture 400-800 kg/cm^2) are notorious for limb breakage. Hence, the large populations of pioneer trees in the forest canopy during the early phases of succession are eventually decimated by catastrophic losses and by the steady encroachment of species with stronger, more resilient branches. For example, oak, beech and sugar maple (modulus of rupture 1150-1250 kg/cm^2) are tenacious of limb. Maximum retention of a broad crown-spread in the canopy is an important part of climax strategy, and requires a large investment in superior wood quality. In conjunction with efficient leaf-mosaics, maximal interception of light by the broad, unbroken canopy of relatively climax trees interferes with germination and establishment on the forest floor of all heliophile species. Thus, a host of potential competitors are nipped in the bud, or in the seed! If less light-requiring species succeed in becoming established, they are often disadvantaged in subcanopy competition with the seedlings and saplings of the extremely shade tolerant climax species.

22. Tyloses are cyst-like occlusions that plug the lumina of non-functional xylem vessels. They tend to slow the internal spread of the mycelium of fungal wood rots that attack the heartwood of living trees. Tyloses are present in most long-lived, relatively climax trees, but are absent in many short-lived, pioneer species. Absence of tyloses may enhance the process of rotting and hollowing of trunks, thus increasing the probability of premature blow-down.

23. Decay resistance of the wood of trees has been largely determined by observations of the durability of lumber in contact with soil (Hough 1898; Brown and Panshin 1940). The soft, pulpy wood of pioneer species decays faster than the hard, dense wood of many relatively climax species. The latter more often possess a biochemical armament of one or more allelochemic or antibiotic substances, such as tannins, other phenolics, alkaloids, *et al.*, which deter attack by insects and fungi. The chemical defenses of stems are strategically concentrated in the inactive heartwood, and in the bark (McKey 1974).

24. Armament by branch-thorns, stipular spines, or epidermal prickles, is confined to the pioneer end of the seral spectrum among

trees of broadleaf deciduous forest. Thorniness is a more frequent option among the more shrubby invaders of openings, as in the huge genus of hawthorns, crab apple (Malus) and plums (Prunus). A few trees pioneering in open situations (osage-orange, honeylocust and black locust) are ferociously armed in the sapling stage and on juvenile shoots accessible to herbivores but not so on branches high in the canopy, which are unarmed. The armed seedlings and lower branches of trees in open, grassy habitats would be otherwise vulnerable to incidental browsing by large herbivores that feed primarily on grasses which are absent in closed-canopy forest. As fitness in energy-budgeting dictates, the genes for spiny armament are turned off above the old "juvenile" zone on the lower trunk of the tree. Selection pressure by browsing herbivores seems to have encouraged only a modest presence of armed trees in the relatively mesophytic North American deciduous forest, compared to xerophytic vegetation such as the thorn forest or thorn woodland of the Southwest. Predictably, the armament strategy should assume a greater importance as available forage for herbivores is limited by increasing aridity.

25. Ray volume, or proportion of wood comprised of parenchymatous tissue arranged in radial fashion, tends to be low in pioneer trees and high in relatively climax species (Myer 1922). Since wood parenchyma serves as a depot for the storage of energy reserves, such as starch, a large ray volume would be compatible with the slow growth and irregular fruiting habit of the conservative, climax way of life. On the other hand, the pioneering strategy of profligate reproduction and rapid growth, which increases the probability of finding and maintaining a temporary place in the sun, necessitates the correlative sacrifice of energy reserves and associated specialized storage tissues. The largest ray volume (up to 31 percent) occurs in oak.

26. Ring porosity is a feature of the wood of many species of temperate dicotyledonous trees, characterized by an exaggerated development of the xylem vessels in the early or spring wood. Many of the vessels produced at this season have diameters more than tenfold greater than vessels formed in the late or summer wood (Brown and Panshin 1940). Relatively homogeneous wood, lacking ring porosity, is referred to as diffuse porous wood, a condition present in nearly all tropical and many temperate dicotyledonous trees. In the deciduous forest of eastern North America, the most shade tolerant, mesophytic trees, such as beech, sugar maple, and basswood, are diffuse porous. Ring porous trees tend to have high light requirements and usually reproduce only in sunny, relatively pioneer habitats, with either moist or dry soil.

Although practically all temperate, broadleaf trees with diffuse porous wood are mesophytic or wetland species, and some are extremely shade-tolerant (e.g., beech, sugar maple (Acer saccharum Marsh.)), many are intolerant of shade, and have high light requirements. These species follow an invasive, pioneering way of life in openings, mainly on mesic sites that favor the eventual development of dense, closed-canopy forest. Examples are sweet gum, tulip tree, sycamore (Platanus occidentalis L.),

gray birch, and various riparian or swamp maples (boxelder, silver maple and red maple, A. rubrum L.). However, many ring porous trees are also successful in open, mesic or wet habitats, including various swamp oak species (pin oak; willow oak, Q. phellos L.; water oak, Q. nigra L.; and others), pumpkin ash (Fraxinus profunda Bush.), water hickory (Carya aquatica Nutt.); nutmeg hickory (C. myristicaeformis (Michx. F.) Nutt.), cottonwood, willow, and water locust (Gleditsia aquatica Marsh.). Thus, in wet or mesic habitats, ring porosity is only an option of heliophile trees, but the most shade tolerant species are diffuse porous.

On the other hand, the most xerophytic trees of the eastern deciduous forest are practically all ring porous. These include the species that penetrate furthest into the arid parts of the Great Plains: bur oak (Q. macrocarpa Michx.), post oak (Q. stellata Wang.), shin oak (Q. havardii Ryd.), and hackberry (Celtis reticulata Torr.). Many xerophytic shrubs of the Plains are also ring porous, including sumac (smooth sumac, R. glabra L.; fragrant sumac, R. aromatica var. serotina (Green) Rehd.), buffalo berry (Shepherdia argentea Nutt.), serviceberry or saskatoon (Amelanchier alnifolia Nutt.), wild plum (Prunus americana Marsh.) and choke cherry (P. virginiana L.). It is interesting to note that most of the successful trees of shelterbelt plantations in the Great Plains are ring porous: osage orange, honeylocust, and ash.

The fact that high-climbing lianes have xylem vessels with anomalously large cross-sectional areas and extremely rapid translocation suggests that ring porosity facilitates rapid rates of water conduction during times of transpiration stress. Because of the sunniness of their habitats, it seems likely that pioneer trees of moist soil, as well as dry, experience frequent transpiration stress. In temperate latitudes, low soil temperatures in spring may impede water uptake, thus increasing transpiration stress, and favoring pioneer or xerophytic tree species with more efficient, ring porous, vascular systems.

Other Seral Strategies

Several additional characters related to succession were not scored, including leaf flushes, oil content of seeds, myrmecophily, and mode of carbon fixation. Some of these traits may prove useful in analyzing tropical forests. Leaf flushes are rhythmic bursts of growth stemming from synchronous bud-break. In the moist tropics, the trait is characteristic of relatively climax forests. Pioneering trees of open habitat tend to have more or less continuous growth in the absence of seasons. The distinction is one of timing, since the latter can be regarded as a flush of very long duration. The climax strategy of rhythmic leaf flushing is conservative of energy because of economy in the synchronous mobilization of resources throughout the tree during the relatively brief spurts of growth. It is correlative with the general climax strategy of slow, long-term growth, outlined above. A second adaptive strategy of herbivore satiation has been suggested for leaf flushes recently (McKey 1974). The simultaneous production of huge biomasses of foliage outstrips

the growth potential of the leaf-eaters specializing on one species, even though in trees, young leaves have lower levels of allelochemic defenses than older leaves (e.g., Feeny 1970). As the leaves mature, the buildup of chemical armament deters sustained growth on the part of the herbivore population (McKey 1974).

In the broadleaf deciduous forests of temperate regions, leaf-flush is strongly seasonal (vernal), but the duration of growth varies along the successional gradient, as in the tropics. Climax trees have relatively brief bursts of growth with fewer leaves per growth interval than pioneer trees. Deciduous trees retain a record of several years on each twig. Preliminary counts of the number of leaf scars per interval (between successive rings of terminal bud-scale scars) show a consistent pattern of relatively few leaves per flush for several years in species scoring high on the climax index scale. Because of the ease of measurement, this character should be incorporated in the index, but insufficient data are at hand.

Oil content of seeds in relation to ecology has been reviewed recently (Levin 1974). Lipids are more efficient forms of food storage than carbohydrates because fats pack more energy per unit weight, in terms of either caloric content or ATP-yield. The optimization of fitness in seeds of K-strategists predicts higher proportions of lipid (oil) reserves in the seeds of trees successful in relatively climax communities (Levin 1974). Coupled with the greater weight of K-selected seeds, high oil-content maximizes the heterotrophic-headstart effect that enhances survival at carrying-capacity densities (as discussed above; cf. seed weight). Thus, lipid content of seeds would appear to be a promising character for the climax index. For example, the high oil content of beechnuts contrasts with the starchiness of acorns. However, quantitative data are not available for many forest species.

