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WHY DO TEMPERATE DECIDUOUS TREES LEAF OUT AT DIFFERENT TIMES? ADAPTATION AND ECOLOGY OF FOREST COMMUNITIES

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With the onset of spring in the deciduous forests of eastern North America, tree leaves do not all emerge in perfect synchrony. Geographic variation in the timing of bud break within species (Lamb 1915; Altman and Dittmer 1962, table 104) can reasonably be attributed to latitudinal climatic trends (Schnelle 1955; Lieth 1974). It is less clear what causes phenological differences among tree species in a particular region (Smith 1915; Ahlgren 1957). Even within single forests, leaf emergence in spring varies over several weeks among coexisting native trees (fig. 1), and species produce leaves at quite different rates during the rest of the growing season. For example, species of *Populus* (Critchfield 1960) and *Betula* (Kozlowski and Clausen 1966) produce a flush of early leaves in the spring followed by a series of individual late leaves through the summer, but species of *Fraxinus* (Gill 1971) and *Carya* (Foster 1931) normally produce only a spring flush of foliage unless defoliated. *Quercus* has a primary flush of spring leaves, which in young trees can be followed by secondary flushes in the summer (Johannestriebe, lammas shoots) even without defoliation (Lavarenne-Allary 1965; Reich et al. 1978; Kriebel et al. 1976).

The proximate control of initial leaf emergence in most temperate deciduous trees is usually the cumulative thermal sum (degree-hours, degree-days) to which buds are exposed after a prerequisite cold period (Lyr et al. 1967; Kramer and Kozlowski 1979; Valentine 1983). Occasionally, as in *Fagus*, which lacks a chilling requirement, bud break is under photoperiodic control (Wareing 1953; Romberger 1963). Although leaf emergence can be advanced a few days by defoliation the preceding year (Heichel and Turner 1976), in general year-to-year variation in the timing of tree phenological stages is low when related to thermal sums rather than calendar days (fig. 2; Lindsey 1963; Taylor 1974). Populations originating from different localities within a species range do differ in their times of bud break when grown in provenance trials. For example, when grown together in Ohio more northern populations of *Acer saccharum* leafed out earlier than populations originating more to the south (Kriebel 1957); conversely, in *Juglans nigra*, populations of more southern origin began growth earlier even in plantations near the northern edge of the species range (Bey 1979). While such intraspecific variations

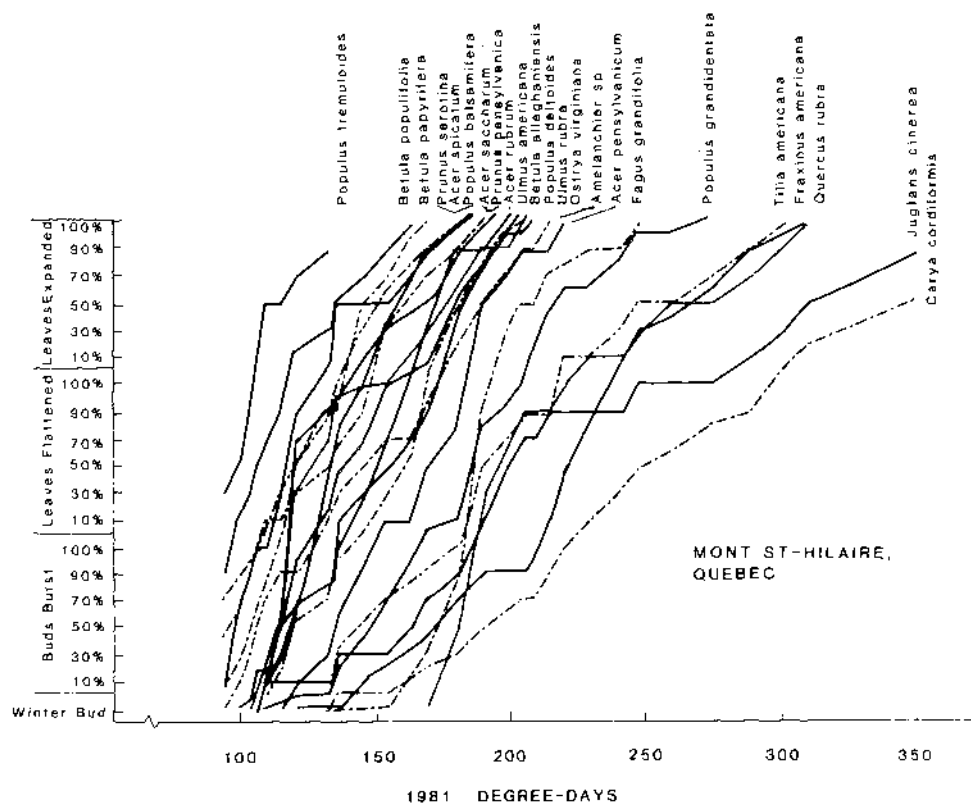


FIG. 1.—Median ($3 \leq n \leq 7$) phenological stages for tree species on the south-facing slope of Lake Hill, Mont. St. Hilaire, Québec (Maycock 1961) plotted through spring 1981. Cumulative degree-days (5°C threshold) are based on data from the Atmospheric Environment Service, Fisheries and Environment Canada, taken at St. Hubert Airport near Mont St. Hilaire.

in leaf phenology are known to be under genetic control (Nienstaedt 1974; Flint 1974), the adaptive significance of such contrasting latitudinal responses is not clear. Indeed there is little in any of these available data to suggest the evolutionary and ecological basis for observed differences in leaf phenology.

A reasonable first assumption is that leaf emergence in temperate trees is ultimately determined by the balance of potential production gains from early leafing set against the danger of leaf damage or loss in late frosts, but this idea alone cannot explain the substantial interspecific variations in leaf phenology at the same site. If the timing of leaf emergence evolved to maximize net production through only such a simple trade-off, then we would generally expect co-occurring tree species to leaf out at the same time. Some variation caused by microtopographic or ontogenetic effects might be anticipated, but certainly not the large differences in timing of leaf emergence which are commonly observed among co-occurring species in natural forests (fig. 1).

