

Pears and persimmons: A comparison of temperate forests in Europe and eastern North America*

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Abstract

Major dimensions of ecological segregation of tree species in cool temperate Europe and E North America appear related to (a) soil pH, (b) large scale 'succession' including topographic sequences of changing moisture stress, and (c) intolerance versus tolerance of canopy competition as involved in 'gap-phase' dynamics. Genera tend to have similar average positions along these dimensions in the two subcontinents.

E North American genera that were probably never present in Europe, and the few opposites, tend to be southern and are concentrated on dry or basic soil. The cause of this trend may involve the isolated expansions of dry climatic areas since the early Tertiary. E North American genera that became extinct in Europe after the mid-Pliocene are typical of habitat intermediate between dry-acid and moist-basic, though generally more moist-acid than dry-basic. These genera also have few species and little overall habitat width. Severe restrictions of their habitats may have occurred. Also, difficulties of migration to and from refugia are suggested by the generally heavier seed of extinct genera and those with strongly southern ranges in Europe or with few species compared to E North America. This relationship is apparent within small winged, medium fleshy and large nutty fruit classes. However, there is little difference in geographic restriction between these classes.

Carpinus, *Alnus*, *Corylus*, *Taxus*, *Pyrus* and *Sorbus* reach 100-1000% greater height in Europe. There are no opposing differences of this magnitude. These trees may be ecological substitutes for extinct *Liriodendron*, *Liquidambar*, *Carya*, *Tsuga* + *Thuja*, *Diospyros*, and a group with smaller fleshy fruits, respectively.

There are other intrageneric differences in height, seed weight, niche width, longevity, etc., that deserve further attention.

Introduction

A dominant theme in most previous comparisons of temperate forests across the Northern Hemisphere has been the differences in diversity of tree taxa. These differences are attributable in large part to the differences in extinction from the relatively

homogeneous 'Mixed Mesophytic' forest during the climatic deteriorations of the late Tertiary and Pleistocene, as indicated by the fossil record (e.g., Van der Hammen *et al.*, 1971; Graham, 1972). It is argued that the greater survival in areas like China was allowed by the continuous and especially mountainous land masses from north to south. Mountains tend to have a greater diversity of habitats, in particular altitudinal zones similar to latitudinal ones, and this may have encouraged north-south migration in response to the changes in temperature. Europe was especially inhospitable in

* Floras used for nomenclature and ranges are Flora Europaea (Tutin *et al.*, 1964-1970) and Gleason & Cronquist (1963).

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this respect. Differences in dryness of climate were probably also important. In E North America there was a southward shifting of trees during the last glacial period though it is still not certain whether temperate trees completely deserted the Appalachians to survive only in more limited areas of high relief on the Coastal Plain. The Plain generally increased in dryness but much of it remained covered by temperate forest which was dominated by *Quercus*, *Carya* and *Pinus* (e.g., Watts, 1979, 1980; H. Delcourt, 1979; P. Delcourt, 1980). In Europe temperate forest probably survived in a much smaller area of mountainous or other moist land around the Mediterranean Sea. Even in interglacial periods, the Mediterranean region has been drier than the American Coastal Plain. During glacial periods the Mediterranean lowlands and C Europe became arid and steppe-like (e.g., van der Hammen *et al.*, 1971; Iversen, 1973; Pignatti, 1978; H. J. B. Birks, unpubl.).

In addition to differences in extinction there were very likely preexisting differences in diversity. China, in particular, has several temperate tree genera that have not been found as fossils elsewhere, e.g., *Bretschneidera*, *Rhoiptelea*, *Sargentodoxa* and *Tetracentron* (Wang, 1961). The completeness of the fossil record may be doubted. Nevertheless, there appears to be some analogy between China and SE Asia as a probable ancient center of taxonomic diversity in tropical rain forest (e.g., Whitmore, 1975).

My primary purpose in this paper is to extend the comparison of existing forests as a preliminary stage to a more detailed synthesis with fossil data. There is now enough information on forests in Europe and E North America to begin exploring similarities and differences in functioning of tree taxa, not just their geographic distributions. Kornas (1965) and others (cited therein) have begun matching forest types. Their studies have been more intensive than attempted here, but more limited in areal extent. I will limit discussion in general to a relatively cool temperate zone: north to the boreal coniferous zone, also excluding subalpine forest, and south to the beginning of evergreen codominance without thorough coverage of southern deciduous species within temperate genera, e.g., *Quercus pubescens* in Europe and *Q. stellata* in E North America. European species that are largely restricted to Russia are excluded.

The basic theoretical interest attached to synthesis of this kind is the insight eventually promised to processes of natural selection over a relatively long time scale. Whatever the exact causes of differences in diversity they must be largely 'historical', since when introduced by man many trees have become naturalized into more or less equivalent habitats in subcontinents outside their current ranges: e.g., *Alnus rugosa*, *Populus deltoides*, *Robinia pseudoacacia*, *Gleditsia triacanthos*, *Crataegus* spp., *Amelanchier spicata* and *Prunus serotina* from E North America to Europe; e.g., *Alnus glutinosa*, *Salix* spp., *Populus* spp., *Crataegus* spp., *Prunus* spp., *Sorbus aucuparia*, *Pyrus* spp. (including *Malus*), *Aesculus hippocastanum* and *Acer platanoides* in the opposite direction (from floras cited above and others). Late successional species are naturalized much less often than early successional ones, but this is presumably due to lack of rapid colonizing ability and/or economic value, being slower to grow. Certainly there are no absolute abiotic differences to explain absences from whole subcontinents. Any local biotic restraints, e.g., competition from existing plants or absence of suitable vectors for pollen or seeds, are likely to be temporary, e.g., until appearance of gaps in the canopy or introduction of animal vectors. These considerations suggest that the differences in diversity can be regarded to some extent as a massive 'natural experiment' allowing insight to the following intimately linked questions concerning any modification of community organization by a reduction in diversity: (a) is there less specialization in habitat or regeneration in Europe; (b) is there any sign of new tree taxa replacing the ones that are absent?

There are a variety of more limited themes possible in this comparative approach, and these are best dealt with in advance. Comparison of composition may suggest differences in climate or soil, though more likely involving glacial refugia than current ranges, as indicated above. Any such differences must be carefully considered in connection with the uncontrolled 'natural experiment' to avoid erroneous conclusions. To the extent that extinction was merely caused by problems of migration to and from refugia, another interest is whether restricted distributions reflect poor dispersal. Finally, a straightforward exposition of the similarities between forests, without necessarily involving histori-

cal questions, is in itself of considerable value. A matching of ecologically equivalent taxa should help reveal the morphological and physiological characteristics that are suitable for a particular 'niche', as opposed to characteristics that merely reflect non-adaptive genetic drift or adaptation to past environments.

This paper is emphatically only a preliminary enquiry of these questions.