Myrmecophily in trees is strikingly correlated with the pioneer phase of tropical forest succession. Thus, the well-known mutualism between ants and various species of *Cecropia* and bull-horn *Acacia* in the American tropics (Belt 1874; Ridley 1910; Janzen 1966) has been a successful strategy for these heliophile fugitives from dense, closed-canopy forests (cf. also the protocooperative *Triplaris* in America and *Macaranga* in southeast Asia). The ants help to slow down succession around the colonizing host trees of open habitats by assiduously weeding out the competing plants that germinate in the vicinity (Janzen 1967, 1969). Insect pests are also repelled by the patrolling ants, thereby enhancing the growth of the host tree, which budgets a modest outlay of food bodies and/or shelter (Janzen 1966).

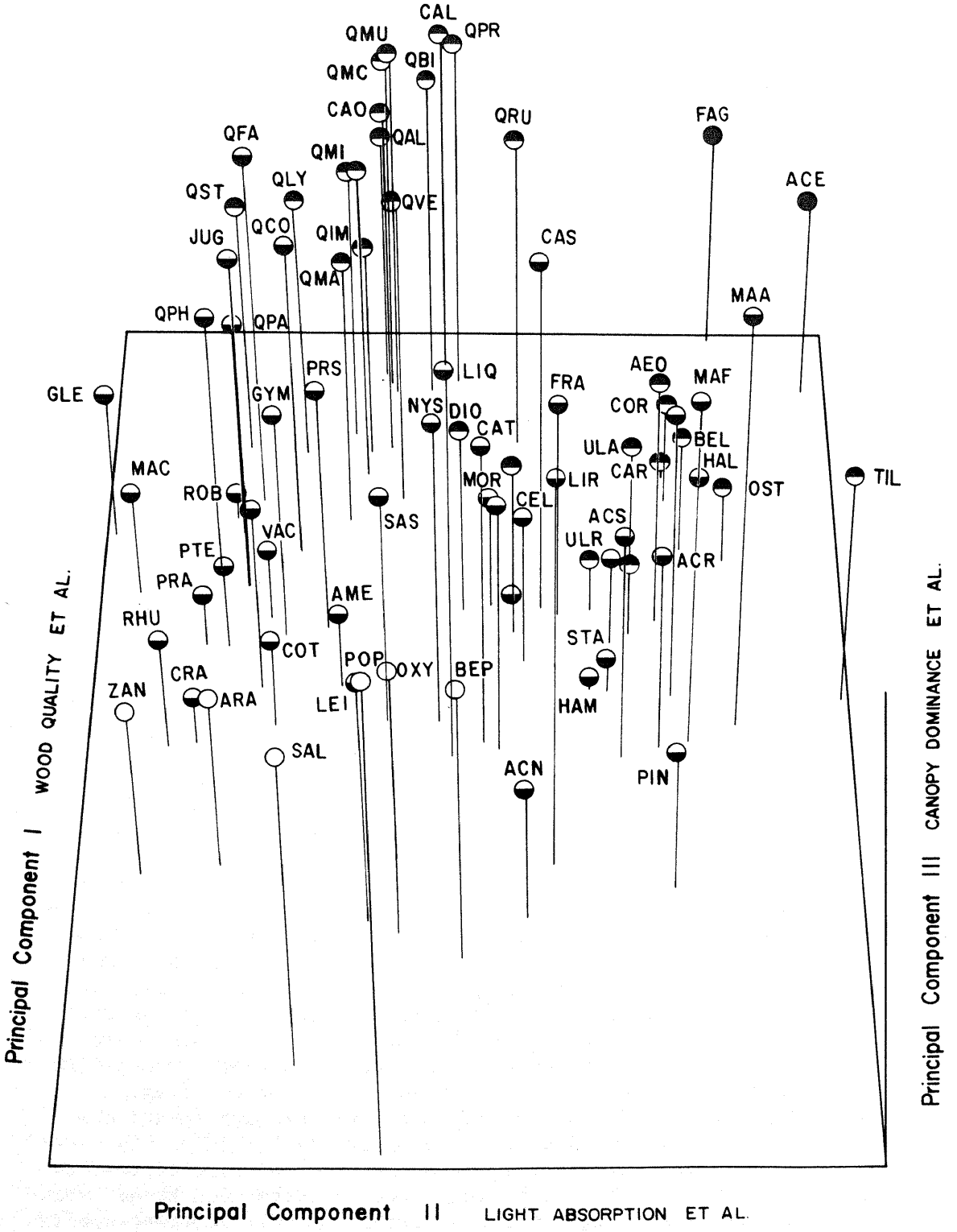
The C_4 or Hatch-Slack pathway of carbon fixation is restricted (in forested regions) to heliophile plants, mainly in the early stages of succession. Shade tolerant plants in forests have the C_3 or Calvin-Benson pathway exclusively. The C_4 plants may be distinguished from C_3 plants, which also include many heliophile pioneers, by the striking

Kranz arrangement of the chloroplasts in and around the bundle sheaths, and by their different (less negative, relative to standard) $^{13}C/^{12}C$ ratios. The known Kranz plants are mainly herbaceous, but some woody plants have the trait (cf. Troughton, Wells and Mooney 1974). In the tropics, the C_4 photosynthetic pathway is known in many pioneering grasses (Downton 1971). It should be sought among the diverse colonizing species of early forest succession. The remarkable efficiency of carbon fixation by the C_4 (relative to C_3) pathway only under high light intensities limits this photosynthetic strategy to open sunny habitats (Chollet and Ogren 1975). Thus, C_4 plants are widely distributed in arid regions and in the xeric, sunny stages of succession in humid regions. Historically, the C_4 pathway may have evolved first under the latter conditions (cf. Wells 1976). The favorable balance of CO_2 uptake relative to transpirational water loss during gas exchange at high temperatures by C_4 plants is well known (Hatch, Osmond and Slatyer 1971; Bjorkman and Berry 1973). The high light requirement of C_4 plants is probably connected with the Kranz restriction of chloroplasts, which is less efficient for light absorption than the more homogeneous deployment of chlorenchyma in C_3 plants.

DISTRIBUTION OF TREES IN ECOMORPHOLOGICAL HYPERSPACE AND AN INDEX OF SERAL POSITION

A sample of 75 species of trees indigenous to the eastern deciduous forest of North America was selected. Most of the principal dominant species, and a nearly complete representation of the more arboreal genera (more than 50), were included in the study. Each species was scored for the 26 ecomorphological characters according to available data, which were segmented into mostly 3 steps per character on a standardized scale of increasing climaxness, as discussed above. The character analysis yielded a 26 x 75 data matrix, from which principal components of variance were extracted and used to generate a 3-dimensional projection of the 75 species of trees in ecomorphological character-space, as an approximation to n-dimensional, seral hyperspace. The distribution of tree species in the 3-D projection (Figure 2) is governed by differential loadings of the 26 characters on the first three principal components used for the Y, X and Z axes with 22.4, 13.9 and 10.9% of trace, respectively.

The first or Y-axis of the projection, which is indicated by the two edges receding from front to rear in perspective, is influenced most by wood density and strength (modulus of rupture). Species with light, weak wood are positioned in the foreground and the heavier, stronger hardwoods are to the rear of the diagram. The second or X-axis, indicated by the parallel front and rear edges, is weighted most for efficiency of leaf arrangement and degree of shade tolerance. The most shade tolerant species with opposite or two-ranked leaves, arranged in thin, planar sprays, are toward the right-hand side of the diagram. Light-demanding species with spiral leaf arrangements are toward the left. The third or vertical Z-axis is indicated by length of the vertical line below each circular symbol for a species, and most represents the height and crown-spread of the tree. Tall species with broad crown-spreads are subtended by longer vertical lines; short, excurrent species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SAL
ACN
PIN
Principal Component I WOOD QUALITY ET AL.
Principal Component III CANOPY DOMINANCE ET AL.
Principal Component II LIGHT ABSORPTION ET AL.

are subtended by shorter lines. In summary then, the principal gradient from pioneer to climax end-members in succession-oriented character-space extends diagonally, from most pioneer in the lower-left, fore corner to most climax in the upper-right, rear corner, and from shorter to longer vertical lines.