As plausible alternatives to this simple but unsatisfactory basis for the observed

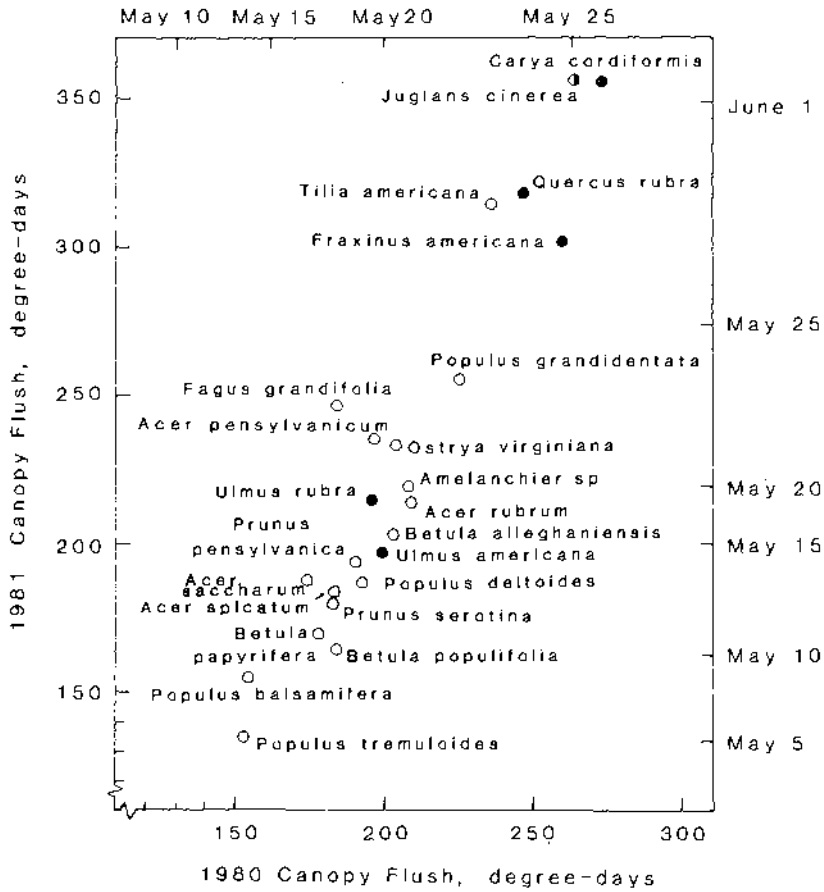


Fig. 2.—Thermal sum required for canopy flush (measured as 100% initial leaf expansion) in 1981 vs. 1980 at Mont. St. Hilaire, Québec. Tree species from the lower left to the upper right flush progressively later. The same individual trees all growing together on the south-facing slope of Lake Hill were monitored in both years. Open circles = deciduous trees with diffuse-porous wood anatomy; half-closed circles = semi-ring-porous wood; closed circles = ring-porous wood. See text for discussion.

diversity in leaf phenology, three broad classes of explanation can usefully be considered: phylogenetic, historical, and adaptive. Phylogenetic explanations predict that closely related species will be similar in leaf phenology. Phylogenetic explanations assume that the Bauplan (in the sense of Gould and Lewontin [1979]) shared by members of a phylogenetic group somehow constrains potential variation in leaf phenology, that present major differences in leaf emergence stem from ancient phyletic divergences involving different and narrowly canalized patterns of leaf phenology. What I am calling historical explanations assume that phylogeny does not set unalterable patterns of leaf phenology, but that insufficient time may have been available for the evolution of phenological characteristics

attuned to present environmental regimes. In the shorter term, historical explanations predict that trees only recently colonizing a region will leaf out in accord with cues more typical of the areas from which they dispersed. On a longer time scale, historical explanations predict that contemporary phenology will reflect adaptation to the paleoenvironments in which the taxon or its immediate ancestors evolved. Finally adaptive explanations predict correlations of leaf phenology with other traits such that the coordinated suite of traits together improves survival and reproduction over other possible combinations of traits. Adaptive explanations assume that timing of leaf emergence can only be understood as part of an integrated syndrome of traits directly involved with leaf function and ultimately tied to reproductive fitness. These three types of explanation are not mutually exclusive, but are qualitatively distinct enough to serve as heuristic alternatives in an initial consideration of why trees leaf out when they do.

A broad-based, comparative approach is most useful to evaluate the likelihood that any of these three classes of explanation applies to leaf phenology. In this paper I review the available data and put forward an evolutionary and ecological interpretation of interspecific variations in leaf phenology. I first consider how consistent the variation and sequence of leafing out is from site to site. Do the tree species in diverse forests generally leaf out over an extended period and are the taxonomic sequences of leaf emergence stable? In other words does *P. tremuloides* always leaf out before *P. grandidentata*? *Acer saccharum* before *J. cinerea*? Or on a broader geographic scale, *A. platanoides* before *J. regia*? Second, I consider whether other plant traits are consistently correlated with time of leaf emergence. Do traits like the timing of cambial growth, flowering, maturation of seeds, or seed dispersal relate to timing of leaf emergence? Are traits intimately related to leaf function like photosynthetic capacity, maximal transpiration rates, vascular anatomy, or plant architecture consistently related to time of leaf emergence? Only with substantial comparative evidence can we begin to assess the adaptive significance for differences in the timing of leaf emergence among co-occurring trees.

LEAF PHENOLOGY IN DIVERSE REGIONS

In a native forest in southwestern Quebec, near the northern edge of the present deciduous forests in North America, there is a regular and temporally extended sequence of leaf development in spring (figs. 1, 2). About a month typically elapses from flushing of early species like *Populus tremuloides* and *Populus balsamifera* to flushing of late species like *Juglans cinerea* and *Carya cordiformis*. Early successional species like *Betula populifolia*, *B. papyrifera*, and *Prunus pensylvanica* leaf early but so do some late successful species like *Acer saccharum* and gap-phase species like *Prunus serotina*. Later-flushing species include canopy dominants in this forest like *Quercus rubra* and *Fraxinus americana* but also gap-phase species like *Populus grandidentata*.

The phenological patterns in Minnesota (fig. 3), at the northwestern edge of the present deciduous forest, are similar to those in southwestern Quebec. Leaves of *Populus tremuloides* and *B. papyrifera* emerge early and leaves of *Fraxinus* and

