Leaf margins and temperature in the North American flora: Recalibrating the paleoclimatic thermometer

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Abstract

For almost a century, leaf margin analysis has been an important method of estimating Cenozoic paleotemperatures. However, the relation between the proportion of toothed versus entire leaves and temperature has so far been calibrated and characterized using relatively small numbers of opportunistically and irregularly collected floras.

Here we present the results of the first systematic spatially-distributed analysis of the relation between leaf margins and temperature for North America.

We used species range maps of native North American dicot trees to derive synthetic local floras for each 50 km grid cell in the USA and Canada, and compared the percentage of entire-margined species with the mean annual temperature in each cell. Leaf margin type for each species was assigned using illustrations from appropriate regional North America floras.

This analysis confirms that high-rainfall areas of the eastern USA and Canada show a strong inverse relationship between toothed margin percentage and mean annual temperature in the range 0–25 °C. The values we estimate are roughly similar to those obtained from floras in east Asia and previous analyses in North America, but the detailed curve is more complex, showing a distinct change in slope above a mean annual temperature of 20 °C. Wetter climate areas of the coastal western USA do not show any significant correlation between leaf margin percentage and temperature. This may relate to the confounding effect of the diverse topography of the West Coast, or it may be caused by the depleted dicotyledonous tree flora of this area.

Like previous studies, this paper demonstrates that there indeed is a strong relationship between leaf margin percentage and temperature on a regional scale in eastern North America. However the relationship does not have the same linear behavior as results obtained from previous analyses. We discuss the implications of the results obtained here for paleoclimatic reconstruction in the content of other leaf margin analyses based on North American sites.
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1. Introduction

It has long been known that trees of cooler climates in the northern hemisphere tend to have toothed leaves, while trees with entire-margined leaves are more common in subtropical and tropical climates.

The adaptive significance of this relationship between leaf form and temperature remains unknown. The

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presence of teeth has been related to herbivory (Brown and Lawton, 1991), to efficiency in the design of distributary networks (Givnish, 1978), and to the deciduous habit (Baker-Brosh and Peet, 1997). Another hypothesis is that the thinner shorter-lived leaves of cooler climates require teeth or lobes to allow them to flex in the wind without tearing (Baker-Brosh and Peet, 1997). Canny (1990), Baker-Brosh and Peet (1997) and Royer and Wilf (2006) have developed an explanation for the adaptive significance of teeth based on their ability to increase transpirative water flow by decreasing the apparent thickness of the aerodynamic boundary layer around leaves, thus supplying extra nutrients to toothed leaves early in the growing season when low evaporation rates due to low temperatures limit photosynthesis.

Despite the continuing uncertainty as to the adaptive significance of teeth, linear models relating P (the proportion of entire leaves in a flora) and MAT (mean annual temperature) have been used to estimate past temperatures from fossil leaf floras since the early 20th century (Bailey and Sinnot, 1915).

In the past 30 years, this relationship has been recalibrated many times using more data from floras in North America by Dolph (1976, 1979), Wolfe (1979, 1993), Wilf (1997), and Kowalski and Dilcher (2003). Leaf margin analysis has also been calibrated from modern floras elsewhere in the world by Herman and Spicer (1996), Stranks (1996), Kennedy (1998), Jacobs (1999, 2002), Gregory-Wodzicki (2000), Kowalski (2002), Kennedy et al. (2002), Greenwood et al. (2004), Traiser et al. (2005) and used to estimate paleotemperatures in the Tertiary (Wing and Greenwood, 1993; Wolfe, 1995), around the K/T boundary (Wolfe and Upchurch, 1986, 1987), and as far back in time as the Albian (Miller et al., 2006).

In addition to examining leaf margins, Wolfe (1993), Wing and Greenwood (1993), Wolfe and Spicer (1999), Huff et al. (2003), and Traiser et al. (2005) have also tried to improve temperature estimation by using multivariate leaf data, but the advantage of a multivariate approach has not been conclusively established, so we have restricted our current consideration to leaf margin analysis.

Most recently, Traiser (2004) and Traiser et al. (2005) have suggested the use of synthetic floras for grappling with the spatial variation in the relationship between leaf physiognomic and climatic variables in western Europe. In addition to considering a number of other variables, including leaf size, they identified a general latitudinal trend in leaf margin percentages, but the narrow temperature range in the moist climates of Northern Europe (southern Europe is dominated by more arid Mediterranean climates with a precipitation-limited winter growing season) limits the applicability of their results in North America, which has a far greater range of temperatures in the moist eastern forest zone, ranging from boreal in Canada to subtropical in southern Florida.

In this study we apply an approach based on that of Traiser (2004) to the North American flora in order to test the applicability of linear models for temperature estimation via leaf margin analysis and use Geographic Information Systems (GIS) to provide a recalibration of the relationship between temperature and leaf margin percentage based on spatial analysis at a continental scale.

2. Regional setting

In North America, temperate and subtropical moist forests occur mainly in the eastern part of the USA and in south-eastern Canada. Smaller areas occur in the mountains and lowlands of the Pacific western USA and Canada.

The tree floras of the eastern and western areas of North America have many genera in common, being dominated, for example, by species of *Quercus* and *Acer*. At a generic level, there are also similarities between the North American mid-latitude tree flora and the tree floras of Europe and eastern Asia. These similarities may have been even more marked in the Pliocene before Quaternary glaciation modified the North American tree flora (Wolfe, 1979).