A general view of the distribution of tree species in the ecomorphological model (Figure 2) supports the individualistic concept of plant communities advocated by Ramensky (1924, 1926), Gleason (1926), Curtis and McIntosh (1951), Curtis (1959), Whittaker (1951, 1956, 1967), McIntosh (1967), inasmuch as exact congruences or discrete clusterings of species appear to be lacking. On the other hand, an unexpected result for a successional model is the arrangement in character-space of convergent sets of species that conform in a general way to the principal "climax" communities of the eastern deciduous forest, as defined by Braun (1950), Clements (1916), Nichols (1913-1920, 1923, 1935), and Oosting (1942). Thus, the swarm of oak and hickory in the upper-left, rear sector of the 3-D projection corresponds to the well-known oak-hickory "association", which has a suspiciously ubiquitous distribution within the deciduous forest formation. However, the chestnut-chestnut oak "association" is not segregated clearly from the oak-hickory in the diagram. Much more striking is the segregation of beech, sugar maple, and basswood from all other species in the upper-right, rear sector of the model (near the corner). This slightly disjunct sorting parallels the comparatively well-marked beech-maple and maple-basswood "associations" of the early ecologists. Also toward the upper-right sector are species of the "mixed-mesophytic association" of Braun (1950), including the magnificent trees of the Appalachian cove forest (silver bell, Halesia carolina L.; Fraser magnolia, Magnolia fraseri Walt.; cucumber magnolia, M. acuminata L.; sweet buckeye). Invasive trees of old fields, forest margins, riverine or other open habitats are distributed in the lower-left, fore of the projection, e.g., gray birch, sumac, plum, hawthorn; cottonwood, willow and boxelder are along the front margin.

Figure 2. Distribution of 75 species of trees in a successional character-space generated from principal components analysis, based on the 26 ecomorphological characters. The "pioneer" extreme is in the left fore corner (lower left of model) and the "climax" extreme is in the right rear corner (upper right of model). An independently derived index based on Euclidean distances generated from the same 26 x 75 matrix is segmented objectively into 4 equal intervals of climaxness: 0-25% (circles unshaded), 26-50% (circles shaded in lower half), 51-75% (circles shaded in upper half), 76-100% (circles fully shaded). However, the 75 species are distributed very unequally among the 4 quartiles, with by far the greater proportion in the 2 middle quartiles. There are only 6 species in the "pioneer" quartile (Populus deltoides, Salix nigra, Betula populifolia, Zanthoxylum clava-herculis, and Oxydendrum arboreum), and only 2 species in the "climax" quartile (Acer saccharum and Fagus grandifolia). Letter-codes for species are given in Appendix. Unlabeled species in figure 2 are (l. to r.): SAP (nr. ROB), CAC (with QMI), ASI (with MOR), ILE (above CEL), CLA (below CEL), CER (nr. ULR), PLA (below ACS), PLO (with COR).

Thus, there are ecomorphological convergences on succession-oriented traits among species of taxonomically dissimilar genera that often occur together in close ecological association. Of course, it should be emphasized that no data concerning associations of species in plant communities entered into the climax index, which is based on functional ecomorphology. Each character of the climax index has its own fitness rationale, and each species has its own, independent, character analysis. Therefore, the correspondence of proximity in successional character-space with coexistence in traditional "climax" associations is indeed remarkable. The equality of climaxness of the traditional associations ("oak-hickory", "beech-maple", etc.) of the deciduous forest of North America is called into question.

Beech and sugar maple are unique in combining: 1. maximal interference with light penetration through their efficiently arranged leaf-mosaics, thus adversely affecting all other tree species growing under their canopy; 2. maximal shade tolerance, thus ensuring their reproduction in their own shade; and 3. sufficient sturdiness and longevity to maintain canopy position and to outlast most associated species. Hence, the ecomorphological model predicts a maximally climax role for beech and sugar maple throughout their wide geographic and ecological ranges within the eastern deciduous forest. Corollary to this view is a successional role for the other "climax associations" of the formation. An exciting possibility is that much of the species richness of the deciduous forest (347 more or less arborescent species in 66 genera of dicotyledons) is sorted out on a seral continuum.

Climax Index

A numerical ordination of tree species according to their succession-oriented ecomorphology is readily derived from the data used to generate the 3-dimensional projection. The simplest approach is the summation of the scoring values for all characters in the vector of each species. The vector sums of the climax index are analogous to the hybrid index of Anderson (1949). The raw-score sums obtained in this way range from 8 (willow) to 51 (beech) on a potential scale of 0 to 53. Data for cottonwood, honeylocust, northern red oak, and beech are summarized in table 1. To express these values as a climax index, the sums were converted to percentages of the maximum possible value; on this scale the range is from 15 (willow) to 96 (beech). If this span of about 80 percentage points is divided into 4 increments of 20 points each, an unequal distribution of species among the 4 categories is observed. In the most pioneer group (15-35%), there are only 9 species; in numerical ordination these are: willow, cottonwood, prickly ash, Hercules club, corkwood, sourwood, sumac, gray birch and boxelder. The second group of relatively pioneer species (36-55%) is by far the largest because of the many species of hawthorn. Otherwise, it comprises 29 species, including tulip tree, sweet gum, silver maple, willow, oak, sour gum (*Nyssa sylvatica* Marsh.), honeylocust, sassafras, pin oak, Kentucky coffee tree, black walnut (*J. nigra* L.), osage-orange, scarlet oak, catalpa, black locust, black cherry, red maple, hackberry, and white ash (*F. americana* L.). The third group (56-75%) has 32 species of intermediate to relatively climax character: for example, cucumber tree, yellowwood, black oak,

sycamore, redbud (Cercis canadensis L.), Spanish oak (Q. falcata Michx.), silver bell, persimmon, American chestnut (Castanea dentata (Marsh.) Borkh.), sweet buckeye, American elm (U. rubra Muhl.), red mulberry (Morus rubra L.), basswood, post oak, shagbark hickory (C. ovata (Mill.) Koch), white oak (Q. alba L.), ironwood (Ostrya virginiana (Mill.) Koch), northern red oak, chinkapin oak, sweet birch (B. lenta L.), flowering dogwood (Cornus florida L.), kingnut hickory (C. laciniosa (Michx.) Loud.).

The most climax group (76-96%) contains only 5 species: hornbeam (Carpinus caroliniana Walt.), 76%; chestnut oak (Q. prinus L.), 79%; swamp white oak (Q. bicolor Willd.), 79%; and sugar maple and beech at 89 and 96%, respectively. The fact that sugar maple and beech are the only species in the top 20 point range (80 to 100%) emphasizes their peculiarly isolated position as the ultimately climax species of the eastern deciduous forest, as discussed above. Most species (61 of the 75 species, or over four-fifths) considered here fall in the intermediate range of successional status on the climax index scale (36 to 75%). Several species receive identical numerical scores, but each species has a unique combination in its vector of characters. If all of the more arboreal species of the eastern deciduous forest (about 324 species distributed in 52 genera, excluding the 14 genera of very shrubby trees) are scored for the 26 succession-oriented characters, the inequality of distribution of species in different ranges of the climax index is greatly enhanced. For example, the second range (climax index 36-55%) is anomalously augmented by a conservative 143 species of hawthorns in the ecomorphologically uniform but taxonomically intricate genus Crataegus (Little 1953). Thus the ecomorphological model of succession indicates a maximum species diversity at the intermediate or earlier mid-seral stages, and minimal diversity at the extreme pioneer or extreme climax stages (Figure 3). Recent measurements of species diversity (Auclair and Goff 1971), based on field data from the well documented succession in the northwestern sector of the eastern deciduous forest (Curtis 1959), are in agreement.

Shade Tolerance-Longevity Subset

A combination of photosynthetic efficiency at low light intensities, efficient leaf arrangements that cast deep shade, and great longevity would insure a climax position in forest succession. Because these traits are of particularly critical importance in determining the seral roles of trees, a subset of 5 characters related to shade tolerance and longevity was selected to consider a simpler, more focused ordination of species. This set has much less discriminant power, but it has greater generality for analyzing succession in forests of widely different physiognomy. The characters selected were shade tolerance of juveniles, phyllotaxy, branch orders, growth rate, and longevity.