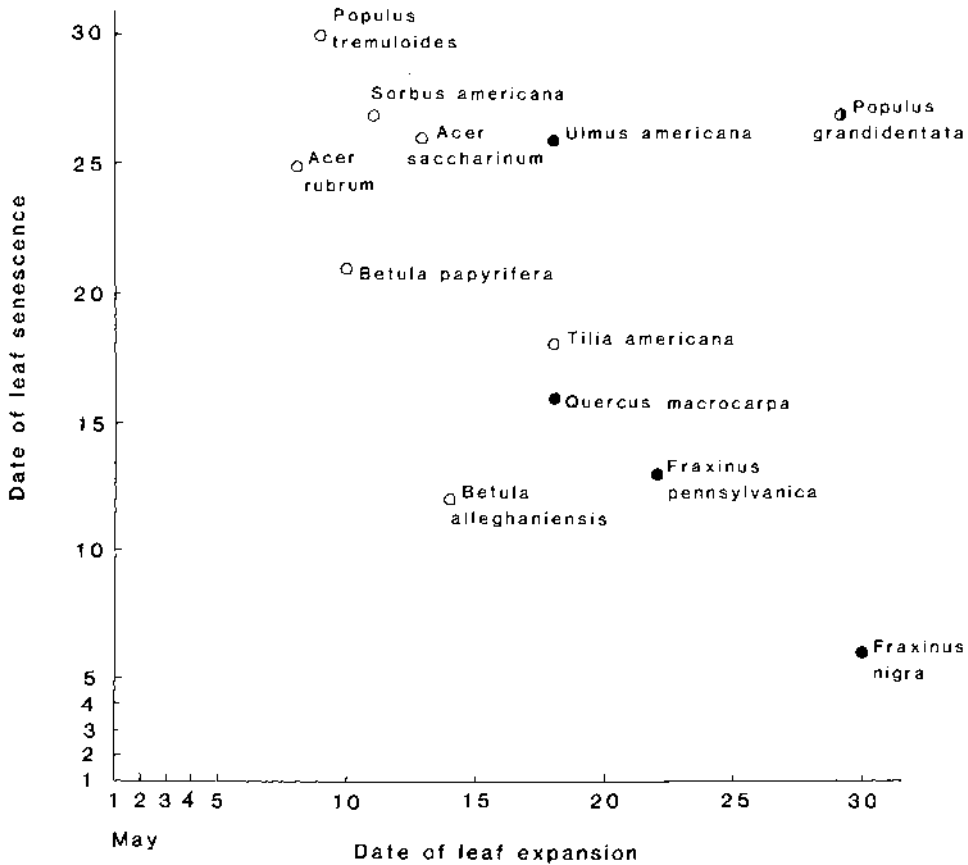


FIG. 3.—Date of leaf senescence plotted against date of leaf expansion for trees in a number of adjacent habitats near Basswood Lake in northeastern Minnesota. Dates are the midpoints of the earliest and latest dates for each species reported by Ahlgren (1957). He studied 5 trees of each species from 1951 to 1956. With the exception of *Populus grandidentata*, trees that leaf out earlier also keep their leaves longer. Symbols as in fig. 2.

Quercus species emerge late. *Populus grandidentata* leaves again emerge notably later than those of *P. tremuloides*. *Tilia americana* flushes relatively earlier than in Quebec, essentially in synchrony with *B. alleghaniensis* and *Ulmus americana* which have intermediate times of leaf emergence in both Quebec and Minnesota. Similarly *Acer rubrum* leafs out relatively earlier in Minnesota than in Quebec.

In northern Ohio (fig. 4), there are good phenological records available for more tree species including many with southerly distributions. Species of *Juglans*, *Carya*, *Quercus*, and *Fraxinus* remain late flushing, but some midwestern and southern species like *Platanus occidentalis*, *Maclura pomifera*, *Gymnocladus dioica*, and *Diospyros virginiana* flush as late or later than these species. *Populus tremuloides* is again the earliest leafing species and *Populus deltoides* follows somewhat later as it also did in Quebec. *Ostrya virginiana* and *U. americana* leaf

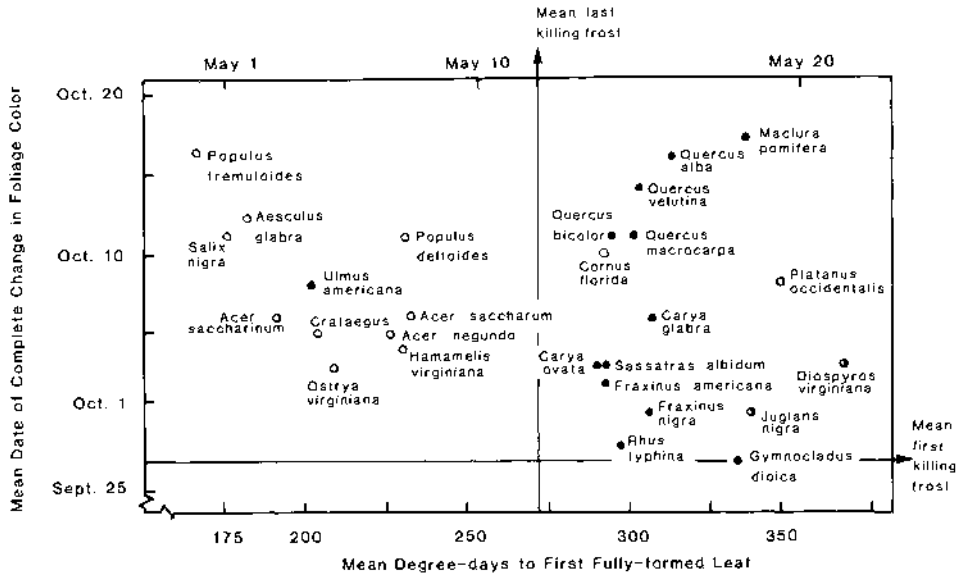


FIG. 4.—Mean date of leaf senescence plotted against mean thermal sums required for leaf emergence at Wauseon, Ohio near the shore of Lake Erie. Calculated from phenological and climatic observations made by Thomas Mikesell from 1883 to 1912 (Smith 1915). Since leaf senescence is at least in part under photoperiodic control and is effected by frosts (Kramer and Kozlowski 1979), only leaf emergence has been expressed in relation to thermal sums. Symbols as in fig. 2.

out relatively early compared to Quebec. *Acer saccharinum* leaves early in both Ohio and Minnesota.

The timing of leaf emergence in these North American forests can also be compared to that of closely related species in the deciduous forests of Europe. I have not yet found detailed phenologic records for single European forests, but some good regional summaries are available (fig. 5). The genera *Quercus*, *Fraxinus*, and *Juglans* again dominate the late-leaving species. *Sorbus aucuparia* is early leafing as is *S. americana* in Minnesota. *Cornus mas* in Europe and *Cornus florida* in Ohio both leaf out just before the late-flushing genera. The wild *Prunus padus* of Europe comes out very early while the cultivated *Prunus domestica*, probably a hybrid of the native *Prunus spinosa* and *Prunus cerasifera* (Polunin and Everard 1976), leafs out considerably later. *Prunus spinosa* leafs out about 5 days later than *Prunus domestica* (Fritsch 1869). *Populus tremula*, in the same subgenus as *Populus tremuloides* and *Populus grandidentata* (Hora 1981), leafs out relatively late as does *Populus grandidentata* in North America. Similarly the European and North American species of *Tilia* all tend to leaf out at intermediate to late times. The phenology of the European species of *Acer*, however, contrasts markedly with that of the North American species. Only *Acer platanoides* is early leafing while all the North American species are early to intermediate. *Betula pendula*, which is more closely related to the North American *B. papyrifera* than to *B. alleghaniensis* (Hora 1981), is early leafing in Austria but not as early over