3. Materials and methods

As a source of data on tree floras, we used the online version of the *Atlas of North American Trees* (Critchfield and Little, 1966; Little, 1971, 1976, 1977, 1978), which has been digitized as shapefiles suitable for GIS analysis by Thompson et al. (1999) and is available on the world wide web at (<http://pubs.usgs.gov/pp/p1650-a/>). All native Canadian and US trees and large shrubs (defined by Little as woody plants >3 m tall in any part of their range) are included in the *Atlas*. The maps are generally thought to be accurate to at least the county level.

The range maps were laid over a grid of squares 50 km on a side covering all of the USA and Canada and the presence or absence of each species in each grid cell recorded. This grid cell size was chosen to allow several hundred independent samples at fine climate resolution, and to minimize the effects of variable topography where a range of temperature zones might confound the analysis. A 50-km-wide sample also exceeds the maximum distance over which leaves might be expected to be transported before being deposited and preserved in the fossil record, and is roughly equivalent to the

implicit county-level accuracy of the original range maps. A larger grid-size would lose data present in the original range maps; smaller would imply greater precision than is really available from the originals.

The 30-year average (1971–2000) climate data (including precipitation and temperature) grid data at half degree latitude resolution were obtained from the U.S. Geological Survey (New et al., 1999). To retrieve climate data for each square used in calculating mean leaf margin value, we calculated distance between centroid of each square and each climate grid cell. Then climate values of each square for leaf margin values were retrieved from the closest climate grid cell.

Each of the 512 broadleaved dicots in the *Atlas* was included. Monocots, conifers, and leafless species (e.g. cacti) were excluded. Leaf margins were classified using Sargent (1905), Britton and Brown (1913), Little et al. (1964, 1974), Gleason and Cronquist (1991), Flora of North America Editorial Committee, eds. (1993-), and Hickman, ed. (1993), as well as web-based resources. Web searches by Latin name usually revealed many high quality images of leaves, plus floral descriptions. Several photographs of each species were inspected before assigning a leaf margin state.

Species were classified as toothed (rather than lobed) if indentations in their leaves were present and extended less than 0.25 of the distance from the outermost margin towards the mid-vein of the leaf. Following the procedure of Wolfe (1993), species with only entire leaves were assigned a value of 1, those with only toothed leaves were assigned a 0. Species in which presence or absence of teeth is a variable trait were assigned a value of 0.5. A list of the categories assigned to each species and whether its leaves are deciduous or evergreen can be found in the Appendix to this paper.

The 'score' for each grid square was obtained by averaging the values obtained for all the species whose ranges overlapped into that grid square.

4. Results

Summary maps and scatterplots (Figs. 1, 2) show that the percentage of entire margins reaches its highest point in the south-eastern USA, and is generally high in the eastern USA, compared to other parts of the continent. There is clear general latitudinal trend, complicated by differences in high relief regions of the west. Grid cells with fewer than 20 species falling within that cell are not colored.

Fig. 1 shows the points coded by mean annual temperature. Because of the very good correlation between latitude and mean annual temperature, this is roughly equivalent to latitudinal coloring, but note, for instance, the cold anomaly where the Appalachian mountain chain in eastern North America is shown by green and light-blue 'tongues' pointing southwest, parallel to the east coast.

Fig. 2 shows the relationship between temperature and leaf margin percentages colored by the proportion of entire leaves. With this coloring scheme, the effect of continentality is also visible: the floras with the smallest proportions of entire leaves (colored orange) are not those with the very coldest mean annual temperatures, but in the continental interior (southern Quebec and Ontario). This suggests that at a given mean annual temperature, more equable continental areas (dryer, with greater mean annual range of temperature) will have fewer entire leaves than coastal regions.

Note that in both of these figures, there is a clear relationship between leaf margin percentage and mean annual temperature for the forest region of the eastern USA and Canada. If the eastern coast is examined independently, the relationship between mean annual temperature and leaf margin percentage becomes even 'stronger', although it remains clearly non-linear (Fig. 3).

Margin percentage changes slowly with respect to temperature between 0 and 20 °C with a sudden curve to a higher portion of entire margins at around 10°, showing reduced continentality. The rate of change with temperature then accelerates at around 20 °C, and keeps a more-or-less linear correlation up to about 25 °C, at the geographical limit of southern Florida. Our plot shows more scatter than is evident in previous work on this subject in China (Wolfe, 1979) and North America (Wilf, 1997), perhaps because more samples, across a diverse range of soil types, elevations, and microclimates were included.

In Fig. 4, we show a comparison of the east-coast subset of our data with six previous studies. In broad terms our results substantiate previous work, but the strongly non-linear relationship evident in our data has not been observed before.

Other previously published studies for parts of North America and eastern Asia have suggested a linear association between temperature and leaf margin percentage (Fig. 4). The relationship that we have found intersects with the linear relationships suggested by other studies at lower and higher temperature values, but curves away from that line at intermediate values. Note that the data points used by Wilf (1997) happen to fall only at extreme values, and the line drawn between them is therefore an interpolation. Our analysis suggests that if intermediate temperature zones were included, the 'true' relationship found by these earlier studies