Similarities of community organization

I have drawn upon much literature and general knowledge of forests in Europe and E North America to construct schemes of ecological segregation for tree genera (Fig. 1). The most concentrated sources for this information that I used are Szafer (1966) and Rackham (1980) for Europe, and Braun (1950) and Campbell (unpubl.) for E North America. Much European work is not in English, but these studies of Poland and England cover virtually the full range of composition. I have tried to overcome any regional biases in these sources by keeping schemes as simple as possible while including all genera. It must be emphasized that the schemes are primarily based on patterns of interspecific association. The interpretations of causation are often provisional, e.g., occurrence of flammable *Juniperus* on calcareous soil may be due to absence of fire as well as soil chemistry *per se*.

As summarized in Figure 1, these descriptive studies suggest that there are two major dimensions of ecological segregation on a relatively large spatial scale: (a) soil pH and associated physicochemical factors; (b) 'succession'. I use the term 'succession' in a relatively broad Clementsian sense, embracing large scale secondary succession following disturbance, and primary succession including the stable or very slowly changing topographic sequences as well as typical hydroseres and xeroseres. These various successions may differ in their vegetation, but there is a degree of association among trees between tolerance of the moisture extremes and colonizing ability on open areas. This association is especially pronounced at the generic level which is emphasized here. This paper treats only tree genera with at least one species reaching 10 m or more in height. However, within this class one can distinguish typically competition-tolerant subcanopy-concentrat-

ed species from less tolerant upper canopy-concentrated species. This distinction is the third major dimension referred to below (Fig. 1). In many cases, it can be viewed as essentially the same as the segregation involving small scale 'gap-phase' regeneration by less tolerant species (Campbell, unpubl.) Cycles of regeneration within patches of forest were probably part of the primaeval scene in many North Temperate areas (Jones, 1945). The assignment of trees to tolerance classes here is similar to the traditional assignments of foresters in both subcontinents (e.g., Zon & Graves, 1911). Most differences here reflect the importance I attach to relative tolerances of closely associated species. For example, both *Salix* and *Populus* are intolerant compared to most trees of later succession, but *Salix* is often concentrated in smaller size classes than associated *Populus* in early succession on moist mineral soil. With this definition, tolerant species do not necessarily succeed intolerants (Campbell, unpubl.). Another possible mechanism for maintaining diversity alluded to below is that involving vectors of dispersal.

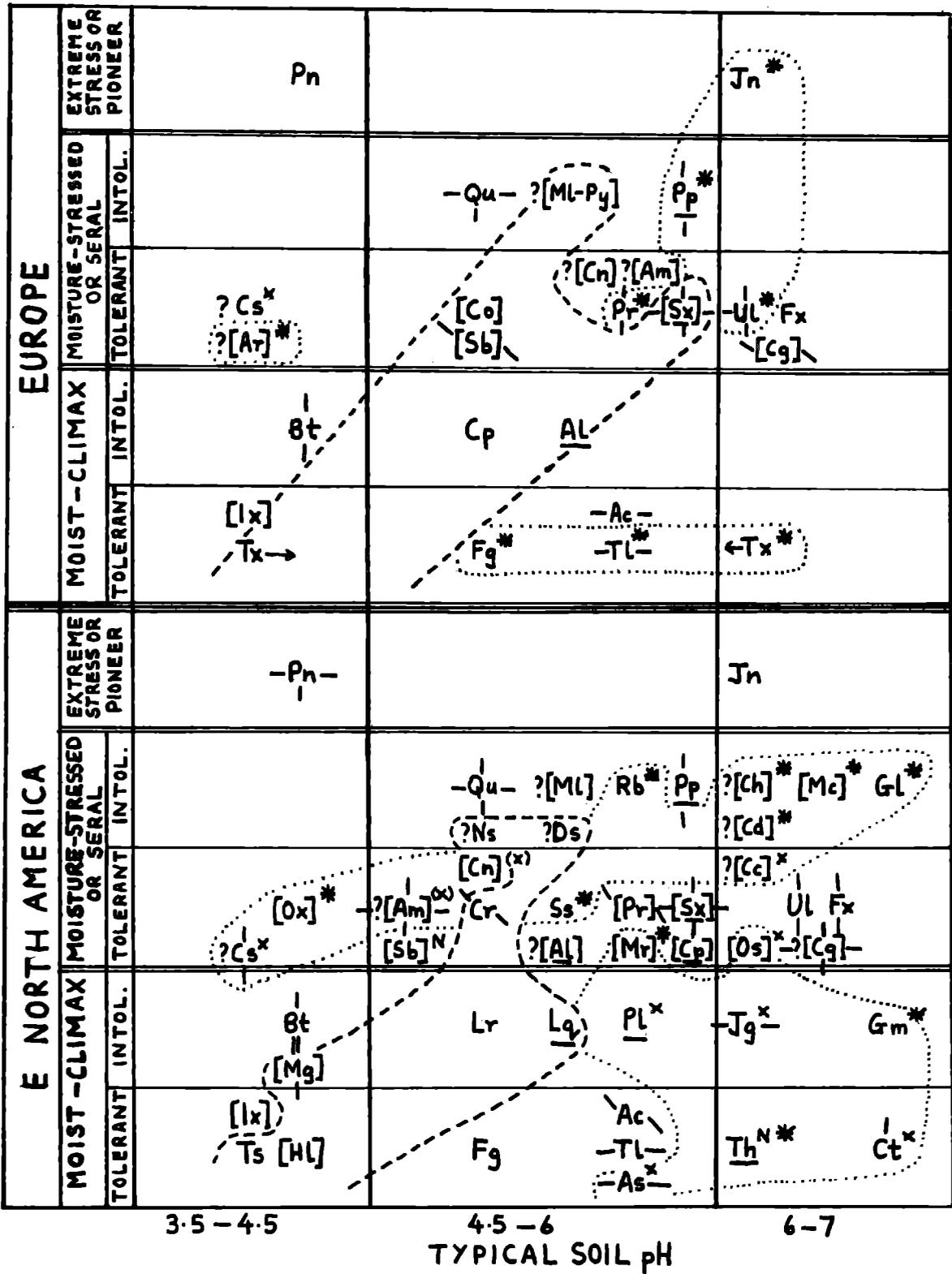
In general species within genera appear to be segregated by habitat as opposed to short secondary succession, gap-phase regeneration, or more subtle 'within-habitat' dimensions. This trend does not seem to be less pronounced in E North America, though Grubb (1977) suggested that in areas like China, with even more intrageneric diversity, differences in 'regeneration niche' are probably more important. Nevertheless, this question deserves more quantitative attention than is possible in this preliminary study.

For genera present as trees in both areas, the similarities in their average positions along the major dimensions are striking (Fig. 1). Other authors have reached similar conclusions from less comprehensive comparisons (e.g., Jones, 1945; Kornas, 1965). This result is not surprising considering the descent of modern forests from a more continuous temperate forest at higher latitude in the Tertiary.