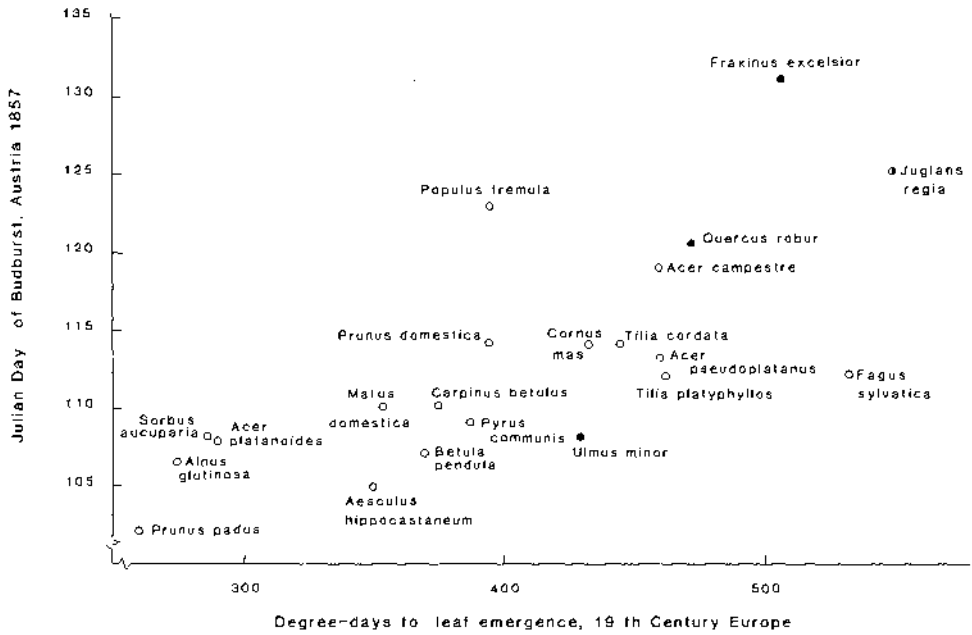


FIG. 5.—Leaf phenology for major European tree species. Median day of budburst in 1857 based on records from 75 stations throughout Austria (Fritsch 1869) plotted against mean thermal sums required for leaf emergence at 31 stations throughout Europe from data in Linsser (1869). Tree species from the lower left to the upper right flush later. Symbols as in fig. 2.

Europe as a whole; *Aesculus hippocastanum*, closely related to the early-leaving *Aesculus glabra* in Ohio, also shows a changing pattern of geographic variation in time of leaf emergence. Overall the temporal sequences of leaf emergence are markedly similar, not only among different sites in North America, but also between related species on the two continents.

With the exception of the European data, these comparisons purposefully have been limited to reasonably comprehensive studies of leaf phenology among native tree species growing together within single forests or localities. This restriction decreases the likelihood that aberrant phenological responses of cultivated or only recently naturalized species will confound the interpretation of any ecological or evolutionary basis for observed differences in leaf phenology. The concordance of phenological trends in Quebec, Ohio, and Minnesota with generalized reports for eastern North America (Lamb 1915; Altman and Dittmer 1962, table 104) supports the validity of comparisons with the available, generalized European data. The sequences of leaf emergence observed in European (Fritsch 1869; Oettingen 1879) and North American (Whitten 1894) botanic gardens where trees from both continents grow together further support the generality of the trends reported here. A few species do shift in their relative timing of leaf emergence from site to site, but these seem to be exceptions to a surprisingly consistent pattern of leaf

emergence through the spring. This overall consistency is also supported by less complete but still useful records of leaf phenology for temperate deciduous forests in Europe (Hoffman and Ihne 1884), Japan (Yanagisawa 1954; Kikuzawa 1983), and eastern North America (Trelease 1884, 1885; Bailey 1887; Mowbray and Oosting 1968).

POSSIBLE PHYLOGENETIC EXPLANATIONS FOR PATTERNS OF LEAF PHENOLOGY

Gould and Lewontin (1979; also see Gould 1980) contend that individual traits may often be nonadaptive, arising not from selection acting to optimize that particular trait but from pervasive developmental or architectural constraints inherent in the phylogenetic history of an organism. If such phylogenetic constraints are operating on the timing of leaf emergence, the observed differences in leaf phenology should be directly related to the phylogenetic relationships of the trees compared here. More closely related trees should leaf out at more closely similar times than distantly related trees.

Considering the phylogeny of the genera represented in the available phenological data (fig. 6), this is not the case. At a suprafamilial level there are no phylogenetic trends whatsoever in time of leaf emergence. Late- and early-leafing trees are represented among both more advanced and more primitive taxa. Relatively advanced families are as likely to be late leafing, like *Fraxinus* in the Oleaceae, as early leafing, like *Aesculus* in the Hippocastanaceae; similarly, less advanced families like Salicaceae include genera that leaf out earlier than comparably advanced genera in the Moraceae. Within single families like Betulaceae evolutionary trends in leaf phenology are well documented (Kikuzawa 1982) and even trees within single genera, like *Populus* and *Betula*, differ more in time of leaf emergence than do many trees from different families (cf. figs. 1–6). Leaf phenology does not appear to be held within narrow limits by phylogenetic constraints; the genetic reorganization necessary to alter timing of leaf emergence apparently occurs with sufficient frequency that leaf phenology can vary considerably among related taxa. Historical or adaptive explanations are therefore more likely than any phylogenetic explanation to account for the observed differences in time of leaf emergence among deciduous trees.

POSSIBLE HISTORICAL EXPLANATIONS FOR PATTERNS OF LEAF PHENOLOGY

Historical explanations rest on the general argument that too little time has elapsed for the evolution of leaf phenology perfectly attuned to local conditions. The argument can be applied on both geologic and recent time scales. On the geologic time scale, taxa not represented in the fossil floras of the north temperate deciduous forest may have more tropical geofloristic origins that gave rise to phenological characteristics which have persisted in modern relatives with more temperate distribution. This possibility differs from a strictly phylogenetic explanation in that phenological traits may persist relatively unchanged in some taxa within a lineage but not necessarily in all. Alternatively, historical explanations may focus on range shifts arising from Pleistocene climatic disruptions as possible