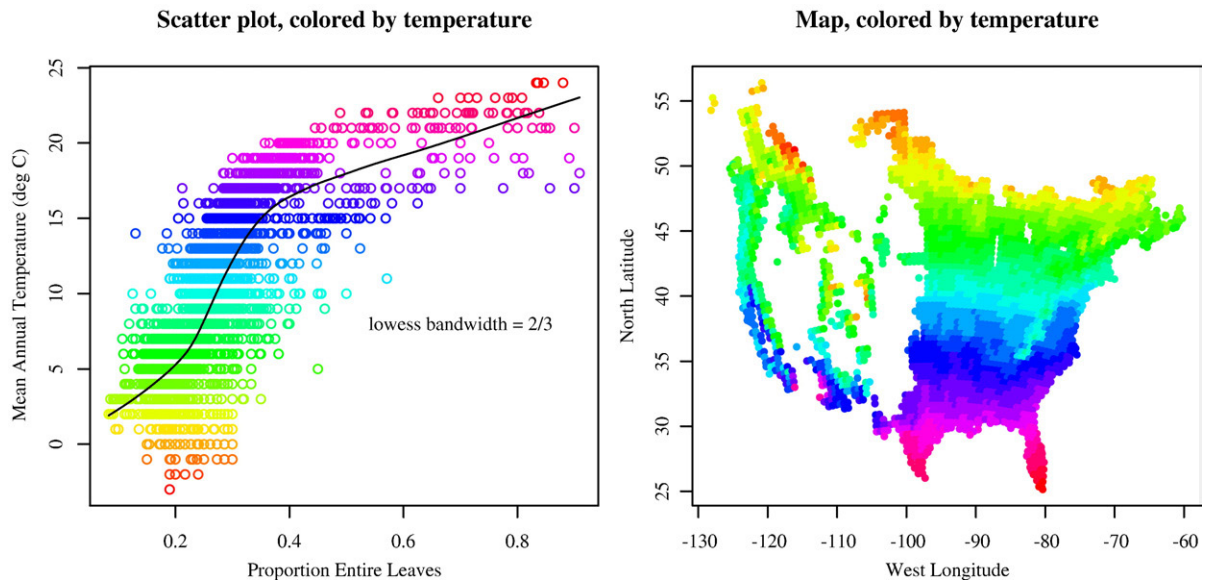## Scatter plot, colored by temperature   ## Map, colored by temperature

Fig. 1. Summary map and scatterplot showing proportion of entire-margined species in the North American native tree flora color coded by mean annual temperature. Black line is lowess non-linear regression line. The color is a continuous spectrum used so that points on the scatterplots can be identified with points on the maps.

might have been arched, as we have found. In retrospect, a close examination of Wolfe and Spicer's complete (173 flora) data set (only partially published in Wolfe, 1993, but available on line as of May, 2007 at <http://www.open.ac.uk/earth-research/spicer/CLAMP/Clamp-set1.html>), including high-elevation floras, does suggest the possible presence of this non-linearity, which we can now document in detail (Fig. 4).

In western North America, areas along the coast with a moist climate of more than 1000 mm mean annual precipitation, between northern California and Alaska, show only a weak correlation with temperature over a range of some 25 °C (Fig. 5). The same is true if the coastal region in general is included, irrespective of rainfall (Fig. 6). (Note that although the slope of the least squares regression lines are statistically different from 0

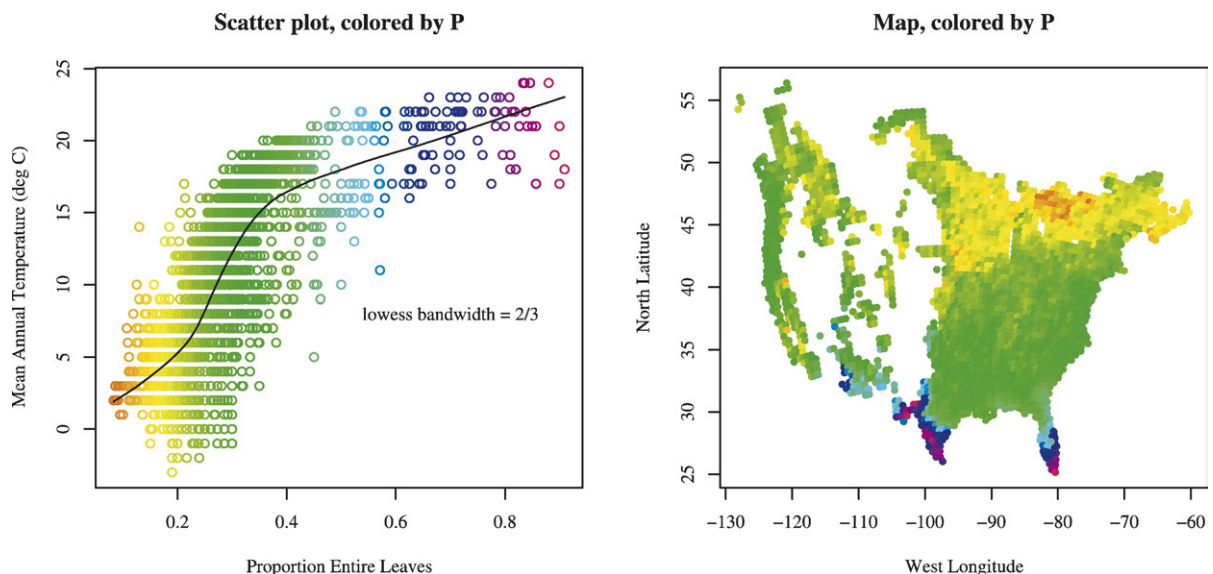## Scatter plot, colored by P   ## Map, colored by P