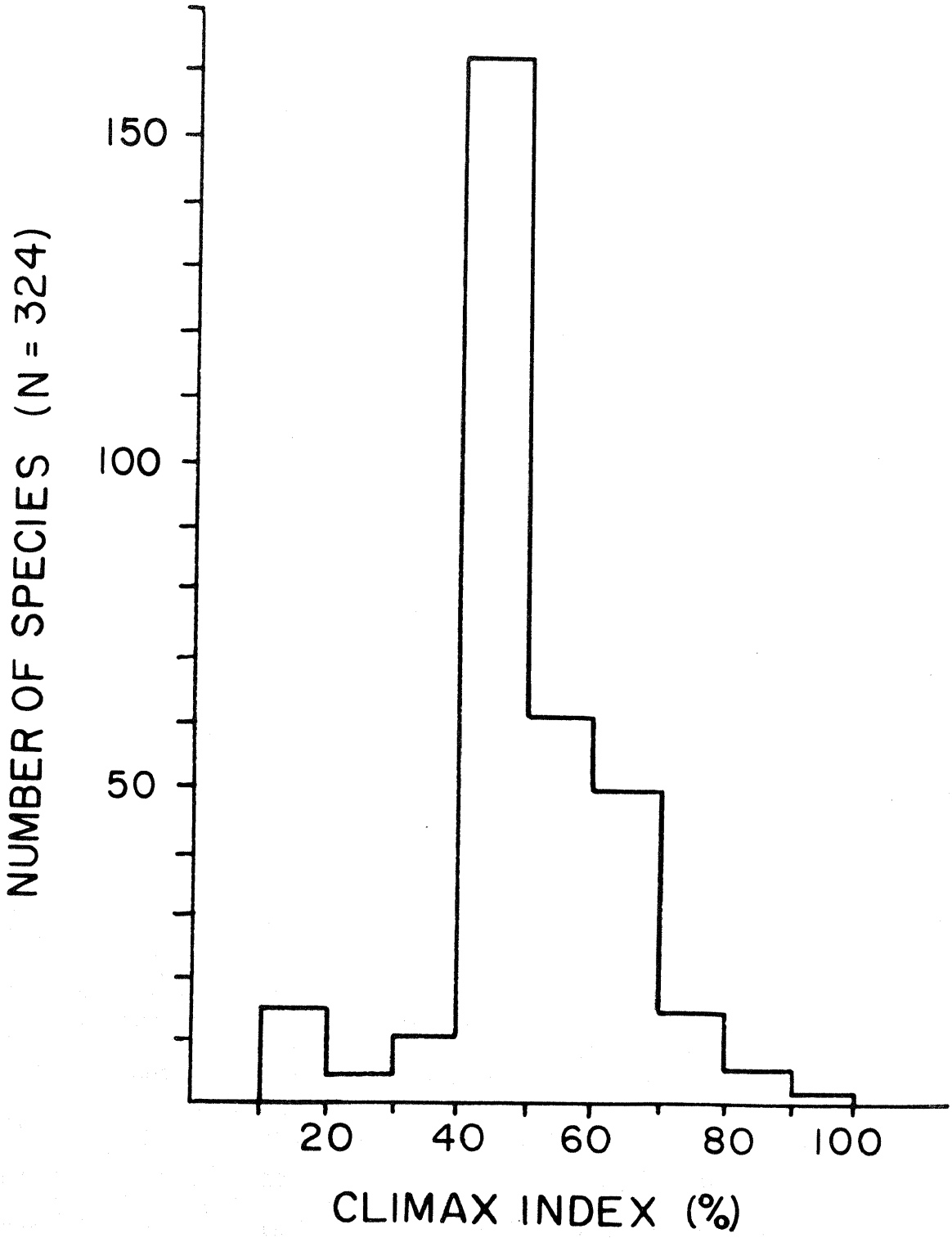
The shade tolerance-longevity subset produces a somewhat similar ordering for most of the species, despite the small sample (< 20%) of the 26 characters in the full climax index. However, important deviations appear consistently in many species of the oak and walnut families, which score especially low in the light-related factors. Thus, the oak (16 species), hickory (3 species) and walnut (2 species) that were examined

Table 1. Character analysis of *Populus deltoides*, *Gleditsia triacanthos*, *Quercus rubra* and *Fagus grandifolia* for 26 characters of the climax index. The Euclidean distance-index numbers are given for comparison (see Figure 4).

	Seral Ecomorphology			
Strategy:	"r"			
Light Absorption Factors	P. deltoides		G. triacanthos	
1. excurrence in youth	excurrent	= 0	deliquescent	= 2
2. branch orders	3-4	= 0	4-5	= 1
3. phyllotaxy	spiral	= 0	spiral	= 0
4. leaf division	undivided	= 3	compound	= 0
5. area of unit blade (cm^2)	100 +	= 2	2.5	= 0
6. leaf orientation	pendulous	= 0	pendulous	= 0
7. stomatal distribution	isofacial	= 0	bifacial	= 2
8. leaf oscillation	present	= 0	absent	= 2
9. cuticle luster	lustrous	= 0	lustrous	= 0
10. pigmentation	yellow-green	= 0	blue-green	= 2
Reproduction Factors				
11. shade tolerance	intolerant	= 0	intolerant	= 0
12 seed weight (mg.)	1.3	= 0	162	= 1
13. dispersal	wind	= 0	mammal	= 2
14. mast periodicity (yrs.)	1	= 0	1-2	= 1
15. age to fruit (yrs.)	10	= 0	10	= 0
16. sex structure	dioecious	= 0	monoecious	= 2
Growth, Longevity, etc.				
17. growth rate (diameter, cm./yr.)	1.5-2.5	= 0	0.5	= 1
18. longevity (yrs.)	100	= 0	120	= 0
19. height (m.)	30	= 1	43	= 2
20. wood density (sp. gr.)	0.34	= 0	0.63	= 2
21. modulus of rupture ($kg./cm^2$)	770	= 0	923	= 1
22. tyloses	absent	= 0	some	= 1
23. decay resistance	low	= 0	high	= 2
24. armament	absent	= 2	present	= 0
25. ray volume (% of wood)	13.7	= 0	18.4	= 2
26. ring porosity	semi-ring	= 1	ring	= 0
Sum		9		26
CLIMAX INDEX (%)		17		49
DISTANCE INDEX (%)		0		41

Table 1. Continued.

Strategy:	Seral Ecomorphology		"K"	
Light Absorption Factors	Q. rubra		F. grandifolia	
1. excurrence in youth	deliquescent	= 2	deliquescent	= 2
2. branch orders	4-5	= 1	5.0 +	= 2
3. phyllotaxy	spiral	= 0	2-ranked	= 2
4. leaf division	lobed (sh.)	= 2	undivided	= 3
5. area of unit blade (cm^2)	100 +	= 2	50 +	= 1
6. leaf orientation	horizontal	= 2	horizontal	= 2
7. stomatal distribution	bifacial	= 2	bifacial	= 2
8. leaf oscillation	absent	= 2	absent	= 2
9. cuticle luster	dull	= 2	dull	= 2
10. pigmentation	blue-green	= 2	blue-green	= 2
Reproduction Factors				
11. shade tolerance	intermediate	= 1	tolerant	= 2
12. seed weight (mg.)	4,325	= 2	284	= 2
13. dispersal	mammal	= 2	mammal	= 2
14. mast periodicity (yrs.)	2-5	= 2	2-3	= 2
15. age to fruit (yrs.)	25	= 1	40	= 2
16. sex structure	monoecious	= 2	monoecious	= 2
Growth, Longevity, etc.				
17. growth rate (diameter, cm./yr.)	0.5	= 1	0.2	= 2
18. longevity (yrs.)	200	= 1	366	= 2
19. height (m.)	45	= 2	37	= 2
20. wood density (sp. gr.)	0.64	= 2	0.63	= 2
21. modulus of rupture ($kg./cm^2$)	990	= 1	1148	= 2
22. tyloses	absent	= 0	present	= 2
23. decay resistance	low	= 0	intermediate	= 1
24. armament	absent	= 2	absent	= 2
25. ray volume (% of wood)	21.3	= 2	20.4	= 2
26. ring porosity	ring	= 0	diffuse	= 2
Sum		38		51
CLIMAX INDEX (%)		72		96
DISTANCE INDEX (%)		62		100


NUMBER OF SPECIES (N = 324)
150
100
50
20
40
60
80
100
CLIMAX INDEX (%)

in this study score, on the average, nearly 30 percentage points less on the subset than on the 26-character climax index. A similar pattern emerges for the legume family (except yellowwood, Cladrastis lutea (Mich. F.) Koch.).

On the other hand, comparatively few species score much higher on the shade tolerance-longevity subset than on the full set of characters. In fact, the only important exception in this anomalous direction is not among the broadleaf angiosperms of the study; it is a needle-leaf conifer, the eastern hemlock (Tsuga canadensis (L.) Carr.). The hemlock receives a full climax index rating of only 64%; but on the shade tolerance-longevity subset this extraordinarily climax tree scores 100%, a level achieved by only two broadleaf species: beech and sugar maple. The hemlock scores lower on the full set of 26 characters because of the several wood properties, excurrent growth, and seed dispersal traits peculiar to conifers as a taxonomic group with a perhaps pioneering ancestry.

Climax Index Based on Distance in Hyperspace

Ecomorphological distance between species in successional character-space was computed on the same 26 x 75 data matrix from which principal components were extracted for the 3-D projection presented above as figure 2. The latter, of course, was based on correlation. The same computational methods developed for measurement of taxonomic distance in phenetic hyperspace (Sokal and Sneath 1963) were used to generate inter-species distances vis-a-vis the phenetic traits involved in plant succession. The two species most ecomorphologically distant from each other happened to be cottonwood and beech. To establish a comparative scale, the distance of each species from beech is expressed as a percentage of this maximal distance in hyperspace. A distance index is obtained simply by taking the inverse values (100 minus the relative distance of each species from beech). The independently computed distance index turns out to be directly comparable to the climax index, described above. The relation between the computationally elaborate distance index (from the multivariate analysis) and the unsophisticated, arithmetical climax index (derived from the sum of character values in the vector of each species) is plotted in figure 4. The two expressions of the same data matrix are obviously strongly correlated ($r = 0.952$; $p = 0.00001$), but the distance index values average about 10 percentage points lower (e.g., see Table 1).