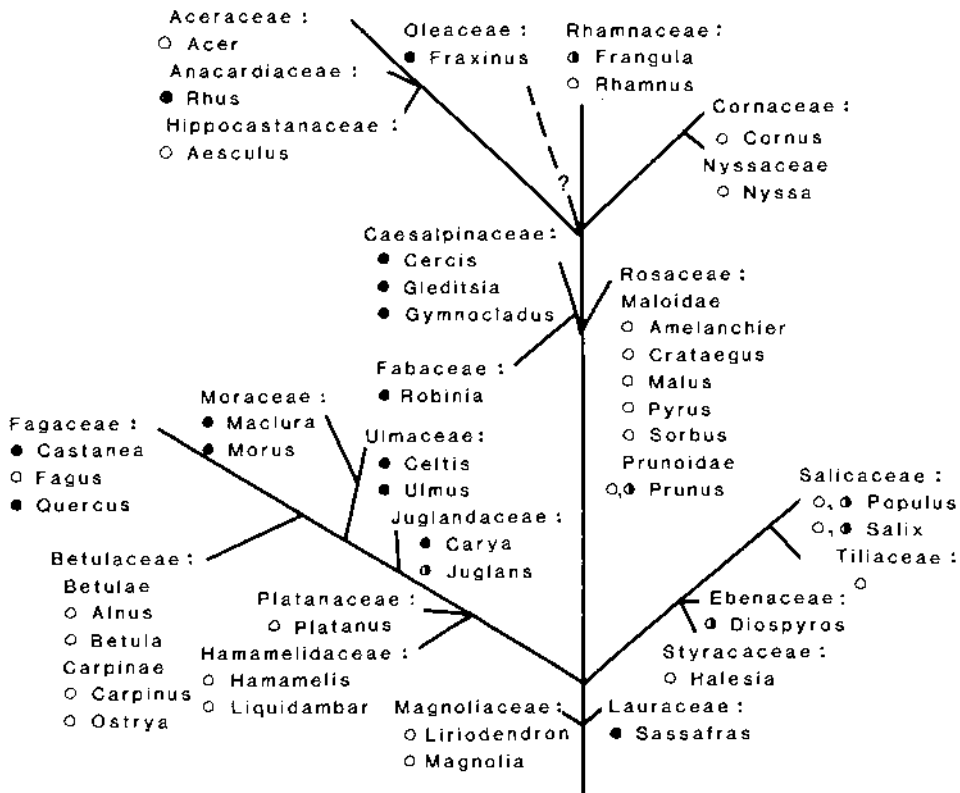


FIG. 6.—Approximate phylogenetic relationships for the genera of trees discussed in this paper adapted from information available in Cronquist (1968, 1981). In many cases the phylogeny is only poorly known, but this diagram does depict the primary relationships between taxa as they are presently understood. Symbols as in fig. 2.

causes of evolutionary disequilibrium in present populations. Historical arguments at both time scales merit consideration, particularly with attention to evidence that can potentially refute the assumptions on which they rest or the predictions that they make.

Essentially all of the families and most of the genera of trees discussed in this paper are represented in Tertiary fossil floras (Graham 1972; Raven and Axelrod 1974). These fossil taxa occur in varying combinations from site to site throughout the present north temperate zone and have been traditionally assigned to either a northern, temperate Arctotertiary Geoflora or a southern, more tropical Neotropical-Tertiary Geoflora (Graham 1972). Although these classical geofloristic concepts have recently been questioned (Graham 1972; Wolfe 1978), it remains clear that our present forest trees stem from ancient lineages that have grown together in various mesophytic forest communities for a very long time (Raven and Axelrod 1974). Both in terms of present phytogeography and fossil floras, certain among these genera can be recognized as primarily tropical or subtropical in their environmental requirements (Graham 1972; Dilcher 1973; Raven and Axelrod

1974). These include *Nyssa*, *Juglans*, *Platanus*, *Diospyros*, *Liquidambar*, *Carya*, *Fagus*, *Liriodendron*, and *Tilia* (Graham 1972). These genera, given their long-standing, more tropical habitat requirements, might be more susceptible to frost damage. We might then expect these genera to leaf out as late or later than others which have occupied primarily temperate habitats throughout their geologic history. In the data from north temperate forests examined here, it is the case that *Tilia*, *Carya*, *Juglans*, *Platanus*, *Diospyros*, and perhaps *Fagus* leaf out late relative to most species of temperate origin. These data thus support a historical view that present phenological differences among forest trees at least in part represent traits of ancient origin only little or not at all modified over long periods of geologic time.

A complement to such essential stasis in a taxon's leaf phenology over long periods of geologic time is the idea that phenologic traits do change over time but perhaps slowly enough that observed leaf emergence times may not be in evolutionary equilibrium with current conditions. In this shorter term historical view, phenological variations may be seen as deviations from an ancient norm for a taxon that is never exactly maintained in the face of environmental fluctuations. In forests of eastern North America recolonized at different times after the retreat of the Wisconsin ice sheet, we might then expect to see differences in leaf phenology attributable to the genotypes favored in the glacial refugia. Before glaciation, tree species presumably had genetically based geographic variation in phenological traits similar to that commonly observed today. As the glaciers advanced, it is unlikely that the full range of this genetic variation was equally if at all represented in glacial refugia; thus, following deglaciation, populations which recolonized more northern regions in eastern North America may be expected to have phenological traits similar to those favored in the environmental regimes where the species survived the Wisconsin ice.

Among the sites discussed in this paper, Ohio was the region colonized soonest after the glacial retreat (Davis 1981). The genera *Acer* and *Quercus*, for example, reentered Ohio between 3,000–4,000 years earlier than Quebec or Minnesota. There is no indication, however, that the phenology of these genera in the later-colonized sites is distinct relative to the phenological sequences in Ohio. The only possible example of such a short-term historical effect that may be noted in the available data is *Carya*. Davis (1981) indicates that *Carya* arrived in Quebec less than 4,000 yr ago compared to 9,000–10,000 yr ago in Ohio. The longer delay in *Carya cordiformis* leaf emergence in Quebec (fig. 2) compared to Ohio (fig. 4) may indicate a relict requirement for a high thermal sum prior to leafing that is not achieved as quickly in the north as it would be to the south. Overall this somewhat limited evidence suggests that Holocene events have had relatively little effect on leaf phenology in a given region, but that much longer-term stasis in species' leaf phenology occurs and provides part of the explanation for observed differences in time of leaf emergence among sympatric trees.

POSSIBLE ADAPTIVE EXPLANATIONS FOR PATTERNS OF LEAF PHENOLOGY

The observed differences in times of leaf emergence may be considered adaptations (in the broad sense of adaptations; see Gould and Vrba [1982]) if in concert

with functionally related traits they contribute toward higher survivorship and reproduction than alternative phenologies. Unfortunately almost no work has been done on the basis for variation in seed yield in forest trees (Farmer 1978). Similarly, although very many studies compare factors affecting variations in growth and survival among a few tree species, only very few allow comparison across most of the taxa discussed here. After an extensive review of the literature, I have therefore had to focus the following discussion on well-documented trends interpreted with reference to more narrowly based studies of related factors. I first sought traits consistently correlated with timing of leaf emergence and then attempted to interpret their possible adaptive significance. Since too little is known of controls on tree reproduction, I have deliberately focused on the contribution of traits to the critical function of leaves: the accumulation of carbon and energy in a terrestrial environment where water availability fluctuates daily and seasonally.

The single most striking correlations that emerge in this literature review are between leaf phenology and the organization of water-conducting tissues in the trunk and branches. Two primary components of the vascular system are involved: (1) variation in the diameter of the principal conducting elements, the xylem vessels; and (2) the proportion of secondary xylem occupied by vessels. Figure 7 illustrates the range of variation in these traits among north temperate hardwoods. Tree species that consistently leaf out early have narrow-diameter vessels in both spring and summer wood and a relatively low proportion of secondary xylem occupied by conducting elements. Later-leafing trees have larger-diameter spring vessels and/or greater numbers of narrow-diameter vessels in their wood. The greater the numbers and the larger the diameters of vessels, the greater is the potential conducting capacity of the xylem (Zimmerman and Brown 1971; Zimmerman 1983). The general relationships between these traits and timing of leaf emergence are summarized diagrammatically in figure 8.