Fig. 2. Summary map and scatterplot showing proportion of entire-margined species in the North American native tree flora color coded by the proportion of entire leaves. Black line is lowess non-linear regression line. The color is a continuous spectrum used so that points on the scatterplots can be identified with points on the maps.
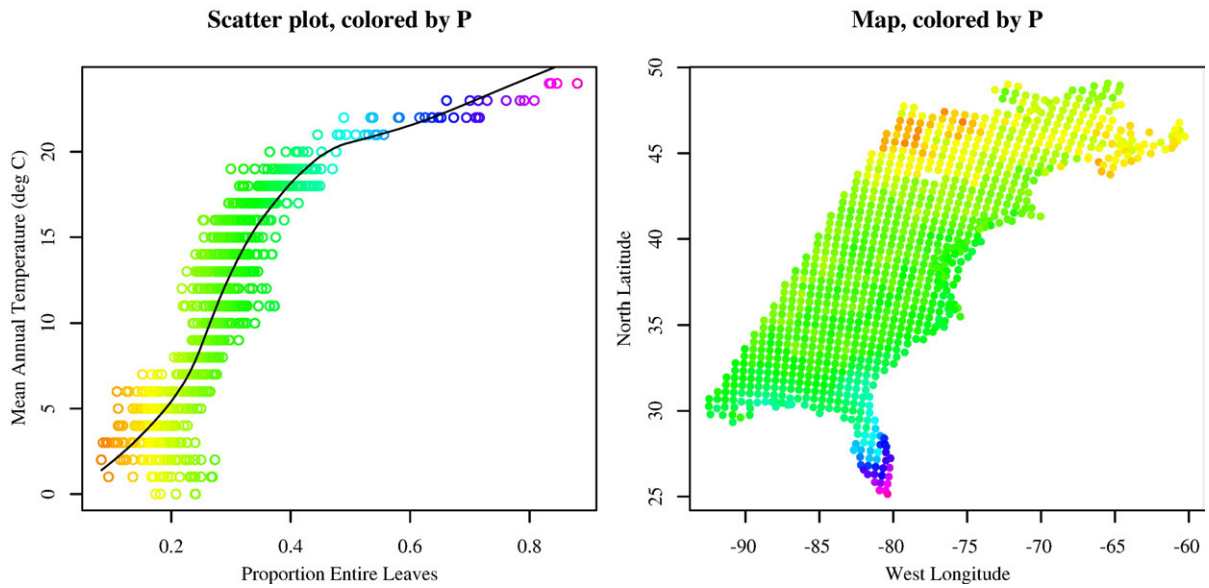
Fig. 3. Proportion of entire leaf margins against temperature in the eastern North American forest region demarcated above. Points color coded as in Fig. 2 by the proportion of entire leaves. Black line is lowess non-linear regression line.
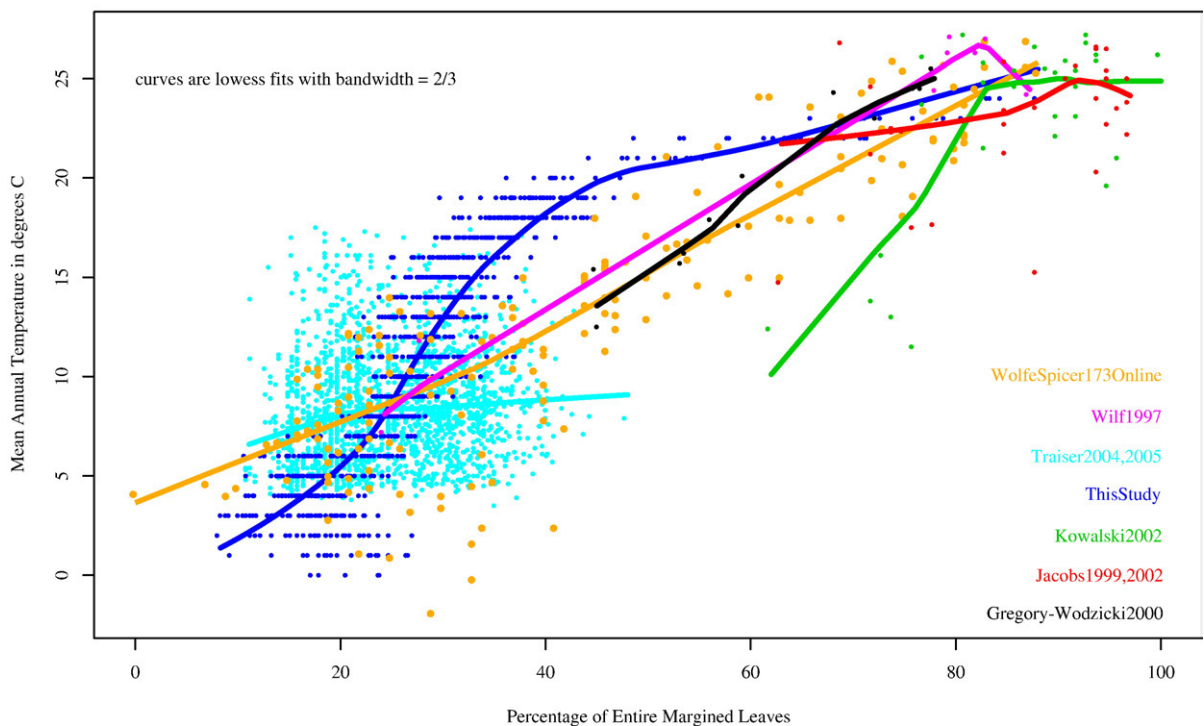

Fig. 4. The results of the present study for eastern North America compared to other previously published studies. Colors here indicate the study from which each data set came as shown in the key in the lower righthand corner of the figure.
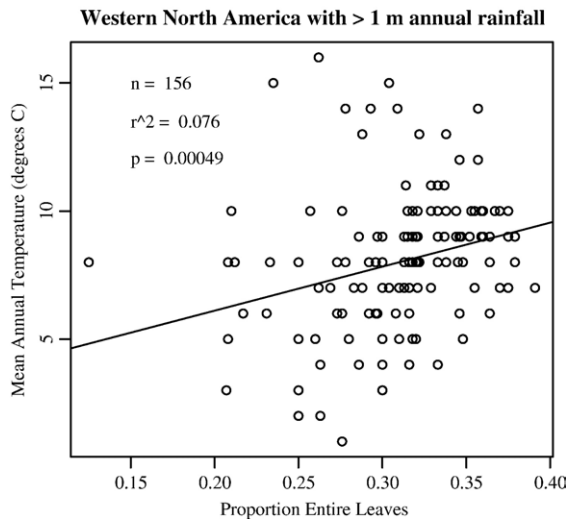
Fig. 5. Scatterplot of margin proportion for areas in western USA with >1000 mm mean annual precipitation. Fitted line is least squares regression.

in both cases, the spatial autocorrelation of the gridded data means that the *p*-value of the regression cannot be trusted.) The poor correlation apparent from these plots (Figs. 5, 6) is surprising because important early studies of the correlation between leaf margins and temperature by Wolfe (1993) were heavily based on data from the western USA.