Differences in taxonomic composition: possible causes

Genera never found in one subcontinent

There are about 15 cool temperate genera in E



North America that are absent in Europe, but only *Arbutus* and *Pyrus* (if separated from *Malus* and *Sorbus*) have the opposite distribution. Some of these E North American genera, and both the European ones, have not been definitely identified as fossil on the other side of the Atlantic. These E North American genera are *Thuja* (with a southern relative in *Chamaecyparis*), *Sassafras*, *Morus* (with southern relative *Maclura*), *Oxydendrum*, *Chionanthus* and the legumes *Robinia*, *Cladrastis*, *Gleditsia* and *Gymnocladus* (*Cercis* being the only woody legume genus in both areas). These omissions could be partially due to inadequacy of the fossil record. Most of these genera are known from other areas of temperate forest in the Northern Hemisphere. At least 'Thuja-like conifers' were found in Europe, though they became extinct relatively early, in the Miocene or Pliocene (Florin, 1966).

These genera that have only been found in one of the subcontinents are all relatively southern and 'successional' except for *Thuja*. It is well known that the frequency of taxonomically close pairs of plant taxa in different subcontinents declines from north to south within the Northern Hemisphere (e.g., Kornas, 1965). However, whether this trend is just due to the greater time of separation in the south, or also due to climatic divergence or other selective forces, is not known. Another feature of these genera, with the exception of *Oxydendrum*, is their concentration on relatively base-rich soil (Fig. 1). Conceivably, this trend is related to the large-scale association between drier climates and more base-rich soils (Eyre, 1963), as in S Europe (cf. Grime, 1979, p. 184) and probably SW E North America (Campbell, unpubl.)

In the case of the legumes one can propose a

taxonomic and ecological match with the European *Laburnum*, *Ulex*, *Genista*, *Cytisus*, *Ceratonia*, etc. These European legumes are also relatively southern; they are also typical of recurrently disturbed grassy or shrubby areas; *Ulex*, *Genista*, etc., are thorny like the American locusts; there are similarities in probable mechanisms of dispersal, e.g., *Robinia* and *Laburnum* by weak wind dispersal of pods (Ridley, 1930), and *Gleditsia* and *Ceratonia* by bovines (Fowells, 1965; van der Pijl, 1969, p. 42). However, the European legumes are little or no more than shrubs. Conversely, shrubby legumes are relatively uncommon in E North America, i.e., *Amorpha* and some *Robinia* spp. Possibly, this difference in maximum stature reflects more frequent disturbance in Europe, whether of climatic or antropogenic origin. Only one other ecological match of genera within a family is possible: E North American *Oxydendrum arboreum* and European *Arbutus unedo* are the only arboreal members of Ericaceae in their subcontinents. Both are small southern trees concentrated on xeric or open ground often on highly acid soil. However, *Arbutus* has evergreen leaves and fleshy fruit.

Combining these ideas into one hypothesis, one may suggest that S Europe, being drier and less forested than the E North American south, has since an early date generated fewer opportunities for trees suited to southern conditions. The opposite may be true for shrubs in the case of the legumes.

Genera that became extinct in Europe

Are there any common characteristics among the extinct genera of Europe that still occur in E North America? These genera are *Taxodium*, *Tsuga*,

Fig. 1. Ecological classification of cool temperate tree genera in Europe and E North America. See text for explanation of vertical 'succession' axis; note that 'climax tolerants' are generally more tolerant of competition than 'moisture-stressed tolerants', etc.

Identification of genera. Pn, Jn, etc.: abbreviations (cf. Table 1). If there is more than one species per genus, radiating lines indicate direction of any dispersion on major axes ('tolerance' only clearly differentiates in Mg.? Cr.? Pr.? Sx). Pp, etc.: generally more hydric than xeric. [] generally not reaching 20 m in height.

Sb^N and Th^N: strongly northern genera in E North America.

Differences between subcontinents.

-----: encloses genera extinct from Europe; or, that have large increases in maximum height or spp. in Europe.

X: much more southern in Europe.

*: E North American genera never found as fossil in Europe; or, in Europe, genera with little change in number of species or latitudinal range.

.....: enclosing X or * in each subcontinent.

Magnolia, *Halesia*, *Liriodendron*, *Liquidambar*, *Carya*, *Nyssa* and *Diospyros* (van der Hammen *et al.*, 1971). Their dates of extinction range from late Pliocene to two or three glacial ages. *Taxodium* may be considered a special case since it is strongly southern and hydric where it occurs today, in E North America and Mexico (Breedlove, 1973). The Mediterranean region probably contained little suitable habitat for this genus during glacial ages and even earlier (cf. Introduction; Michaux *et al.*, 1979). All of the remainder are somewhat southern except for *Tsuga* and, marginally, *Carya*. Also, there is a curious concentration along the diagonal of the two-dimensional scheme of habitat gradients (Fig. 1) from the moist-acid corner towards the dry-basic, though excluding *Juniperus* and others at the latter extreme. One can understand the survival of *Juniperus*, as compared to those like *Tsuga* at the other extreme, in terms of the drier and perhaps more basic Mediterranean conditions. The diagonal concentration should perhaps be viewed in terms of the probable association between dryness and acidity within moist temperate climatic regions. The extinction of taxa with intermediate preference suggests that intermediate habitat was especially rare during the glacial ages. Dry-acid conditions were presumably concentrated in the restricted mountainous refugia of the Mediterranean region. Though most of the lowlands were too dry for forest, it is conceivable that moist-basic forest existed close to watercourses, perhaps disjunct from leached mountain slopes. There is some vegetational evidence that similar edaphic discontinuities occur today within some rugged Appalachian areas and nearby (Campbell, unpubl.).

Alternatively, one might argue that competition from the dominant genera either side, typically *Quercus-Castanea* on dry-acid ground and *Fagus-Acer* on moist-basic, combined with increased environmental fluctuations to 'squeeze' out the intermediates (cf. theory of May, 1973). It may be significant that except for *Tsuga* these extinct genera are not among the major dominant trees in late successional or climax forest of E North America.

Several of the extinct genera are major dominants in early successional forest or gap-phase regeneration, but this ability is unlikely to have encouraged survival by itself. Climatic fluctuation and migration over millenia may well favor different characteristics than those favored by local dis-

turbance from wind, fire, water, etc. Indeed, the fruits of these genera are mostly rather large and specialized compared to the small sweet-fleshed or winged fruits of more extreme pioneers like *Crataegus*, *Prunus*, *Juniperus*, *Betula*, *Populus* and *Salix* (Table 1).

One further distinguishing characteristic of these genera is their low numbers of species (Table 1; Fig. 2). There is generally only one sympatric species per genus within most of each subcontinent, and no more than four within E North America as a whole.