The seasonal variation in vessel diameter, which is an integral part of the observed relationship between leaf phenology and organization of the vascular system, has long been recognized by wood anatomists. Variation in vessel diameter is sufficiently stable within species that this trait figures strongly in all keys for wood identification (Core et al. 1979; Panshin and deZeeuw 1970; Wappes 1932). These diagnostic variations in wood anatomy are traditionally classified as diffuse-porous (low variance in the diameters of vessels produced through the growing season), semi-ring-porous (a gradual seasonal change from larger- to smaller-diameter vessels), or ring-porous (a distinct dichotomy between large-diameter early-season vessels and small-diameter or nonexistent late-season vessels). The reader unfamiliar with wood anatomy may wish to examine the micrographs in Core et al. (1979) to appreciate just how distinctive the contrast between diffuse- and ring-porous wood can be. Most trees, both temperate and tropical, are diffuse-porous (Metcalf and Chalk 1950). Ring-porous taxa are more common in temperate regions but do also occur in the tropics (Chowdhury 1964; Van der Graaff and Baas 1974). Carlquist (1980) has recently gone beyond this tripartite classification and recognized 13 basic wood types considering variation in both conducting elements and associated fibers and parenchyma in the secondary xylem. Carlquist (1975) also reviews ecological implications of the wealth of

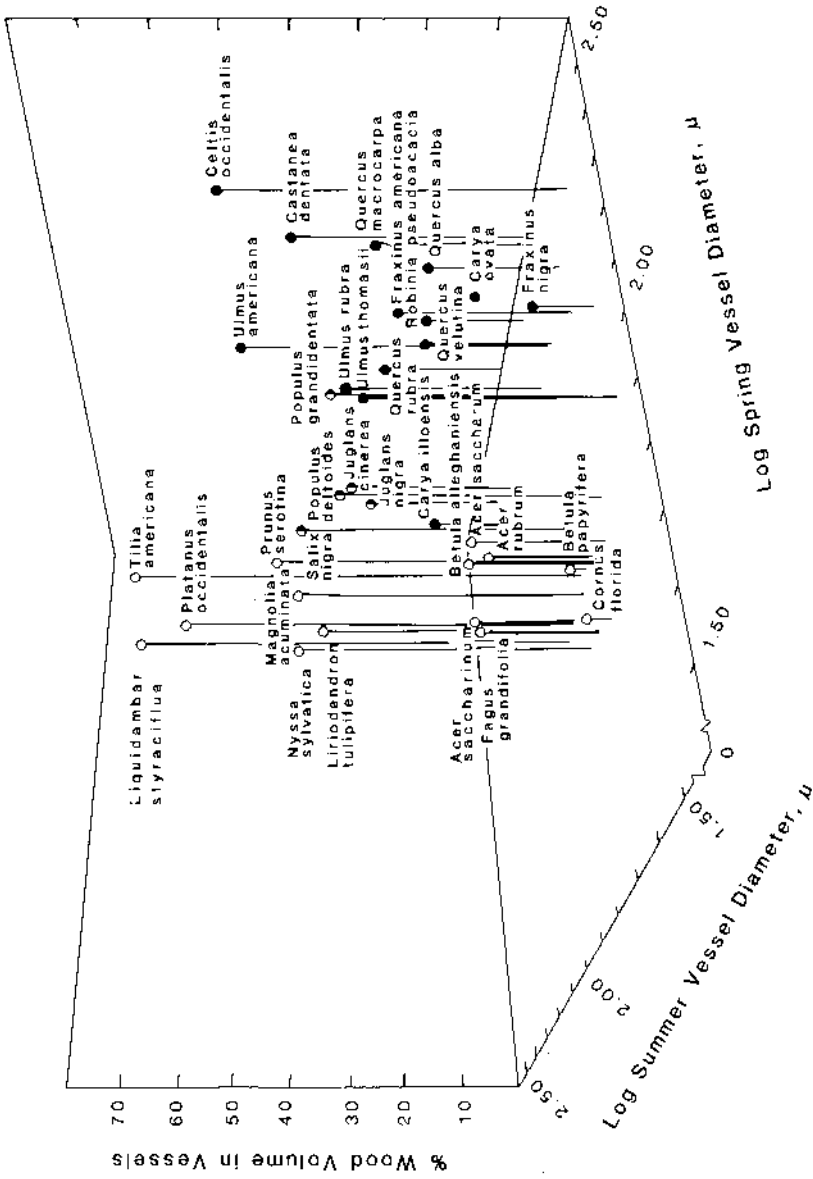


FIG. 7.—Variables affecting a tree's capacity to transport water: that mean spring and summer vessel-diameters in microns and the percentage of wood volume represented by vessels. Larger-diameter vessels transport water with less resistance but greater danger of cavitation (Zimmerman and Brown 1971); the more vessels per unit volume the greater the potential volume of water transported per unit time. The data are from French (1923). Symbols as in fig. 2.

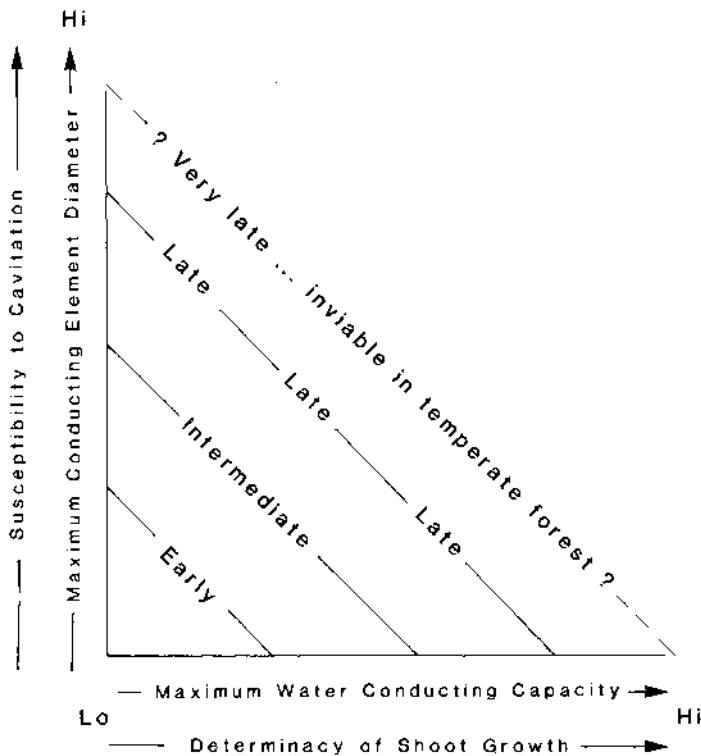


FIG. 8.—The relationship between timing of leaf emergence and characteristics of the tree's water transport system. Trees with larger vessels are more susceptible to cavitation and those with more and/or larger vessels have the greater potential rates of transport of water to the leaves. This maximal transport rate is intended to be that achieved prior to any cavitation. See text for a discussion of these relationships.

variation in vessel length and sculpturing. Without considering these refinements, there is a general but not inviolable trend among temperate deciduous trees for semi-ring-porous and ring-porous species to leaf out after most diffuse-porous species.