Figure 3. Frequency distribution plot of 324 species of trees on the climax index gradient. Most of the broadleaf-deciduous trees (or arboreal shrubs) in 52 genera indigenous to eastern North America are included. The modal class at 40-50% climaxness comprises 163 species, or about half the total number. Note that the most pioneer percentile (0-10%) is unoccupied, and that the most climax percentile (90-100%) has only one species (Fagus grandifolia at 96%).

The regression serves also as a scatter diagram that emphasizes the unequal distribution of tree species on the ecomorphological gradient, with relatively few extremely pioneer or climax species (Figure 4). Although the great bulk of the species are concentrated toward the center of the ellipsoid, each species has its own individualistic position in the scattergram. Thus, the uniqueness of the character vector of each species is better expressed in this plot (or even better in figure 2) than by the numbers of the climax index or distance index. The unequal distribution of the 75 principal species among the 4 quartiles of the Euclidean distance index is indicated also in figure 2.

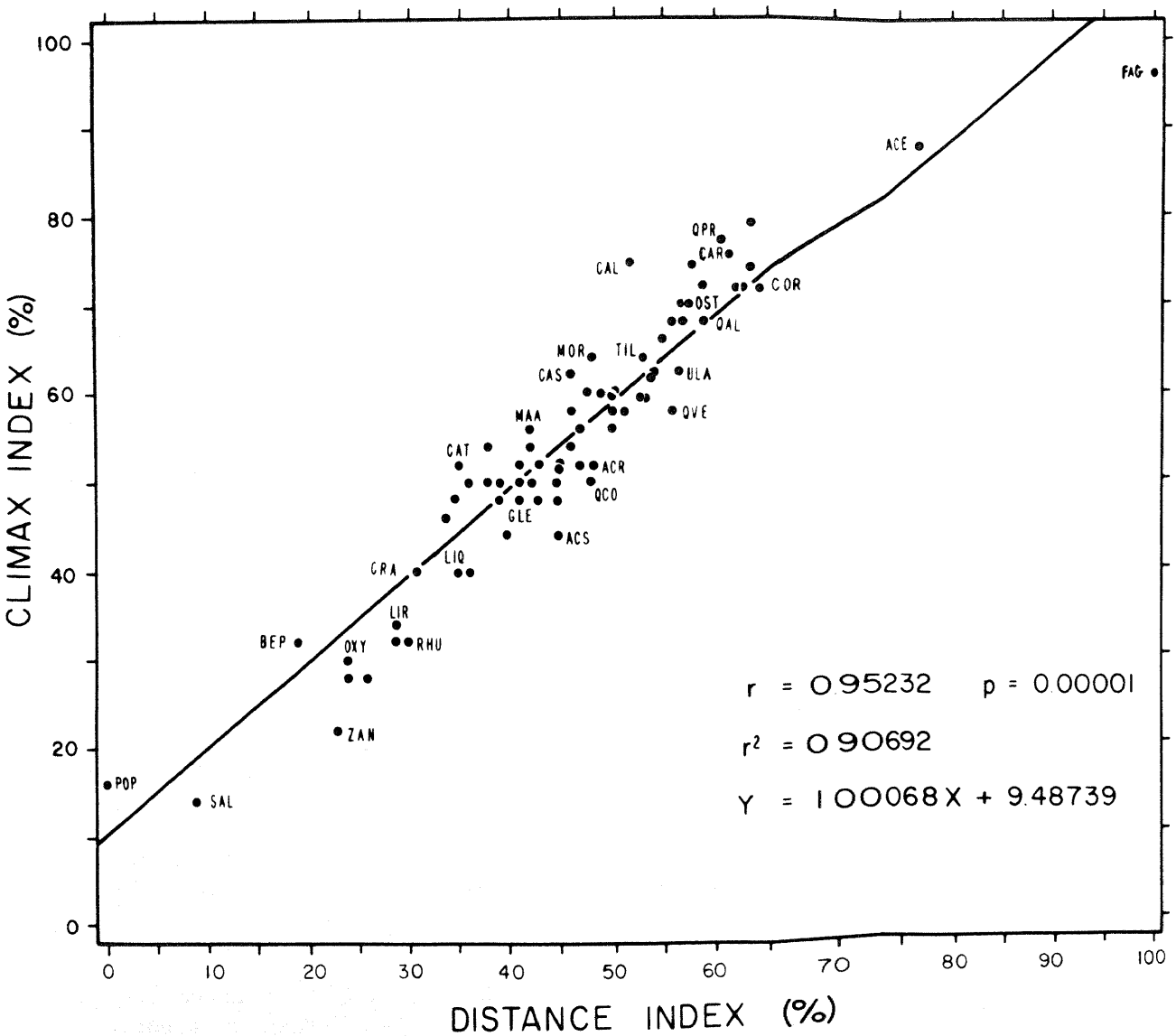


Figure 4. Regression of the arithmetical climax index on the Euclidean distance index for 75 species of the eastern deciduous forest. Letter-codes for species are given in Appendix. The climax index (y) averages about 10% higher than the distance index (x); the linear equation is very nearly y = x + 9.5.

IMPLICATIONS FOR ORDINATION OF FOREST COMMUNITIES

The continuity of the successional process contributes very largely to the theory of vegetational continua. The individualistic, but overlapping, seral ecomorphologies of forest trees (Figure 2) suggest that successional replacements in species-rich forests should be protracted, gradual rather than stepped, and with alternative sequences likely in the most diverse intermediate phases. The braided-stream metaphor of Cooper (1926) is an appropriate simile for the complexities of succession.

The continuum theory of vegetation of the Wisconsin school (Curtis and McIntosh 1951; Bray and Curtis 1957; Curtis 1959) was a refreshing departure from the typological thinking that had dominated plant ecology, and it was developed from objective, random sampling of stands, with no a priori views on the complex successional relations in the deciduous forests of southern Wisconsin. An ingenious, geometric, 3-dimensional model projected the sampled stands into a character-space generated from their quantitative species-compositions (Bray and Curtis 1957). A lack of clustering of different forest stands was apparent, nor was it possible to perceive a simple, linear sequence. The fact that the atmospheric continuity of stand distribution in Euclidean space stemmed largely from successional relations was shown by the strong correlation of the X and Z axes with post-settlement and gap-phase successions, respectively (Bray and Curtis 1957). The ordination of stands on the X-axis was essentially the same as in the original linear sequence of the continuum index (Curtis and McIntosh 1951).

Curtis himself suggested that suppression of the ancient Indian tradition for annual burning of the prairies and forests, following European settlement in the 19th century, had initiated the grand sequence of forest succession observed throughout the Middle West in the 20th century (Curtis 1959). In an elaborate account of the historical literature, he correlated the cessation of regional burning with fragmentation of the natural vegetation due to clearing and cultivation. Even at the time of settlement in the early 19th century, the "prairie peninsula" of southern Wisconsin was really a mosaic or patchwork of prairie and forest. The denser stands of trees were in topographic positions (scarps or hill-slopes, streams) sheltered from the destructive, wind-driven fires that swept through the tall-grass prairies on the more level, open surfaces (cf. Wells 1965, 1970a, 1970b, 1970c).

The most rapid forestation of prairie (following settlement, partial clearing, and cessation of fire) occurred where black oak or bur oak "grubs" (sprouting burls or stumps) had survived the regime of fire as low shrubs hidden by the tall grass. Apical dominance asserted itself after release from the drastic prunings of the prairie fires, and the shrubby burls grew into trees. Also, occasional trees of bur oak had

escaped destruction by grass fire because of their thick, insulating bark; and open groups of bur oaks formed savannas. These grassy oak-openings were filled in with dense stands of black oaks and white oaks after the fires ceased (Cottam 1949). The scattered, open-grown bur oaks with their massive, spreading, gnarled limbs persist among the numerous, excurrent, forest-grown, young trees as anomalous holdovers in the succession from savanna to forest. After canopy-closure, reproduction of oak and hickory dwindles, but invasion by basswood, sugar maple, or beech has taken place in many stands; and these shade tolerant species have come to dominate both understory and canopy.