Low numbers of species also occur within genera not recorded as fossil in Europe, perhaps involving restrictions in habitat or range (see above), and within genera restricted in Europe to partially 'historical' refuges in the south (see below). The only oligospecific genera that are widespread as trees in both E North America and Europe are *Fagus* and *Carpinus*, and even these may be 'historically' absent from some parts of Britain (Rackham, 1980). The only restricted genera that are multispecific are *Carya* and *Magnolia*, both extinct from Europe. However, E North America is especially rich in *Carya* spp.: this genus is very unusual in having less species in E Asia, i.e., only one in China (Wang, 1961). Furthermore, the number of *Magnolia* species in E North America does not reflect, as in other multispecific genera, a great variety of habitats; instead, their ecological segregation may involve their large differences in maximum size, leaf size and species of pollinator (Thien *et al.*, 1975). This general lack of radiation with respect to habitat within extinct genera elaborates the argument above based on their intermediate average habitat. For contrast, *Betula*, *Quercus* and *Prunus* are not far from being intermediate on average, but they are multispecific, relatively wide in the range of habitats occupied, and they survived the Pleistocene. Why oligospecific genera should be concentrated in intermediate habitat (Fig. 2) is an interesting question but outside the scope of this paper.

Genera that are more southern in Europe

The list of genera absent from cool temperate Europe could be added to from those with native ranges restricted to the south in the region, i.e., mostly in the southeast: *Castanea*, *Juglans*, *Aesculus*, *Platanus*, *Ostrya*, *Celtis* and *Cercis*. These gen-

Table 1. Fruit characteristics of genera in relation to geographic differences*.

Type of fruit	Never found in Europe	Extinct in Europe	Strongly southern in Europe	Wide-ranging but with fewer spp. in Europe	Wide-ranging and similar number of spp.	Large increase in height or spp. in Europe
Winged	<u>Thuja</u>	<u>Liriodendron</u> ^a	<u>Platanus</u> ^b	<u>Acer</u> ^a	<u>Ulmus</u> ^(a)	<u>Alnus</u>
	1-0	1-0	1-1	6-3	3-4	3-2
	<u>Oxydendrum</u>	<u>Halesia</u> ^a		<u>Fraxinus</u> ^a	<u>Populus</u>	<u>Salix</u>
	1-0	1-0		4-1	4-4	12-23
		<u>Liquidambar</u> ^b		<u>Pinus</u> ^(a)		
	1-0		6-2			
	Tsuga		Betula			
	2-0		6-3			
Fleshy	<u>Chionanthus</u> ^a	<u>Diospyros</u> ^a	<u>Celtis</u> ^(a)	<u>Ilex</u>	<u>Prunus</u> ^(a)	<u>Taxus</u>
	1-0	1-0	2-1	4-1	8-6	1-1
	<u>Sassafras</u> ^(a)	<u>Nyssa</u> ^a		<u>Cornus</u>	<u>Juniperus</u>	<u>Sorbus</u>
	1-0	1-0		8-2	2-1½	2-8/5 ^c
	<u>Morus</u>	<u>Magnolia</u> ^b		<u>Crataegus</u>		<u>Arbutus</u>
1-0	4-0		30 ^c -6		0-1	
			<u>Malus</u>		<u>Pyrus</u>	
			3-1		0-5	
			<u>Amelanchier</u>			
			3-1			
Nutty	<u>Gymnocladus</u> ^(a)	<u>Carya</u> ^a	<u>Aesculus</u> ^a	<u>Quercus</u> ^(a)	<u>Fagus</u>	<u>Corylus</u> ^(a)
	1-0	6-0	2-1	14/6 ^d -3	1-1	2-1
	<u>Gleditsia</u>		<u>Juglans</u> ^a		<u>Tilia</u>	<u>Carpinus</u>
	1-0		2-1		3-3	1-1
	<u>Robinia</u>		<u>Castanea</u> ^a			
3-0		2-1				
<u>Cladrastis</u>		<u>Ostrya</u>				
1-0		1-1				
		<u>Cercis</u>				
		1-1				

* Letters underlined in genera are abbreviations used elsewhere. Below names are numbers of species in cool temperate E. North America and Europe, including shrubs and borderline southern (e.g., *Quercus stellata*) or northern (e.g., *Fraxinus nigra*) species.

a Seed weight over 0.01 (winged), 0.1 (fleshy) or 1 (nutty) gm. From U.S.D.A. (1948).

(a) Borderline seed weight. b Complex fruit with seeds released gradually

c Excluding apomictic microspecies. d Excluding subgenus *Erythrobalanus*.

era all extend to colder latitudes in E North America. However, at least the first four have become naturalized in some places well north of their native ranges in Europe. Thus, this component of north-south difference within Europe may be somewhat analogous to the transatlantic difference in being largely 'historical'. It is significant that *Castanea*, *Juglans* and *Aesculus* are the genera with largest seeds in Europe and E North America, which may well have contributed to a slow rate of dispersal.

Also, probably none of the remainder have particularly well-dispersed fruit (Table 1).

Another feature of this group as a whole appears to be concentration on relatively base-rich soil (Fig. 1), which could reflect prevailing soil conditions in southern Europe (see above). *Castanea* is exceptional: its optimum habitat in the south occurs at high elevation where soils are generally more leached. These two types of distribution may partially indicate the nature of glacial refugia. Thus,

they could be used to support the suggestion above that rarity of intermediate habitat contributed to extinctions.

In E North America recolonization of the north appears to have been more complete. However, *Castanea* was still slower to do this than others (Davis, 1976; Watts, 1979). Also, *Robinia* and others have been recently expanded in range by man, though only in the case of *Maclura* has this process changed a strongly southern species into a more widespread one. *Maclura* has an interglacial record from near Toronto, confirming its wide potential (Terasmae, 1960). Possibly its current postglacial restriction to the southwest, with a very unusual range, is due to extinction of native horses shortly after glacial retreat, since its fruit is unique in size and dispersal by large quadrupeds, especially horses (Ridley, 1930; personal observation).

Genera with fewer species in Europe

Like the number of genera, the number of species within genera is less in Europe on the whole (Table 1). However, some of the differences probably existed before the climatic deteriorations (cf. Tanai, 1972). There needs to be more collection and synthesis of data to compare in detail the intrageneric taxonomies and histories, as Tanai has begun in Japan. Only some general observations are possible.