The entire-margin trait is correlated with the trait of evergreen-ness-entire leaved species also tend to be evergreen. Examination of the relationship between percentage of broadleaf evergreen leaves and temperature, geography, and percentage entire leaves (Fig. 7) reveals expected patterns: there are more broadleaf evergreen species in low latitudes, high temperatures and where most of the leaves are entire. Percentage of evergreen species does not, however, do as good a job at predicting temperature as percentage entire-margin species. Since it is usually impossible to determine whether a fossil leaf was deciduous or not, the observation that deciduousness is not a better temperature predictor than teeth is irrelevant. It is more interesting to consider using percentage entire margins to predict deciduousness in the fossil record. This seems a reasonable procedure, subject to the relatively broad scatter in the plot of percent broadleaf deciduous and percent entire in the lower left corner of Fig. 7.

Comparing the maps in Figs. 2 and 7, we can also see that while percentage entire produces relatively horizontal colored bands, percentage broadleaf evergreen shows crescent-shaped bands running north

along both coasts of North America. This implies that coastal regions are identifiable by a particularly high ratio of evergreen species to entire species, in other words, near the coasts, there are more evergreen species than would be expected based on the number of entire species. Since deciduousness may be related to cold winter temperatures and physiological drought, this effect is not hard to explain by reference to the milder (more equable) and wetter climates near large bodies of water.

5. Discussion

The results obtained in this study in some respects confirm previous findings on leaf margin analysis. In other respects, however, they call for a reappraisal of earlier published conclusions on the nature of the temperature relationship.

On one hand, the positive relationship between entire leaf margin percentage and temperature is confirmed as being robust in the extensive forest area of eastern North America, between around 0 and 25 °C. Given the scatter of the data points, it would appear possible to designate temperature to within about ±3 or 4 °C between about 0 and 20 °C (given the outer margins of the scatter of points). This is slightly less accurate than previous studies had suggested (accuracy to within ±2.5 °C), but still appears likely to give useful conclusions about paleotemperatures, especially in combination with other sources of evidence. The scatter decreases markedly at temperatures above 20 °C, at least in eastern North
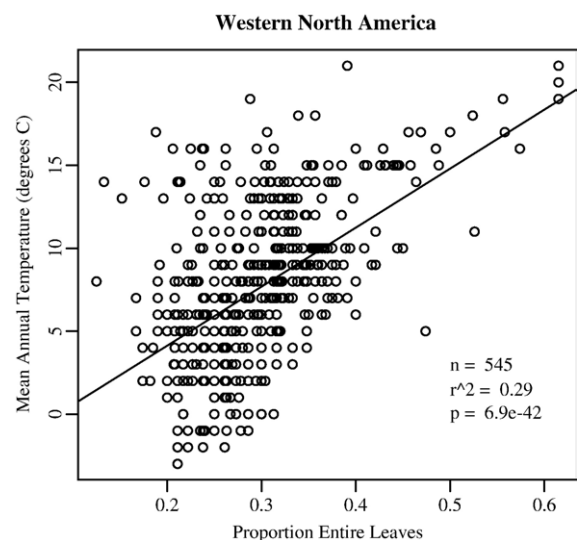