Thus, a gradient of decreasing fire and drought resistance, and decreasing light requirement, is traced from treeless prairie or oak-opening of thick-barked, fire-resistant bur oak, through shade intolerant, sprouting hardwoods (black oak, white oak, shagbark hickory, et al.) to the thin-barked, very fire-sensitive, and very shade tolerant beech and sugar maple. Curtis (1959) cautiously regarded the latter as the closest approach to "climax" in the deciduous forest in Wisconsin. Similar conclusions as to a seral continuum culminating in sugar maple or beech have been reached in other sectors of the eastern deciduous forest of North America, as in New Jersey (Buell et al. 1966).

Since most of the more abundant tree species range widely east of the Mississippi (cf. Little 1971), the successional relations among them are critical to an understanding of the entire formation. Much of the bewildering complexity of composition of the deciduous forest of eastern North America (347 more or less arborescent species in 66 genera of dicotyledons) is distributed along an elaborate seral continuum. Ordination of communities on the basis of species composition is a first step, but it has its limits. For example, gap-phase succession produces heterogeneous mosaics which may be melded in random samples, thus creating anomalous "associations" of species with very different ecological behavior. More direct, biological criteria from the functional morphology of the plants themselves would provide a better basis for ordination. Hence, a wide application of the ecomorphological, climax index model is apparent.

SERAL ECOMORPHOLOGY AND THE EVOLUTION OF XEROPHYTISM

Ecomorphological traits that confer fitness to the pioneering way of life in open, sunny, and relatively xeric habitats of humid climates are conspicuously prevalent in the climax vegetation of arid regions. Prominent examples are division of the leaf into numerous leaflets, reduction in area of unit blade, and spiny armament of stems. These features appear as options of seral trees in mesophytic forests, but are developed as dominant themes in the xerophytic woody plants of desert shrubland, thorn woodland, and some tropical deciduous forests and savannas. Floristically, the combination of compound microphylly and spiny armament is most richly represented in the cosmopolitan legumes, especially in Mimosaceae and Caesalpinaceae; but one or both characters are

common in many other families with large contingents of xerophytic woody plants; e.g. Bombacaceae, Burseraceae, Rutaceae, Zygophyllaceae. Sometimes a biochemical armament of terpenes, alkaloids, or other unpalatable or toxic substances, augments (as in Rutaceae) or replaces (as in Burseraceae) the more obvious thorn defense. The leaf characters are evidently connected with reduction in heat load and transpiration, while armament characters are a deterrent to browsing herbivores. The suite of characters increases in prevalence with increasing aridity, especially in subtropical latitudes, as insolation, potential evapotranspiration, and demand for scarce browse increase in that direction.

Other notable leaf characters related to insolation and gas exchange are vertical orientation of blade and isofacial stomatal distribution. These traits are seemingly anomalous, but rather analogous, in their occurrence in the extreme riparian pioneers of mesophytic, broadleaf forest (Salicaceae) and in upland, xerophytic sclerophylls of semiarid regions (manzanita, Ericaceae; Eucalyptus, Myrtaceae). The traits probably evolved originally in connection with pioneering strategy in forest vegetation, as adaptations to photosynthesis under high light intensities, as discussed above (cf. stomatal distribution; see also the C_4 pathway of carbon fixation.

Another striking ecomorphological character of some shade intolerant xerophytes is the extreme development of apical dominance, as in the giant stem succulents (Cactaceae, Euphorbiaceae) and rosette trees (Agavaceae, e.g.) of subtropical latitudes. In the undisturbed, denser phases of thorn woodland, the dominant, broad-crowned trees (such as Bursera, Juliania; or Acacia, Cercidium, Lysiloma, and other legumes) tend to form a more or less closed canopy. Here the adaptive significance of extreme excurrence in many tall, cactoid succulents becomes apparent. Only by channeling energy resources into the vertical elongation of gigantic columns can the CAM (crassulacean acid metabolism) succulents penetrate small gaps in the thorn woodland canopy and fully exploit the advantages of their xerophytic but sunlight-requiring, photosynthesis-transpiration strategy. Like the heliophile, emergent giants of the tropical rain forest, they escape the unfavorable light conditions below the canopy by jutting above it in skyscraper fashion.

I would suggest that, secondarily, the great columnar cacti of the thorn forests of Mexico have spread into scantily vegetated, desert regions, much too arid for canopy closure. For example, some very arid sectors of the Sonoran Desert are penetrated by the huge saguaro (Carnegiea gigantea (Engl.) Brit. & Rose) and cardon cactus (Pachycereus pringlei Brit. & Rose) which stand out as monumental colossi, unnecessarily taller than the sparse growth of creosote bush, bur sages, and other low shrubs. On the other hand, there is a much richer development of giant succulents in the tall and dense thorn woodlands of southern Mexico, where 5 genera and about 30 species attain gigantic size, erecting their tall columns high above the canopy of legumes, elephant trees, etc. (Wells, original; Britton and Rose 1920).

Mesophytic forests are the dominant theme of the paleobotanical record over most of the span of geological time since the great flowering of the Angiosperms during the Cretaceous period. In North America, relatively xerophytic vegetation appeared in the Southwest during the mid-Tertiary, but did not expand as regional desert until late in the Neogene, perhaps not until the interglacials of the Pleistocene (Axelrod 1950, 1958; Wells 1970c). The elaborate physiognomic and floristic diversity (including much endemism) of the present North American desert vegetation suggests a longer history for the evolution of xerophytes than that indicated by the rather scanty fossil record (Wells 1966, 1970, 1977; Axelrod 1967). Since many xerophytic traits are extreme developments of lines foreshadowed in the seral ecomorphology of pioneer plants growing in humid regions, the first steps toward xerophytism may have evolved in the early seral stages of a mesic forest setting. The most likely places for the evolution of the more extreme xeromorphic characters under humid conditions would have been on sunny scarps with bedrock outcrops (cf. Winterringer and Vestal 1956; Wells 1962; Axelrod 1972), where indefinitely protracted and very diverse, "xerarch" successions may be enacted on the varied lithological suites exposed by erosion.

DISTRIBUTION OF PLANT FAMILIES ALONG THE ECOMORPHOLOGICAL GRADIENTS OF FOREST SUCCESSION

If species in the same genus, or in related genera, tended to displace to widely different sectors of the successional gradient from pioneer to climax, then families would have broad, relatively uninteresting, seral distributions. On the other hand, if there were much ecological parallelism among related species, then different families might tend to displace to different successional positions. Within limits, both strategies are apparent on the basis of comparative ecomorphology, but a trend toward displacement of families along the seral gradient exists in temperate deciduous forest (Figure 5).

The Salicaceae is a family narrowly specialized as pioneers. Their exceedingly numerous, very light, parachuted seeds confer great mobility; and their fast growth in full sun enables them to exploit ephemeral habitats opportunistically. But the correlative legacy of soft, weak, nondurable wood and extreme intolerance of shade insures brief longevity and a transient role in the early stages of forestation, even though the cycle is constantly regenerated (e.g. in riverine habitat, on new burns and other open sites).

On the other hand, there are no families specializing at the climax extreme of the seral spectrum (climax index >80%). Only two families of very wide seral amplitude even penetrate this ecomorphological niche, vig. Aceraceae (with sugar maple) and Fagaceae (with beech). Most of the species in these families have sorted out in the middle range of the climax index, between 30 and 80% (Figure 5). Similarly, all of the other

families with trees in the temperate deciduous forest sort out (with considerable overlap) in this middle interval, with a few families almost bridging the gap to the pioneer end of the spectrum (to the Salicaceae at 15-17%). The ultimately climax way of life, with its limited mobility, slow growth, great longevity and extreme degree of photosynthetic efficiency at very low light intensities, is an adaptive peak reached by very few taxa, at least in temperate forests.

Apparently, r-selection is a more probable evolutionary route than K-selection for plants (cf. Figure 1, for the uneven, r-skewed distribution of seed weight); but there is an extensive middle ground where the