In about half of the genera that occur in E North America and Europe the reduction of species number in Europe is by a factor of $\times 1.5-3$ (Table 1). Most other genera differ little, but two or three have considerably more species in Europe. There is little or no association between the degree of difference and whether fruit is winged, fleshy or nutty. However, within the winged class genera with seed weight typically under 0.01 g do not have much reduction of species in Europe (*Ulmus*, *Alnus*, *Salix*, *Populus* and *Platanus*) with the exception of *Betula*, a genus concentrated on moist-acid soil (cf. discussion above). Within the nutty class (with or without bracts) those with seed weight under 1 g do not have much reduction (*Tilia*, *Fagus*, *Carpinus* and *Ostrya*). Within the fleshy class there is no relationship with seed weight, but those without much reduction in Europe may have somewhat sweeter flesh, i.e., *Sorbus*, *Prunus*, *Juniperus* and *Taxus*, while those with especially great reduction

of about $\times 4-5$ may be relatively unattractive to birds, i.e., *Crataegus*, *Ilex* and *Cornus* (cf. Ridley, 1930, p. 414, etc; Van der Pijl, 1969, p. 30, etc.; Stiles, 1980).

The exceptional proliferations of species in *Quercus* and *Crataegus* in cool temperate E North America by about $\times 5$ may involve special stimulations of speciation by climate or disturbance. If subgenus *Erythrobalanus* is excluded from the comparison of *Quercus* species, leaving only *Lepidobalanus*, the difference is roughly halved. *Erythrobalanus* is even more peculiarly American than *Carya* (see above), being completely absent elsewhere and not even recorded as a fossil in Europe. There is a curious tendency for species in *Lepidobalanus*, *Erythrobalanus* and *Carya* to occur as mixed triplets with similar habitat and range, suggesting some kind of species-complexing in their origin (unpubl.; cf. Whittaker, 1969). Conceivably, the intermediate degree of fragmentation of moist temperate forest in E North America by dry climate actually stimulated speciation within genera that dominate on moderately dry sites, i.e., *Quercus* and *Carya* (cf. Introduction). The large number of species in *Crataegus* has been attributed to changes in ploidy, apomixis and perhaps recent forest clearance by man, with microspecies originating in different areas and subsequently hybridizing (Stebbins, 1967, p. 549). Though the exceptional proliferations of *Salix* and *Sorbus* species and perhaps others in Europe may have similar explanations, alternatives will be discussed in the next section.

Differences in biology of taxa: evidence for substitution

Direct selection by abiotic environment

One might imagine that the conditions in Europe during climatic deteriorations led directly to evolutionary changes within some tree taxa. In particular, since problems of migration were probably a major cause of extinction, one might expect decreases in generation time or seed size in Europe. Also, if the narrow intermediate habitats of extinct genera are indicative of glacial conditions, one might expect increases in widths of habitat niches within surviving taxa.

However, as Table 2 shows, there is no consistent

Table 2. Changes in maximum height and seed weight of genera across the Atlantic*.

Change in seed weight	Genera with over 15% increase in maximum height in E.N. America	Genera with less than 15% change in maximum height	Genera with over 15% increase in maximum height in Europe
Genera with over 15% increase in average seed weight in E. North America	Pn (5/5) Jg (2/7) Bt (3/5) Ix (4/3) Fg (3/2)	?Cg (5/-) ?Sx (3/-) ?Ul (4/-)	?Al (10/15)
Genera with less than 15% change in average seed weight	?Pp (-/4) ?Jn (-/3) ?Cc (-/2) ?Os (-/3)	Qu Pr ?Te ?Am	
Genera with over 15% increase in average seed weight in Europe	Cs (50/4) Cn (25/3) Pl (3/5)	Ac (6/-) Fx (9/-) As (2/-) ?Ct (5/-)	?Sb (8/10) Py (15/15) Cp (13/15) Co (20/33) Tx (7/100)

* Based on U.S.D.A. (1948) and other miscellaneous sources, e.g., floras were used to compare seed weights with linear dimensions. The rough percent increases divided by 10 are shown in parentheses (seed weight/height) after each genus abbreviation (cf. Table 1). Many figures are tentative given the inadequate data for several genera; ? indicates most tentative. For cultivated species in Europe (in Pr, Py, Jg, Cs, Co) lowest reported seed weights or values equal to half the average (similar where data are sufficient) were used.

transatlantic difference in maximum tree size or seed weight. Also, as discussed in the previous section, the number of species within each genus is lower in most cases in Europe. Thus, the average habitat width of genera is probably no greater. It is possible that the habitat widths of individual species are greater in Europe, but there are few quantitative data that are readily available to test this idea.

Though there are no clear overall trends, there are various opposing differences in maximum height and seed weight, some of which are quite striking. This variety may be fruitfully considered in relation to a more tangible hypothesis: that some differences in biology are due to ecological substitution for trees that never existed or that became extinct in Europe. As will be seen, some return to discussion of direct selection by abiotic environment may be possible after elaboration of this hypothesis.

Evidence for substitution

(a) Large differences in maximum size or species number within genera

The most striking differences in biology within cool temperate woody genera across the Atlantic Ocean are the 100–1000% increases in maximum height of the following, from E North America to Europe:

- (1) *Carpinus* from ca. 10 m to 25 m;
- (2) *Alnus* from ca. 10 m to 25 m;
- (3) *Corylus* from ca. 3 m to 10 m;
- (4) *Taxus* from ca. 2 m to 20 m;
- (5) *Pyrus*, if included with *Malus*, from ca. 10 m to 20 m;
- (6) *Sorbus* from ca. 10 m to 25 m.

About 11 genera differ in maximum height by less than 15% (Table 2). About 12 genera are more than 15% taller in E North America (Table 2) but none is as much as 100% taller. The increase in maximum height of legumes in E North America is about 200%, but this comparison is familial not generic, and it may be related to special disturbed and/or southern conditions, as discussed already.

Salix also deserves consideration. Though not much taller, *S. fragilis* in Europe is reported to reach stem diameters of 1 m, in contrast to *S. nigra* in E North America which only reaches about 0.5 m and is generally more multiple-stemmed.

Pyrus (plus *Malus*), *Sorbus* and *Salix* are also exceptional in that their numbers of species in Europe are high compared to E North America. The differences are about $\times 2$ –3, even excluding apomictic microspecies in *Sorbus* (Table 1). Moreover, the remaining genera with large increases in size do not include any with large decreases in species number. In *Sorbus* at least there appears to be a larger range of habitats occupied and much less restriction to colder latitudes in Europe (Fig. 1). In

Carpinus, and perhaps *Alnus*, there is probably a decrease in tolerance of competition from canopy trees (cf. Baker, 1949; Forbes, 1955; McVean, 1956; Rackham, 1980). Such decrease is understandable if the larger species in Europe are geared to faster growth (cf. Marks, 1975).