Fig. 6. Scatterplot for areas in western USA regardless of annual rainfall. Fitted line is least squares regression.
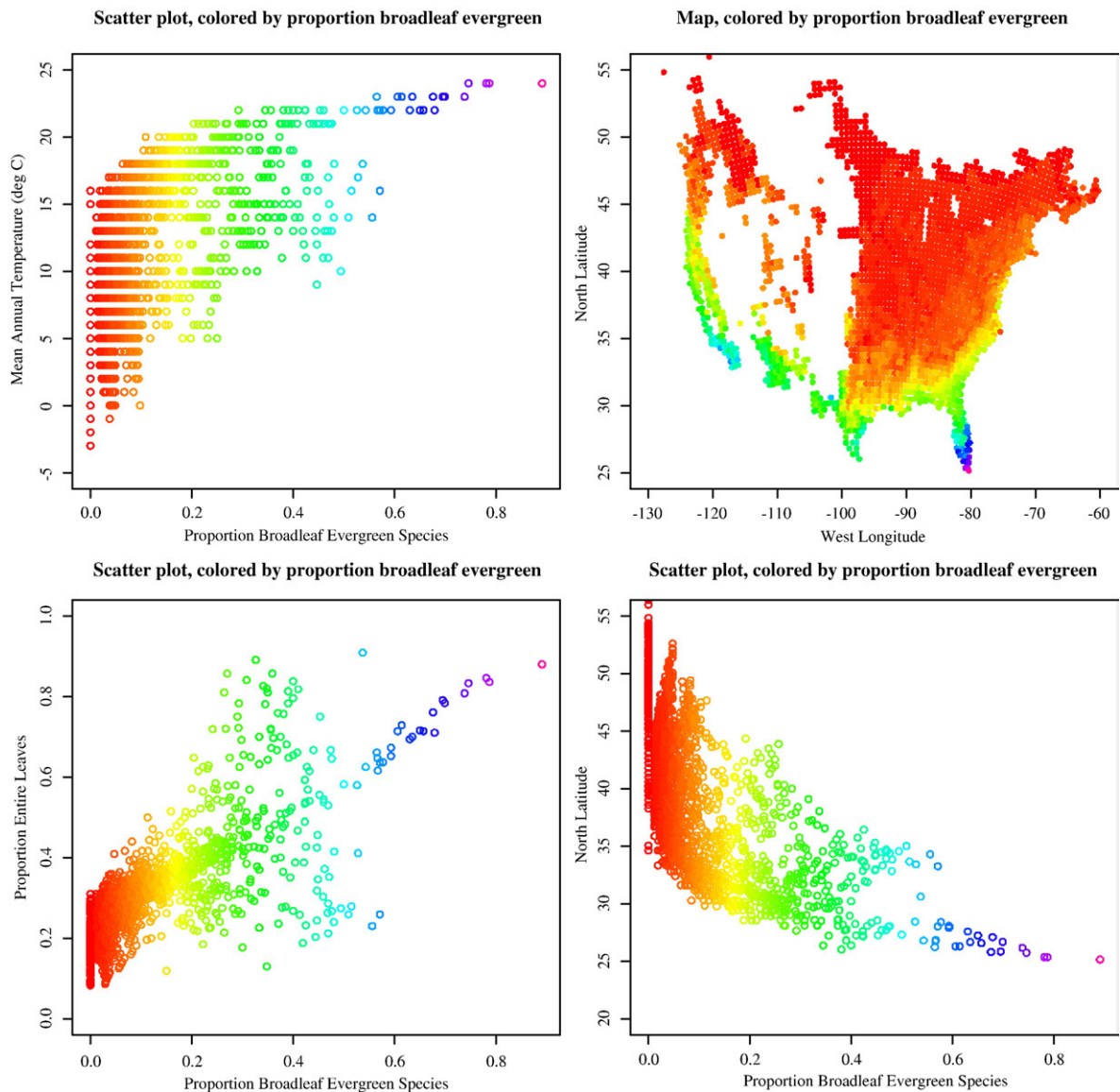
Fig. 7. Map of percentage of broadleaf evergreen species (where there are more than 20 species to a grid cell) and scatterplots showing the bivariate relationships among percentage broadleaf evergreen, percentage entire, mean annual temperature, and latitude.

America. In land areas experiencing MAT of 0–20°, precision seems to be within ±1 °C, although this apparent precision may partly be due to less heterogenous range of environments (in terms of soils) in the warmer parts of the south-eastern USA. Many of these data points are from the Florida Peninsula which is mostly limestone. If the soil environments had been more heterogenous, it is possible that scatter would have been greater.

This spatial analysis reveals limits in accuracy of temperature estimates due to scatter and non-linearity, which are not evident in smaller data sets. The 'bulge'

away from the straight line at intermediate temperatures may call for reassessment of some earlier paleotemperature estimates from the fossil record that were based on leaf margin analysis. It is possible that the flattening of the curve that also brings about the 'bulge' relates in some way to the swampy soil conditions common in Florida and along the Gulf Coast. Kowalski and Dilcher (2003) have noted that swampy environments tend to have different proportions of entire-margined species than non-swampy environments. However, although swamps are widespread across southern Florida, this is by no

means the case throughout northern Florida, and in Texas where the mean annual temperature is greater than 20 °C, above the inflection point of the curve. Hence, it seems unlikely that swampy soils alone cause this trend.

For the western coast of North America, the lack of any strong correlation with temperature is quite unexpected. Although this area contains very variable topography, one might have expected that the lowland flora would have had at least some detectable effect in producing a latitudinal trend. Some of the earlier classic studies in leaf margin analysis by Wolfe (1979, 1993) were also based in the western USA, and showed a strong correlation with temperature.

It is possible that the nature of the sampling in the western USA by Wolfe (1993), on local deciduous stands of particular physiognomy, identified a linear relationship which is not evident when sampling is more thorough and regular. Wolfe pointed out that the lowland floodplain settings supporting forests in modern arid areas are just the sort of facies that preserve plant fossils. On the other hand, the vagaries of taphonomy and preservation of fossil leaf floras surely require that error analysis of the relationship between temperature and leaf margins use a wide range of forest types. Thus, our result here may provide a more realistic interpretation of the variation found in the fossil record. The lack of a broad scale effect in the western USA may also be partly due to depletion of the western USA moist climate flora, which during glacial phases was caught between mountains to the east, and aridity (Adams and Faure, 1997). The resulting extinctions of species of both moist climates and warmer climates may have left behind fewer forms with entire margins. In this sense, interpretation of Tertiary fossil leaf floras from the western USA might be more accurate if based on training data from the eastern USA, which is not so depleted.

Although the GIS approach used here is very different from obtaining species lists from individual sites as previous authors did and therefore diversities will be inflated by counting range-through taxa, we do not see any reason why this should bias the proportion of leaves with entire margins. If anything, the broad scale sampling used here should be expected to yield a more accurate representation of 'true' relationship between leaf form and temperature than sampling local sites, which are subject to the vagaries of microclimatic variation. We suggest that the smaller sample numbers and rather more selective or *ad hoc* sampling used in previous studies has disguised the 'true' non-linear relationship apparent in eastern North America. It is unclear whether the correlation in eastern Asia would be the same or different if more data points from intermediate temperatures were added in.