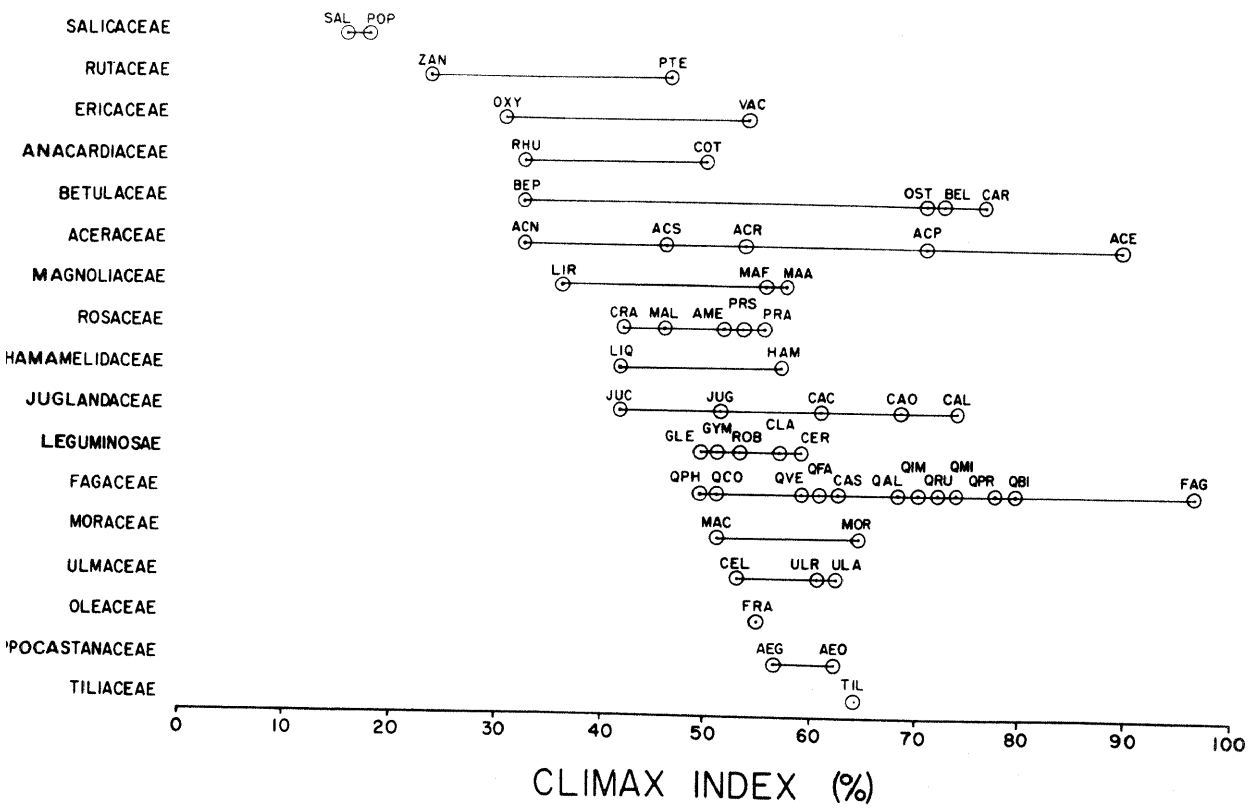


Figure 5. Distribution of plant families on the ecomorphological gradient of the climax index, including most represented by 2 or more species in the present study. Letter codes for species given in Appendix. Although the Salicaceae is narrowly specialized at the pioneer extreme, there is no corresponding family specializing at the climax extreme. Instead, there is a wide displacement of confamilial species along the gradient in several families that have penetrated the climax niche.

two strategies are evenly balanced. Indeed, most of the taxa scored in this study are an ecomorphological patchwork of pioneer and climax traits. Although some taxa attain the same climax index score, nevertheless, no two attain it in exactly the same way. In response to diverse selection pressures from different parameters of the same n-dimensional environment, different parts of the plant have evolved to different extents (possibly at different rates) in n different ecomorphological directions. Thus, the Juglandaceae has a relatively climax reproductive strategy with heavy, K-selected seeds; it has relatively climax wood properties which confer considerable longevity; but the heliophile foliage morphology, inefficient light absorption strategy, and low shade tolerance tip the balance away from the climax end of the successional spectrum. The same is true of many oaks in the Fagaceae.

A semantic problem arises because many species of oak range far beyond the climatic region of the mesophytic, broadleaf-forest succession under discussion here. Some oak take over climax status (relative to species available) by default of the more shade-tolerant, mesophytic, climax species (e.g., beyond the range of beech and sugar maple in the southwestern sector of the eastern deciduous forest in Kansas and Oklahoma). However, oak-dominated forests are more open-canopied and have a greater diversity of species in the understory than the dense, ultimately climax forests that are monotonously dominated by beech and sugar maple (cf. Curtis 1959; Auclair and Goff 1971). In other words, although some oak forests are climax (in a stability sense), they are not as climax (in an ideal, ecomorphological sense) as a beech forest; and wherever full sympatry occurs, succession from oak to beech is predicted by the climax index model.

Since maximal overlap of families occurs between 30 and 80% on the climax index scale (Figure 5), seral ecomorphology indicates maximal species diversity for intermediate stages of succession (cf. also Figures 2, 3 and 4). Recent analysis of deciduous forest succession vis-a-vis species diversity in the Great Lakes region provides clear empirical support (Auclair and Goff 1971). Intuitively, this should be so, because ecological succession of plants from pioneer to climax is sequential and gradual, and lacks sharp breaks within the sere. The intermediate stages of succession have many early pioneer species as holdovers, and some late climax species begin to appear, along with numerous intermediate species. Clements had a name for it: mictium, or seral mixture. The rise to canopy dominance of the shade-tolerant, and maximally shade-producing, climax species creates a light environment hostile to heliophile species of earlier stages, and their reproductive decline eventually results in the local demise of the latter. Hence, climax forests should have relatively low species diversity, but for very different reasons than for early pioneer stages, which are at the bare beginnings of the sequential colonization process. Also, it follows from the overlapping seral ecomorphologies of plant families and their component taxa (Figure 5), that succession in forests of high species diversity should be a continuous process without discrete "stages", and with stochastically alternative pathways to climax.

Distribution of Families Within the Successional Gradients of Tropical Forests

The species-rich, broadleaf evergreen forests of the tropics offer superb testing grounds for the ecomorphological model of plant succession. A preliminary survey of the great diversity of tropical families suggests a similar pattern of distribution on the successional gradient from pioneer to climax. As in temperate forests, relatively few families are narrowly specialized at the pioneer extreme, but most have broad seral distributions in the pioneer to intermediate, or intermediate to climax, ranges. The wealth of Angiosperm families in the tropics increases the probability that some might specialize narrowly at the climax extreme of seral ecomorphology, a niche apparently too narrow for any temperate family. It will be interesting to test this by obtaining the necessary suites of ecomorphological data on entire families in the tropics.

At the pioneering end of the seral spectrum, there are beautiful tropical analogs to the Salicaceae. The outstanding example is the Bombacaceae (cf. also the unrelated Cochlospermaceae), which has converged on the Salicaceae on the same suite of ecomorphological traits, and in some respects surpasses it. Thus, the Bombacaceae are fast-growing, exceedingly light-wooded (e.g. balsa), short-lived, shade-intolerant trees, producing large quantities of very light, long-hairy, mobile seeds. As in cottonwood and willow, the r-strategy increases the probability that the light-requiring propagules will reach the sunny safe-sites of widely scattered, ephemeral openings in the dense and somber forests. Some Bombacaceae (e.g. kapok) quickly attain gigantic stature as emergents above the top canopy of slower-growing trees, a vantage point whence the cottony seeds are broadcast to the winds.

Other pioneering, arboreal families of the tropics are Casuarinaceae, Chloranthaceae, Cochlospermaceae, Polygonaceae (Triplaris), Rutaceae, Simaroubaceae, Sterculiaceae, and the monocotyledonous Palmae and Pandanaceae. Also, the Moraceae includes some extremely pioneer trees in the American genus Cecropia and in its African analog, Musanga cecropioides (both are placed in Urticaceae by Airy Shaw 1965). The two genera are a remarkable example from tropical rain forest of intercontinental parallelism on seral ecomorphology (rapid growth, soft, weak wood; dioecious, wind-pollination; fecund, mobile dispersal; shade intolerance). The pioneering genus Trema (Ulmaceae) is ecomorphologically analogous, and has attained an even wider, pantropical distribution somewhat like kapok (Ceiba pentandra (L.) Gaertn.) in the Bombacaceae.

Thus, at all taxonomic levels: family, genus, even species, there are examples of r-selected pioneers of forest succession with wide world-distributions in the ocean-sundered tropics. The mobility that adapts them to an invasive way of life on the local, successional scene may predispose them to the vagaries of long-distance, perhaps even intercontinental, dispersal. The ecomorphological model of succession also

predicts restricted distributions -- a greater prevalence of narrow endemism -- among relatively immobile, K-selected species, genera, families, specializing in the more climax phases of the seral continuum.

SUMMARY

The seral ecomorphology of angiosperm trees is factored into 30 functional characters, and the fitness rationale of each character is defined as explicitly as possible. The 26 characters used fall into 3 main suites. 1. Light Absorption Factors: apical dominance, branch orders, phyllotaxy, leaf division, area of unit blade, leaf orientation, stomatal distribution, leaf oscillation, cuticle luster, pigmentation. 2. Reproduction Factors: shade tolerance, seed weight, dispersal mechanisms, mast periodicity, age to fruit, sex structure. 3. Growth, Maintenance and Longevity Factors: growth rate, longevity, height; wood density, modulus of rupture, tyloses, decay resistance or chemical armament, spiny armament, ray volume, ring porosity (wood and armament characters). Several other characters not used are discussed: leaf flushes (maintenance), oil content of seeds (reproduction), myrmecophily (biotic armament), C_4 photosynthetic pathway-Kranz anatomy, and anemophily (reproduction; suggested for tropics under sex structure).