(b) *Ecological matches with absent genera.*

Should these differences in size be regarded as resulting from some obscure historical event, or are they due to substitution for tree taxa that are absent? Because of the lack of detailed data for comparison at present, one cannot propose with certainty which absent taxa from Europe are most similar to the hypothetical substitutes. One should perhaps consider the several potentially cool temperate genera that became extinct in Europe which do not occur in E North America today, surviving mainly in E. Asia: i.e., *Eucommia*, *Pterocarya*, *Actinidia*, *Sciadopitys*, *Cryptomeria*, *Alangium*, *Platycarya*, *Koelreuteria*, *Ailanthus*, *Metasequoia* and perhaps others. However, one cannot assume that these genera were abundant in cool temperate forests of E North America or Europe (cf. Graham, 1972). Indeed, several of them became extinct in Europe at relatively early dates, in the Miocene or Pliocene (Florin, 1966; van der Hammen *et al.*, 1971), suggesting relatively warm temperate associations. Furthermore, there are some remarkable similarities between the genera with size increases and some extinct genera that survive in cool temperate E North America. Though these similarities cannot of course prove the hypothesis of substitution, they do build it to the point where it may be more seriously tested in the future using more modern and fossil data from throughout the Northern Hemisphere.

The most similar genera in E North America to those with size increases in Europe are now individually discussed. Except for *Carya*, *Alnus*, and *Pyrus*, the numbers of species within matched groups are similar, generally only one per genus (Fig. 2). The special abundance of *Carya* species in E North America has been discussed already; this abundance may not have occurred in Europe.

(1) *Carpinus* in Europe is similar to extinct *Liriodendron* in its concentration on sites with intermediate moisture stress and soil pH, in its moderate intolerance of shade, and its fairly high persistence in secondary succession. Neither extends in range or relatively continental areas dominated by

Quercus and others. Thus, both are similar in habitat and range to *Fagus*, though neither extends as far north. *Carpinus* has greater sprouting ability, but with repeated cutting both give way to other trees. Both have medium-sized seeds with some kind of wing, but the seed of *Carpinus* is lighter by about $\times 1/4$ and its wing is a bract subtending a nutlet rather than being directly attached. *Carpinus* in E North America is often associated with *Liriodendron* (e.g., Meijer *et al.*, 1981).

(2) *Alnus* in Europe is similar to extinct *Liquidambar* in being centered on average pH (though perhaps wider), its concentration on fairly swampy or flooded sites (see also the matching by Kornas (1965) of whole communities), and its intolerance of shade. However, *Alnus* extends to higher latitudes and altitudes. Both have a strong ability to resprout after removal of stems, though *Alnus* largely coppices from stumps while *Liquidambar* largely suckers from roots. Both have more or less winged seed that is probably liberated rather slowly from fruits and suited to dispersal by water (cf. Ridley, 1930), but the seed of *Alnus* is lighter by about $\times 1/5$ – $1/10$ and the fruit of *Liquidambar* is more complex. *Alnus* in E North America is often associated with *Liquidambar* (e.g., Kornas 1965; Meijer *et al.*, 1981).

(3) *Corylus* in Europe is similar to extinct *Carya* in its wide pH range with decline on very acid soils, its importance in subcanopy of *Quercus* forest on somewhat disturbed, mid-successional or dry sites, and its moderate tolerance of shade. *Corylus* coppices vigorously, but *Carya* only moderately. Both have nuts but those of *Corylus* are lighter by about $\times 1/4$ – $1/20$. *Corylus* in E North America is often associated with *Carya* (e.g., Meijer *et al.*, 1981).

(4) *Taxus* in Europe has a more complex match. It is similar to extinct *Tsuga* in being able to grow on acid moist soil in oceanic climate, along with somewhat calcifuge trees like *Ilex* and shrubs like *Rhododendron* (cf. Pignatti, 1978). Also, *Taxus* and *Tsuga* are among the most shade-tolerant and most heavily shading trees in their respective subcontinents, sharing obvious similarities of foliage and tree form. However, *Taxus* is also common on calcareous soils, apparently somewhat disjunct edaphically from its acid sites, though still in oceanic climate. *Taxus* may pioneer on these calcareous sites but it can also form long-lived forest with little evidence of change except for a sensitivity to grazing by rabbits (Smith, 1980). Instead of *Tsu-*

ga, an E North American match for *Taxus* on these sites appears to be *Thuja*, which does not have definite fossil records in Europe. *Thuja* is typical of wet to moist or occasionally rocky base-rich soils in northern oceanic climate (with *Chamaecyparis* a possible southern match). It is also very shade-tolerant and has similar foliage and tree form. Curiously, its successional behaviour is also a subject of keen interest; it would probably be able to spread over a remarkably large upland area if grazing by deer were to cease (Grigal & Ohmann, 1975). Regeneration of *Taxus*, *Tsuga* and *Thuja* is almost all by seed, which is small and winged in *Tsuga* and *Thuja*, but medium-sized and with very sweet surrounding flesh in *Taxus*. Finally, it is of considerable interest that the shrub form of *Taxus* in E North America is particularly common under *Tsuga* and *Thuja* (e.g., Braun, 1950; Wenger, 1976; Rogers, 1980).

In the search for a cause linking the two site types of *Taxus* some comparison with *Quercus petraea* may be worthwhile. *Q. petraea* has a similar edaphic distribution (e.g. Tansley, 1939) which may be attributed to tolerance of low P (R.E. Hughes, pers. comm.), since this tolerance has been suggested by experiment (Newnham & Carlisle, 1969), and on some calcareous soils P may be as important a limiting factor as it is on typical acid oceanic soils (P. J. Grubb, pers. comm.). Conceivably, the evergreenness of *Taxus*, *Tsuga* and *Thuja* is of value in tolerance of low nutrient supply (cf. Monk, 1966). *Acer saccharum* is the other very shade-tolerant tree concentrated on moist base-rich soils in the range of *Thuja* in E North America. Compared to that of *A. saccharum*, the foliage of *Thuja* is reported to be lower in P and K concentration by about $\times 1/3$ but similar in Ca, Mg and N (Fowells, 1965). In swamps dominated by *Thuja* nutrient supply is probably very low (Reiners & Reiners, 1970).

(5) *Pyrus* (pears) in Europe is similar to extinct *Diospyros* (persimmons). Both appear to have intermediate or wide pH range (but *Pyrus* occurring more on base rich soil), considerable tolerance of drought, early to mid-successional behaviour, and low or intermediate tolerance of shade. However, detailed information is lacking; both are relatively non-gregarious, especially *Pyrus*. Both are strong sprouters. Both are unique among large temperate trees of their subcontinents in having fruits with the syndrome of features that is particularly conducive

to dispersal by larger mammals (cf. Ridley, 1930; van der Pijl, 1969), i.e., large size with several moderately large seeds in a yellowish flesh that ripens rather suddenly near the time it falls to the ground, loosing tannic astringency, becoming browner, and gaining fragrance and sweetness. The similarities in etymology are also curious (Indo-European and Algonquian)!