If the non-linear functional relationship obtained here reflects the 'true' relationship between leaf margin percentage and temperature, what are the implications? Many of the estimations of temperature against margin percentage in fossil leaf floras may have to be recalibrated, with new conclusions regarding paleoclimate. It appears from the scatterplot of eastern North American data (Fig. 3) that for mean annual temperatures between about 12 and 19 °C, the earlier calibrations tended to underestimate temperatures by between 3 and 5 °C. However, for warmer climates above about 20 C, the earlier linear models seem to have overestimated temperature by 1 or 2 °C.

The results of the present study confirm that leaf margin analysis can be useful in paleotemperature analysis in some areas, such as the eastern USA. However, the relationship may be unreliable in regions that are floristically depleted or have complex topography, such as the western USA. In regions where the relationship is strong, it should be used with caution, because of non-linearity in the relationship and the evident scatter within the data. Our findings emphasize that interpretation of paleotemperatures from fossil leaf floras is best done in combination with other indicators (such as general floristics and a combination of other leaf characteristics).

Acknowledgments

Appendix A

Presence of teeth and deciduous habit by species. Toothed margins scored as: 1 = entire, 0 = toothed, 0.5 = sometimes toothed; deciduous habit scored as: D = deciduous, E = entire, B = both, ? = unknown or indeterminate.

List of species included and their margin scores (1 = entire, 0 = toothed, 0.5 = sometimes toothed).

Species	Type	Species	Type
Acacia berlandieri	1	Licaria triandra	1
Acacia choriophylla	1	Liquidambar styraciflua	0
Acacia farnesiana	1	Liriodendron tulipifera	1
Acacia macracantha	1	Lithocarpus densiflorus	0

Appendix A (*continued*)

Species	Type	Species	Type
Acacia rigidula	1	*Lyonia ferruginea*	1
Acacia roemeriana	1	*Lyonothamnus floribundus*	0
Acacia tortuosa	1	*Lysiloma latisiliquum*	1
Acacia wrightii	1	*Lysiloma microphylla*	1
Acacia greggii	1	*Maclura pomifera*	1
Acer barbatum	0	*Magnolia ashei*	1
Acer circinatum	0	*Magnolia grandiflora*	1
Acer glabrum	0	*Magnolia acuminata*	1
Acer grandidentatum	0	*Magnolia fraseri*	1
Acer leucoderme	0	*Magnolia macrophylla*	1
Acer macrophyllum	0	*Magnolia pyramidata*	1
Acer negundo	0	*Magnolia tripetala*	1
Acer nigrum	0	*Magnolia virginiana*	1
Acer pensylvanicum	0	*Malus angustifolia*	0
Acer rubrum	0	*Malus coronaria*	0
Acer saccharinum	0	*Malus diversifolia*	0
Acer sacchrum	0	*Malus ioensis*	0
Acer spicatum	0	*Manilkara bahamensis*	1
Aesculus californica	0	*Mastichodendron foetidissimum*	1
Aesculus glabra	0	*Maytenus phyllanthoides*	1
Aesculus octandra	0	*Metopium toxiferum*	1
Aesculus parvia	0	*Morus microphylla*	0
Aesculus parviflora	0	*Morus rubra*	0
Aesculus sylvatica	0	*Myrcianthes fragrans*	1
Alnus maritima	0	*Myrica pensylvanica*	0.5
Alnus rugosa	0	*Myrica californica*	0
Alnus oblongifolia	0	*Myrica cerifera*	0
Alnus rhombifolia	0	*Myrica heterophylla*	0
Alnus rubra	0	*Myrica inodora*	1
Alnus serrulata	0	*Nectandra coriacea*	1
Alnus sinuata	0	*Nemopanthus collinus*	0
Alnus tenuifolia	0	*Nyssa aquatica*	0.5
Alvaradoa amorphoides	1	*Nyssa ogeche*	1
Amelanchier alnifolia	0	*Nyssa sylvatica*	0.5
Amelanchier arborea	0	*Olneya tesota*	1
Amelanchier interior	0	*Osmanthus americanus*	1
Amelanchier sanguinea	0	*Ostrya chisosensis*	0
Amelanchier utahensis	0	*Ostrya knowltonii*	0
Amphitecna latifolia	1	*Ostrya virginiana*	0
myris balsamifera	1	*Oxydendrum arboreum*	0
Amyris elemifera	1	*Parkinsonia aculeata*	1
Annona glabra	1	*Persea borbonia*	1
Aralia spinosa	0	*Photinia arbutifolia*	1
Arbutus texana	1	*Picramnia pentandra*	1
Arbutus arizonica	1	*Pinckneya pubens*	1
Arbutus menziesii	1	*Piscidia piscipula*	1
Arctostaphylos pringlei	1	*Pisonia rotundata*	1
Ardisia escallonioides	1	*Pistacia texana*	1
Artemisia tridentate	0	*Pithecellobium unguis-cati*	1
Asimina parviflora	1	*Planera aquatica*	0
Asimina triloba	1	*Platanus racemosa*	0
Avicennia germinans	1	*Platanus wrightii*	0
Baccharis halimifolia	0.5	*Platanus occidentalis*	0
Betula nana	0	*Platanus wrightii*	0
Betula populifolia	0	*Populus arizonica*	0
Betula uber	0	*Populus angustifolia*	0
Betula alleghaniensis	0	*Populus balsamifera*	0
Betula lenta	0	*Populus deltoides*	0