The 26 traits are used to define successional character-space in which 75 principal species of broadleaf trees of the eastern deciduous forest are plotted. Each species was scored for each character, giving a 26 x 75 data matrix from which principal components of variance were extracted. The three components with the largest percent of trace were used as axes for a 3-dimensional projection of the relative positions for the 75 species of trees. Also computed were distances between species in seral hyperspace, generated from the same matrix. The Euclidean distances, when converted to a scale relative to the two most distant species (cottonwood and beech), proved to be correlated with a relative scale derived from the arithmetical sums of the character scores in the vector of each species. The latter are a readily obtained and immediately useful climax index. Most of the species (61 of the 75) fall in the intermediate range of the successional scale, with only 9 and 5 species in the relatively pioneer and relatively climax intervals, respectively. The regression of climax index on distance index serves as a scatter diagram which shows a similarly unequal distribution of tree species on the ecomorphological gradient. Although most of the species are concentrated toward the center of the ellipsoid, each species has its own individualistic position in the scattergram. In like manner, the distribution of 75 species of trees in the 3-dimensional model generated from the principal components analysis supports the individualistic concept of plant communities, inasmuch as exact congruences or discrete clusterings of species are lacking.

However, an unexpected result for a successional model is the arrangement in character-space of convergent sets of species that approximate

the principal "climax" communities or "associations" of the eastern deciduous forest (oak-hickory, beech-maple, etc.). The equality of climaxness of the traditional "climax" associations is called into question. In the ecomorphological model, beech and sugar maple are uniquely isolated from all other species at the climax extreme (80-100% on the climax index scale). The two unrelated taxa are unique in combining: 1. maximal interference with light penetration through their efficiently arranged leaf mosaics, thus adversely affecting all other tree species growing under their dense canopy; 2. maximal shade tolerance, thus ensuring their reproduction in their own somber shade; and 3. sufficient sturdiness and longevity to maintain canopy position and to outlast most associated species.

There are no families specializing entirely within the climax niche, which is penetrated by only two (Fagaceae and Aceraceae), both of very wide seral amplitude in the deciduous forest. On the other hand, there is a family, Salicaceae, specializing at the pioneering extreme of seral ecomorphology. Their exceedingly numerous, very light, parachuted seeds confer great mobility; and their fast growth in full sun enables them to exploit ephemeral habitats opportunistically. But the correlative legacy of soft, weak, non-durable wood and extreme intolerance of shade insures brief longevity and a transient role in the early stages of forestation.

Numerous families specialize in the intermediate range of seral ecomorphology; hence, there is maximal species diversity in this range of succession. The rise to canopy dominance of the few most shade-tolerant, and maximally shade-producing, climax species creates a light environment hostile to heliophile species of early to intermediate stages, resulting in the demise of the latter. Hence, climax forests should have relatively low species diversity, but for very different reasons than for early pioneer stages, which are at the bare beginnings of the sequential colonization process.

The ultimately climax way of life, with its limited mobility, slow growth, great longevity, and extreme shade tolerance is an adaptive peak reached by very few taxa, at least in temperate forests. As can be seen in the strongly r-skewed modal distribution of seed weights among 82 tree species, by far the greater proportion have very light seeds, averaging less than 0.1 gram. Thus, the pioneering r-strategy appears to be a much more probable evolutionary pathway for trees than the climax K-strategy.

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APPENDIX

The 3-letter codes in Figures 2, 4 and 5 designate the following 79 species of broadleaf deciduous trees of eastern North America.

CODE	SPECIES	CLIMAX INDEX %
ACE	*Acer saccharum* Marsh.	88.8
ACN	*Acer negundo* L.	32.1
ACP	*Acer pensylvanicum* L.	70.0
ACR	*Acer rubrum* L.	52.9
ACS	*Acer saccharinum* L.	45.4
AEG	*Aesculus glabra* Willd.	56.6
AEO	*Aesculus octandra* Marsh.	62.3
AME	*Amelanchier arborea* (Michx.) Fern.	51.0
ARA	*Aralia spinosa* L.	28.3
ASI	*Asimina triloba* (L.) Dun.	51.0
BEL	*Betula lenta* L.	71.7
BEP	*Betula populifolia* Marsh.	32.1
CAC	*Carya cordiformis* (Wang.) Koch	60.5
CAL	*Carya laciniosa* (Michx.) Loud.	73.6
CAO	*Carya ovata* (Mill.) Koch	68.0
CAR	*Carpinus caroliniana* Walt.	75.5
CAS	*Castanea dentata* (Marsh.) Borkh.	62.3
CAT	*Catalpa speciosa* Warder	52.9
CEL	*Celtis occidentalis* L.	52.9
CER	*Cercis canadensis* L.	58.6
CLA	*Cladrastis lutea* (Michx.) Koch	56.6
COR	*Cornus florida* L.	71.7
COT	*Cotinus obovatus* Raf.	49.1
CRA	*Crataegus crus-galli* L.	41.5
DIO	*Diospyros virginiana* L.	60.5
FAG	*Fagus grandifolia* Ehrh.	96.2
FRA	*Fraxinus americana* L.	54.8
GLE	*Gleditsia triacanthos* L.	49.1
GYM	*Gymnocladus dioica* (L.) Koch	51.0
HAL	*Halesia carolina* L.	60.4
HAM	*Hamamelis virginiana* L.	56.6
ILE	*Ilex montana* T. & G.	58.6
JUC	*Juglans cinerea* L.	41.5
JUG	*Juglans nigra* L.	51.0
LEI	*Leitneria floridana* Chapm.	28.3
LIQ	*Liquidambar styraciflua* L.	41.5
LIR	*Liriodendron tulipifera* L.	35.8
MAA	*Magnolia acuminata* L.	56.6
MAC	*Maclura pomifera* (Raf.) Schn.	51.0
MAF	*Magnolia fraseri* Walt.	54.8
MAL	*Malus coronaria* (L.) Mill.	45.4

CODE	SPECIES	CLIMAX INDEX %
MOR	*Morus rubra* L.	64.2
NYS	*Nyssa sylvatica* Marsh.	49.1
OST	*Ostrya virginiana* (Mill.) Koch	70.0
OXY	*Oxydendrum arboreum* (L.) DC.	30.2
PIN	*Pinckneya pubens* Michx.	47.2
PLA	*Planera aquatica* Gmel.	62.3
PLO	*Platanus occidentalis* L.	58.6
POP	*Populus deltoides* Bartr.	17.0
PRA	*Prunus americana* Marsh.	54.8
PRS	*Prunus serotina* Ehrh.	52.9
PTE	*Ptelea trifoliata* L.	45.4
QAL	*Quercus alba* L.	68.0
QBI	*Quercus bicolor* Willd.	79.3
QCO	*Quercus coccinea* Muenchh.	51.0
QFA	*Quercus falcata* Michx.	60.5
QIM	*Quercus imbricaria* Michx.	70.0
QLY	*Quercus lyrata* Walt.	68.0
QMA	*Quercus marilandica* Muenchh.	60.5
QMC	*Quercus macrocarpa* Michx.	73.6
QMI	*Quercus michauxii* Nutt.	73.6
QMU	*Quercus muehlenbergii* Engelm.	71.7
QPA	*Quercus palustris* Muenchh.	51.0
QPH	*Quercus phellos* L.	49.1
QPR	*Quercus prinus* L.	77.4
QRU	*Quercus rubra* L.	71.7
QST	*Quercus stellata* Wang.	66.1
QVE	*Quercus velutina* Lam.	58.6
RHU	*Rhus copallina* L.	32.1
ROB	*Robinia pseudoacacia* L.	52.9
SAL	*Salix nigra* Marsh.	15.1
SAP	*Sapindus drummondii* H. & A.	41.5
SAS	*Sassafras albidum* (Nutt.) Nees	49.1
STA	*Staphylea trifolia* L.	52.9
TIL	*Tilia americana* L.	64.2
ULA	*Ulmus americana* L.	62.3
ULR	*Ulmus rubra* L.	60.5
VAC	*Vaccinium arboreum* Marsh.	52.9
ZAN	*Zanthoxylum clava-herculis* L.	22.7

ABOUT THE AUTHOR

Philip V. Wells received a B.A. in biology from Brooklyn College in 1951, M.S. in plant physiology from the University of Wisconsin, Madison in 1955, and Ph.D. in plant ecology from Duke University in 1958. He taught at University of California, Santa Barbara and California Polytechnic College before his present position (1962-) as professor of botany and systematics and ecology at University of Kansas. In 1966-67, he served as visiting professor and director of the Botanical Garden, University of California, Berkeley. Publications in plant ecology, paleoecology, systematics and evolution number about 45.

For reprints write: Dr. Philip V. Wells
Department of Systematics and Ecology
Snow Hall
The University of Kansas
Lawrence, Kansas 66045