The functional implications of large versus small vessels first discussed by Zimmerman and Brown (1971; Zimmerman 1983) provide a proximate explanation for the tendency of ring-porous trees to leaf out later in the temperate forest environment. Individual large-diameter vessels can transport water more rapidly than small-diameter vessels at a given xylem potential because larger capillaries offer less resistance to flow (Zimmerman and Brown 1971). Larger vessels, however, are also more susceptible to breakage of the continuous capillary stream required to transport water up a tree; cavitation, caused by either extreme transpiration loads in summer or freezing in winter, stops conduction in the affected vessel and is generally irreversible (Zimmerman and Brown 1971). Since most of the conducting capacity in ring-porous trees is in large-diameter vessels that cavitate in winter, new xylem must be initiated before newly emerging leaves can

be supplied with water. Lodewick (1928) and Wareing (1951) have shown that cambial activity begins earlier in ring-porous than diffuse-porous species and that it precedes leaf emergence. Thus as the winter ends and temperatures again allow metabolic activity, diffuse-porous trees with relatively little cavitation of their conducting elements can potentially leaf out before ring-porous species which must first rebuild their functional xylem. Unfortunately this offers no explanation as to why many diffuse-porous species like *Tilia* and *Platanus* with abundant narrow vessels affording relatively large potential conduction capacity should leaf out as late as, or even later than, many ring-porous species.

A second set of correlates between shoot growth patterns and the timing of leaf emergence offers a possible proximate explanation for the range of leaf phenologies observed among diffuse-porous taxa. The ring-porous species of temperate trees in the genera *Carya*, *Quercus*, *Fraxinus*, and *Gymnocladus* that have been studied all have determinate shoot growth in which a single brief flush of leaves and associated shoot elongation occur each growing season (Marks 1975; Moore 1909; Kozłowski 1964; Hoffman and Lyr 1973; Kozłowski and Ward 1961; Foster 1931; Gill 1971). Young individuals of *Quercus* do show multiple episodes of shoot growth within a season but these are also a series of brief periods of growth rather than a steady, continuous shoot elongation (Reich et al. 1978; Kriebel et al. 1976; Lavarenne-Allary 1965). In contrast diffuse-porous tree species may to varying degrees have indeterminate shoot growth in which a relatively few leaves emerge early in the season followed by a series of individual late leaves produced on a gradually elongating shoot through the summer (Kramer and Kozłowski 1979; Hoffman and Lyr 1973). Indeterminate shoot growth has been reported in such diffuse-porous genera as *Acer*, *Aesculus*, *Alnus*, *Betula*, *Cornus*, *Liriodendron*, *Magnolia*, *Oxydendrum*, *Populus*, *Prunus*, *Salix*, and *Sorbus* (Moore 1909; Sharik and Barnes 1976; Kikuzawa 1978, 1983; Critchfield 1971, 1960; Kozłowski 1964; Kozłowski and Ward 1961; Kozłowski and Clausen 1966; Marks 1975; Steingraeber 1982; Power et al. 1982). In an earlier analysis, Marks (1975) associated indeterminate growth with early successional species, but recent data on *B. alleghaniensis* (Sharik and Barnes 1976) and *A. saccharum* (Steingraeber 1982; Powell et al. 1982) suggest that later successional species have only lesser degrees of indeterminacy perhaps grading into strictly determinate growth at the extreme. The phenological data reviewed here (figs. 1-6) also show that species with greater degrees of indeterminate growth tend to leaf out earlier. It is reasonable to hypothesize that the timing of leaf emergence in diffuse-porous species is predicated on the consequences of late spring frosts in indeterminate versus more nearly determinate species. Highly indeterminate species that leaf out early risk only a few leaves to late frost while a more nearly determinate, diffuse-porous species that leafed out at the same time might lose essentially its entire annual complement of leaves. Although the proximate basis of leaf emergence timing in diffuse-porous species may well rest on such avoidance of excessive damage by late spring frosts, it remains unclear why shoot growth patterns ultimately should be linked with variation in the conducting capacity of diffuse-porous woods as well as with leaf phenology (cf. fig. 8).

This puzzling aspect of the interrelationship among shoot growth pattern, wood anatomy, and leaf phenology cannot be resolved with the data presently available in the literature on other aspects of leaf function. There is only a weak indication (figs. 2, 5) that early-leafing species keep their leaves longer into the fall. Chabot and Hicks (1982) review some of the implications of such variation in leaf longevity. Beyond this there are no consistent correlations of shoot growth pattern, wood anatomy, and leaf phenology with stomatal frequency (Salisbury 1927; Ticha 1982), leaf nitrogen concentrations which approximately indicate photosynthetic capacity (Ricklefs and Matthew 1982), shade tolerance (Baker 1949), tolerance to flooding (Teskey and Hinckley 1978*a*, 1978*b*), maximum stomatal conductances (Körner et al. 1979; Hinckley et al. 1978), stomatal sensitivity to water stress (Bunce et al. 1977; Federer 1977; Bazzaz 1979), maximal rates of stem flow (Zimmerman and Brown 1971; Hinckley et al. 1978), freezing resistance of overwintering buds (Sakai and Weiser 1973), frost tolerance of young foliage (Tryon and True 1964), relative allocation of biomass to leaf tissues (Tritton and Hornbeck 1982), canopy architecture (Whitney 1976; Steingraeber et al. 1979; White 1983), tree size at maturity, or tree longevity (Altman and Dittmer 1962, table 103). More data on these and other traits related to leaf function are required before the proximate causes of leaf phenology in diffuse-porous trees can be fully understood from either an ecological or evolutionary viewpoint.