(6) These E North American matches for genera with large increases of size in Europe, and the previously discussed matches of genera within the legumes and ericads, leave only the following E North American genera that are so far unmatched in Europe: extinct *Halesia*, *Magnolia* and *Nyssa*, and never-found *Sassafras*, *Morus* and *Chionanthus*. These genera are all somewhat southern, oligospecific except for *Magnolia* (see above), bird-dispersed except for *Halesia*, and relatively early successional or responsive to canopy gaps except for *Halesia*. The lack of an obvious match for *Halesia* is of minor interest here since the genus is relatively southern in E North America. The species of *Sorbus* in Europe may provide matches for the bird-dispersed genera just listed. *Sorbus* spp. number about 5–8 in Europe, though the full species status of some may be doubted (see above). Like those of the absent bird-dispersed genera, their fruits are fleshy and cover a similar range of sizes. Their dispersal ecology must be similar. Their seed weights are also variable but they are less than those of the absent genera by about $\times 1/10$ on average, excepting that of *Morus* which is lighter. They also occupy a similar range of habitats and are generally non-gregarious. However, since detailed biological data are very few, these comparisons cannot be taken very far at present. Since *Sorbus* is taxonomically close to *Pyrus*, there may be some overlap between these matches and that proposed under (5) above, in which *Pyrus* has an excess of species.

Further matches may perhaps be looked for involving genera that are restricted to the south in Europe but not in E North America, i.e., *Castanea*, *Juglans*, *Aesculus*, *Platanus* and some smaller trees (see above). However, there has been much less time for competitive release in these cases. Interglacial periods with temperate forest extending to its current northern limits have lasted only about 10–30% of the whole Pleistocene (Davis, 1976) Nevertheless, the larger maximum stem diameter and species number of *Salix* in Europe may be tentative-

ly linked with the absence of *Platanus* in the north. These trees are both largely concentrated along watercourses in pioneering situations (see also the matching of forest types by Kornas (1965)). Where they do occur together, *Salix* is generally succeeded by *Platanus*, though it may persist in lower strata (personal observation in E North America). Again, the trees are similar in regeneration, both with considerable sprouting ability and small wind-dispersed seeds, though seed weight in *Salix* is lower by about $\times 1/20$ and the fruit of *Platanus* takes some time to break up. *Platanus* may also be considered somewhat analogous to *Alnus* (see above).

(c) *Relationship of seed weight to ecological substitutions and other factors*

In most of the 15 or so matches of tree species across the Atlantic, seed weight is less in European counterparts by $\times 1/4$ – $1/20$. This trend provides support for the idea that the surviving European trees were able to migrate more easily to and from refuges. The matches involving trees that were probably absent in Europe well before the Pleistocene, perhaps from the beginning, are as follows, from E North America to Europe: *Thuja* to *Taxus*; *Morus*, *Chionanthus* and *Sassafras* to *Sorbus* spp.; within Leguminosae; within *Ericaceae*. These cases include all but one (*Tsuga-Taxus*) of the increases in seed weight in Europe: *Thuja-Taxus*, *Morus-Sorbus* sp., and *Oxydendrum-Arbutus*. These exceptions are understandable since this preexisting component of floristic difference may not have involved problems of migration as were encountered in the Pleistocene. Nevertheless, even in the cases of *Taxus* and *Arbutus* there may be superior dispersal over long distances due to the fleshy bird-dispersed fruit not found in their E North American counterparts. One might speculate that this dispersal is related in some way to the fact that they are the most strictly oceanic trees in Europe and have relatively fragmented distributions, along with *Ilex*, another bird-dispersed tree (cf. Pignatti, 1978).

Though seed weight within most matches decreases in Europe, there is a moderating tendency for increases to occur within the genera that have increases in height (Table 2; $P \approx 0.1$ in a $3 \times 3 \chi^2$ test). The explanation may be simply that the height of a tree compensates for seed size by exposing seed more efficiently to wind or animals. This relaxation

of selection for small seed through its advantage in dispersal may allow more selection for large seed through its advantage in establishment. It is also possible that this latter selective force increases as part of the syndrome of 'K-selection' (selection under competitive stress) that is associated with the size of a plant (Harper, 1977, p. 665).

The group of genera that have moderate decreases in maximum height in Europe tend to have more decreases in seed weight than those with little change in height (Table 2). This association gives more significance to these changes in height, which might otherwise be considered solely a result of the smaller areal sample of ancient undisturbed forest in Europe. These decreases in height and seed weight could be indicative of a general 'r-selection' not obscured by ecological substitution as in the genera with massive increases in height. As well as general reduction in competition due to climatic disturbance and extinctions, another cause of these changes might be the need for migration over long distances. This latter possibility would return discussion to consideration of direct selection by the abiotic environment.

The invocation of 'r-selection' in Europe fits in with the apparent association between intolerance of canopy competition (Fig. 1) and decrease in maximum height and perhaps seed weight in Europe (Table 2). Of the seven genera with more than 35% decrease in typically reported maximum height, all are among 'intolerants' except perhaps for *Castanea* whose tolerance is uncertain. Of the seventeen genera with lesser decreases in height or with negligible changes, only *Juniperus* and *Quercus* are among 'intolerants'. If the comparison is extended to whole families, the legumes show the greatest decreases in height ($\times 1/3$) and seed weight ($\times 1/15$) on average. The legumes are probably especially dependent on canopy openings as already discussed. Thus, the ecology and/or genetic system of these intolerant trees may have been conducive to further 'r-selection' following the environmental disruptions in Europe.

There are some large intrageneric increases in seed weight in Europe that are not associated with increases in height (Table 2). Possibly, another factor in the selection of seed weight has been the relatively dry southern European environment, through the advantages of weight in allowing penetration of dry soil surfaces or grassy litter. This idea

agrees with the fact that genera with at least 100% increase in mean reported seed weight are relatively drought-tolerant, i.e., *Castanea*, *Cornus*, *Corylus*, *Pyrus*, and perhaps *Carpinus* and *Fraxinus*, though the latter are borderline in both respects. The only genus with a decrease of this magnitude is *Alnus*, which is among the least drought-tolerant genera, being largely restricted to flooded sites.

(d) *Wider niches of individual species*

Even if all these proposed substitutions fill 'gaps' in the community organization of European forests, there would still appear to be a large reduction in the occupied number or subdivision of equivalent niches. Though absent genera may be largely matched, there are still large differences in species number within many genera. Also, the apparent graduation of trees like *Carpinus* into higher strata should either lead to wider stratal niches or to a 'gap' in the lower strata.