Given the limited evidence available we cannot infer that the observed times of leaf emergence among temperate deciduous trees contribute to maximal lifetime reproductive efforts. On a proximate level, late leafing in ring-porous trees is linked to the susceptibility of large-diameter vessels to cavitation and the consequent necessity of cambial activity preceding spring leaf emergence. Despite the suggestion by Gilbert (1940) that ring-porosity evolved as an adaptation to strongly seasonal water availability, it is difficult to recognize the current adaptive value of ring-porosity when so many ring-porous trees like *Quercus* typically occupy xeric habitats; surely by leafing late the oaks miss the opportunity to fully exploit the spring groundwater resource which in xeric habitats could potentially enhance growth and reproduction. Similarly, variations in leaf emergence among diffuse-porous trees correlate with differences in seasonal patterns of leaf production and shoot growth. Early-leafing species have more indeterminate shoot growth that makes relatively few leaves vulnerable to late frosts. Nonetheless the resources available for growth and reproduction in later-leafing, diffuse-porous trees like *Tilia*, *Platanus*, *Nyssa*, *Magnolia*, and *Liquidambar* potentially could be increased by earlier leaf emergence. Unlike ring-porous species, these late-leafing, diffuse-porous species have ample conducting capacity to supply water to their emerging leaves and yet seem not to have evolved the strongly indeterminate shoot organization of the early-leafing diffuse-porous species. It therefore does not seem possible at this time to attribute adaptive value to the timing of leaf emergence in contemporary temperate forest environments. We may certainly analyze the present ecological implications of leaf phenology, but we cannot explain its evolutionary origin as an adaptation maximizing potential growth and reproduction in contemporary temperate forest environments. Instead present

differences in the phenology of leaf emergence among temperate deciduous trees can best be explained historically and may only perhaps eventually be understood as adaptation to ancient rather than contemporary environments.

DISCUSSION

In large part our difficulties in interpreting the evolutionary basis for differences in leaf phenology among temperate deciduous trees probably stem from the transience of the forest communities we study. Davis (1976, 1981) reviews the evidence for the instability of temperate forests during the Quaternary. Each glacial cycle spans 50,000–100,000 yr with only 10,000–20,000-yr interglacial periods. During these relatively brief interglacial periods deciduous forest trees that have survived glaciation as isolated populations south of the ice disperse into the glaciated regions (Delcourt and Delcourt 1979, 1981). Rates of dispersal vary among species such that competitive interactions in forest communities can be altered drastically during the course of the interglacial period. Davis (1976) gives the Holocene example that chestnut reached one end of its modern range in eastern North America 3,000 yr earlier than it reached the other. In Europe, where the record of previous interglacial periods is better studied, it is also clear that not even the same forest communities develop in each interglacial period (Davis 1976, 1981; Frenzel 1968; Wright 1977). Our analysis of the evolutionary history and adaptive significance of traits in forest tree species must inevitably be muddled by the ephemeral selection regimes which have typified the Quaternary history of temperate forests. The Tertiary paleoenvironments that shaped the traits we study may bear little direct resemblance to the habitats in which species have alternatively survived the glacial and interglacial periods of the last 2½ million yr. Presumably there is some congruence between the ancestral environments in which traits evolved and the environments in which a tree can successfully colonize, grow, and reproduce, but we should not expect to discover perfect adaptation to the contemporary forest environment. The consistent correlations we have observed between growth pattern, wood anatomy, and timing of leaf emergence probably arose in response to various selection regimes in Tertiary forests. Co-occurring species have achieved their common ability to colonize and survive in contemporary forests through diverse combinations of traits that quite likely evolved in equally diverse habitats all somewhat different from the one they now share.

It seems reasonable to consider that many other traits may be in similar evolutionary disequilibrium among temperate forest trees. For example, tree-herbivore interactions seem less likely to represent tightly coevolved relationships as envisioned by Rhoades and Cates (1976) than something akin to the more haphazard and diverse pest communities that rapidly build up on newly introduced tree crops (Strong 1974, 1979). Similarly forest succession, while it may be predictable in terms of species autecologies (Solomon et al. 1981), most likely arises from interactions in chance assemblages of species rather than from coevolved partitioning of resources in space and time. We must anticipate a certain vagueness (*sensu* Strong 1984), a considerable measure of stochasticity, in

the ecology of transient species shaped by long and not necessarily shared evolutionary history. More complete comparative analyses of traits contributing to the success of trees in contemporary forests should be undertaken to test this supposition. In terms of leaf phenology, data from the species-rich mesophytic forests of southeastern North America could provide an especially useful extension of the tentative generalizations arising from the present analysis. Further studies involving not only a more extensive geographic sample of broadleaf, deciduous forests but also additional traits will yield some interesting ecological generalizations, and may help elucidate the evolutionary basis of the observed traits.

SUMMARY AND CONCLUSIONS

1. The time of spring leaf emergence varies consistently among deciduous tree species in the north temperate forests of both eastern North America and Eurasia. The time of bud break among different tree species growing together in the same forest typically spans several weeks and the taxonomic sequences of leaf emergence are very similar from region to region.

2. Tree species that leaf earliest have only narrow-diameter xylem vessels (diffuse-porous wood anatomy) and relatively low numbers of vessels per unit wood volume. These include most members of the genera *Populus*, *Betula*, *Salix*, *Alnus*, *Ostrya*, *Acer*, *Carpinus*, *Prunus*, and *Aesculus*. Later-leafing trees are characterized by having distinctly larger-diameter xylem vessels produced in their early, spring wood (ring-porous wood anatomy) and/or, especially in diffuse-porous species, relatively high numbers of vessels per unit wood volume. Both these traits contribute to greater maximum potential water conduction capacity. Among diffuse-porous species earlier leafing is also associated with greater indeterminacy of shoot growth; the earliest-leafing taxa initially flush only a few early leaves followed by a series of individual morphologically distinct late leaves on some shoots through the summer (heterophylly).

3. By virtue of their large vessel diameters, ring-porous species gain potential conduction capacity but also are more susceptible to cavitation of xylem water columns during winter, which renders the affected vessels nonfunctional. As a result cambial activity must precede leaf emergence in ring-porous species; this explains the relatively late leafing of ring-porous genera like *Fraxinus*, *Quercus*, *Rhus*, *Ulmus*, *Sassafras*, *Morus*, *Maclura*, *Carya*, and *Juglans*.

4. No comparable functional explanation can be discerned for the late-leafing, diffuse-porous species, which have high numbers of narrow vessels providing good conducting capacity not prone to winter cavitation. These include *Nyssa*, *Platanus*, *Liquidambar*, *Tilia*, and *Fagus*. The inability of these species to leaf earlier may stem from the tropical to semitropical paleoenvironments in which they are believed to have evolved. The earlier-leafing, diffuse-porous genera primarily originate in the more temperate Arcto-tertiary flora and have indeterminate shoot growth, which functions to minimize losses to late frosts.

5. The traits of temperate trees that evolved in diverse and poorly known paleoenvironments do not necessarily represent optimal adaptations to contemporary conditions. While we can analyze the ecological implications of variation in

leaf phenology, we should not assume that a tree's phenological characteristics necessarily lead to its maximum potential growth and reproduction. The Quaternary history of the temperate forests has been one of repeated disruptions by glaciations such that present forest communities must be seen as transient assemblages rather than stable sets of coevolved species. Evolutionary disequilibrium should be anticipated not only in leaf phenology but also in many other traits of temperate forest trees.

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