Thus, if the 'niche' view is accepted one might expect to see a general widening of ecological tolerances in response to the competitive release. For example, my general impression of *Fraxinus* is that *F. excelsior* occupies a relatively wide range of moisture conditions in Europe, perhaps approaching the combined range of the four species in cool temperate E North America. Does the ecology of the large prickly fruit of *Aesculus hippocastanum* in Europe combine the ecologies of the smaller prickly fruit of *A. glabra* and the large smooth fruit of *A. octandra* in E North America? One might even expect to see incipient speciation related to such expansion within trees more tolerant of Pleistocene climates and migrations. For example, in Europe a subspecies of *Juniperus communis* ranges over much of the lowland area, whereas the other is restricted to montane and other special sites similar to conditions in the boreal and arctic regions where the species has a Holarctic distribution. Is the lowland form a recent substitute for a species like *J. virginiana*, which ranges over most of E North America and only in the boreal transition is replaced by *J. communis*? Unfortunately there are insufficient data at hand, even on modern ecological tolerances, to begin a detailed comparative survey of all species in the two subcontinents.

A remark on differences in longevity

In view of the several genera with lower maxi-

mum height in Europe, and the rarity of old forest, it is surprising that reported typical longevities of genera are virtually all greater in Europe (e.g. U.S.-D.A., 1948; Möller, 1957; Altman & Dittmer, 1962; Fowells, 1965; Spector, 1965; Biological Flora of the British Isles in the Journal of Ecology since 1946). Generally, the difference is by $\times 1.5-3$ and in no case is longevity reported to be lower in Europe. However, most data on 'typical longevities' are vague. Jones (1945) did not mention any general trend in comparing temperate forests throughout the Northern Hemisphere, though he did note that *Abies* is relatively short-lived in E North America. Nevertheless, it seems unlikely that these large differences are purely due to different impressions of 'longevity'. Longer life with smaller maximum height in some genera would imply that growth rates are reduced, at least late in life. However, could there be different trends in maximum diameter and its growth?

Theoretically, there is a type of selection for differences in longevity that is not exactly the same as 'K- versus r-selection' and which might help explain these confusing trends. Giesel (1974) showed that if reproductive success is low during a period of falling population density, then reduced and delayed reproduction leading to greater longevity should be favored by natural selection. It is likely that such conditions have been more prevalent in Europe considering the greater fragmentation of temperate forest since the early Tertiary. Are reproductive efforts lower in Europe? This is another physiological question which is outside the scope of the current paper.

General discussion and conclusions

Some differences in the trees present on either side of the Atlantic support the idea that increasing dryness of climate since the early Tertiary has played an important part in fragmenting old oceanic temperate forest and causing separate evolution of forests in drier or more continental areas. E North American genera never found in Europe even as fossil or *vice versa*, and genera with exceptional proliferations of species in one of the subcontinents, tend to be relatively southern, tolerant of drought or disturbance, and typical of base-rich soil. These trends can be attributed to less historical connection of drier climatic areas with more base-rich soil. The

number of European trees involved in this trend is smaller, presumably due to the smaller area of temperate forest in the south as a source for origin of species or as a refuge during cold periods. Extinction of genera in Europe was greater among those typical of moist-acid oceanic forest as opposed to dry-basic forest. Most extinct genera are also somewhat southern where they occur today.

Within relatively cool temperate moist-acid oceanic forest, most extinction of genera in Europe occurred among those typical of habitat intermediate between moist-basic and dry-acid. Genera in this zone of the habitat gradients tend to have fewer species. In contrast, genera that may be restricted to southern Europe largely by slow dispersal tend to be typical of habitat either side of this intermediate zone. The causes of these trends are obscure, but it is likely they involve fairly profound relationships between community organization, evolution and/or environmental pattern, especially in glacial refuges.

The ecology of seed dispersal has received relatively little attention due to practical difficulties, and perhaps lack of appreciation of the important role that dispersal may play in overall ecology (cf. Harper, 1977). Historical biogeography offers some immediate insight to the long-term importance, though only through circumstantial evidence. Sufficiently detailed pollen maps to measure migration rates are now becoming available, and these will allow fuller insight. The results of this paper strongly suggest that small-seeded trees can migrate faster over long distances on average, since they are less restricted in range. However, this association only applies within winged, nutty and perhaps fleshy classes. There is remarkably little overall difference between these classes in their numbers of species and in their degree of apparent restriction by difficulties of migration (Table 1), although seed weights and seed numbers per crop differ greatly. These similarities might support the general concept that trees have divided the available agents of dispersal through competitive evolution. Stiles (1980) subdivided bird-dispersed woody plants in E North America in relation to season, size and nutrient content of fruits, features which he presumed to differentiate the types of dispersal. Again, there is little clear relationship between his types and the biogeographic differences studied in this paper; the sweetest fruits may have fared relatively well in Europe (see above), but Stiles did not emphasize sweetness in his

scheme as an independent dimension. The fact that there is only one genus in each subcontinent with the archetypal syndrome of characters indicating dispersal by larger mammals (*Pyrus* and *Diospyros*) provides further support for the notion of a balanced subdivision with respect to dispersal agents.

There is evidence that some trees with superior long-distance dispersal have responded greatly to extinctions of particular genera, or substitute for those that were never present in Europe. These trees appear to have experienced a change in size from understory to canopy, and in most cases an increase in seed size. Otherwise their ecological characteristics are similar to those of smaller congeners in E North America, which are often associated in their various habitats with the genera absent from Europe. The apparent substitutes in Europe are also similar in methods of regeneration to their proposed matches, except for having seeds that are probably better dispersed. In the case of *Corylus* as a proposed substitute for *Carya*, there is support for this idea from some fossil evidence that suggests a genetic change during the Pleistocene. There is a systematic increase in the abundance of *Corylus* during interglacials after the Cromerian, which is not explicable in terms of changing abiotic environment (West, 1970). Coincidentally, *Carya* became extinct at about that time (van der Hammen *et al.*, 1971). There are no other reports of such systematic changes, though there has been little analysis with these detailed questions in mind.

Excluding these genera with 100–1000% increases in maximum height in Europe, there is a general moderate decrease in height and seed weight, especially among genera more dependent on openings in canopy for regeneration. These trends may reflect some accentuation of 'r-selection', either due to diffuse competitive release without full substitution, or in response to pressure for migration over long distances. Though differences in height and seed weight are roughly associated, large somewhat independent increases or decreases in seed weight seem related to tolerance of dry versus wet conditions. Selection for large seeds may have been accentuated by the relatively dry southern European conditions.

The study of evolution in trees is clearly problematic due to the long generation time. It is very rare for populations to be studied in detail. However, the observations of Waldron *et al.* (1976) suggest an increase of about 10–20% in juvenile growth rate

after 70 yr in an escaped population of *Pyrus communis*. Consideration of changes that appear to have occurred since deforestation by man may provide more circumstantial evidence (Marie-Victorin, 1938; etc.). For example, *Betula pendula* appears to have evolved a faster life cycle including change from tree to shrubby habit on the north German plains by comparison with adjacent mountainous areas; these changes are attributed to human disturbance (Stern & Roche, 1974, p. 231). Thus, the changes in growth suggested during the Pleistocene are quite possible. Further synthesis of current ecological observations, historical and fossil data will surely make valuable advances in this field.

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