Species	Type	Species	Type
Betula nigra	0	*Populus fremontii*	0
Betula occidentalis	0	*Populus grandidentata*	0
Betula papyrifera	0	*Populus heterophylla*	0
Bourreria ovata	1	*Populus tremuloides*	0
Bourreria radula	1	*Populus trichocarpa*	0
Bumelia celastrina	1	*Prosopis juliflora*	1
Bumelia lanuginose	1	*Prosopis pubescenes*	1
Bumelia lycioides	1	*Prunus alleghaniensis*	0
Bumelia tenax	1	*Prunus americana*	0
Bursera fagaroides	0.5	*Prunus angustifolia*	0
Bursera microphylla	1	*Prunus caroliniana*	0
Bursera simaruba	1	*Prunus emaginata*	0
Byrsonima lucida	1	*Prunus fremontii*	0
Caesalpinia mexicana	1	*Prunus hortulana*	0
Calyptranthes pallens	1	*Prunus ilicifolia*	0
Calyptranthes zuzygium	1	*Prunus lyonii*	0
Canella winterana	0	*Prunus mexicana*	0
Canotia holacantha	0.5	*Prunus munsoniana*	0
Capparis cynophallophora	1	*Prunus myrtifolia*	0
Capparis flexuosa	1	*Prunus nigra*	0
Carpinus caroliniana	0	*Prunus pensylvanica*	0
Carya floridana	0	*Punus serotina*	0
Carya myristicaeformis	0	*Prunus subcordata*	0
Carya texana	0	*Prunus umbellata*	0
Carya aquatica	1	*Prunus viriniana*	0
Carya cordiformis	0	*Psidium longipes*	1
Carya glabra	0	*Ptelea crenulata*	0.5
Carya illinoensis	0	*Ptelea_trifoliata*	0
Carya laciniosa	0	*Quercus agrifolia*	0
Carya ovata	0	*Quercus ajoensis*	1
Carya pallida	0	*Quercus alba*	1
Carya tomentosa	0	*Quercus arizonica*	1
Castanea alnifolia	0	*Quercus arkansana*	0
Castanea dentata	0	*Quercus bicolor*	0
Castanea ozarkensis	0	*Quercus chapmanii*	0
Castanea pumila	0	*Quercus chrysolepis*	0.5
Castanopsis chrysophylla	0	*Quercus coccinea*	0
Catalpa speciosa	0.5	*Quercus douglasii*	0
Catalpa bignonioides	0	*Quercus dunnii*	0
Ceanothus arboreus	0	*Quercus durandii*	0
Ceanothus spinosus	0	*Quercus ellipsoidalis*	0
Ceanothus thyrsiflorus	0	*Quercus emoryi*	1
Celtis lindheimeri	0.5	*Quercus engelmannii*	0
Celtis laevigata	0	*Quercus falcata*	0
Celtis occidentalis	0	*Quercus gambelii*	1
Celtis reticulata	0	*Quercus garryana*	1
Celtis tenuifolia	0	*Quercus georgiana*	0.5
Cephalanthus occidentalis	1	*Quercus glaucoides*	1
Cercidium floridum	1	*Quercus graciliformis*	0
Cercidium microphyllum	1	*Quercus gravesii*	1
Cercis cannadensis	1	*Quercus grisea*	0
Cercis occidentalis	1	*Quercus havardii*	1
Cercocarpus betuloides	0	*Quercus hypoleucoides*	1
Cercocarpus breviflorus	1	*Quercus ilicifolia*	1
Cercocarpus ledifolius	1	*Quercus imbricaria*	1
Cercocarpus traskiae	0	*Quercus incana*	1
Chilopsis linearis	1	*Quercus kelloggii*	0

Appendix A (*continued*)

Species	Type	Species	Type
Chionanthus virginicus	1	*Quercus laevis*	0
Chrysobalanus icaco	1	*Quercus laurifolia*	1
Chrysophyllum oliviforme	1	*Quercus lobata*	1
Citharexylum berlandieri	1	*Quercus lyrata*	0
Cladrastis kentukea	1	*Quercus macdonaldii*	1
Clethra acuminata	0	*Quercus macrocarpa*	1
Cliftonia monophylla	1	*Quercus marilandica*	1
Clusia rosea	1	*Quercus michauxii*	0
Coccoloba diversifolia	1	*Quercus mohriana*	1
Coccoloba uvifera	1	*Quercus muehlenbergii*	0
Colubrina arborescens	1	*Quercus myrtifolia*	1
Colubrina cubensis	1	*Quercus nigra*	1
Colubrina elliptica	1	*Quercus nuttallii*	1
Condalia globosa	1	*Quercus oblongifolia*	1
Condalia hookeri	1	*Quercus oglethorpensis*	1
Cordia boissieri	0.5	*Quercus palustris*	1
Cordia sebestena	0.5	*Quercus phellos*	1
Cornus racemosa	1	*Quercus prinus*	0
Cornus rugosa	1	*Quercus pungens*	1
Cornus sessilis	1	*Quercus rubra*	0
Cornus alternifolia	1	*Quercus rugosa*	0
Cornus drummondii	1	*Quercus shumardii*	0
Cornus florida	1	*Quercus stellata*	1
Cornus glabrata	1	*Quercus tomentella*	0
Cornus nuttallii	1	*Quercus toumeyi*	1
Cornus occidentalis	1	*Quercus turbinella*	0
Cornus stolonifera	1	*Quercus velutina*	0
Cornus stricta	1	*Quercus virginiana*	1
Corylus cornuta	0	*Quercus wislizeni*	0
Cotinus obovatus	1	*Rapanea punctata*	1
Cowania mexicana	1	*Reynosia septentrionalis*	1
Crataegus chrysocarpa	0	*Rhamnus crocea*	0
Crataegus saligna	0	*Rhamnus betulaefolia*	0
Crataegus succulenta	0	*Rhamnus californica*	0
Crataegus tracyi	0	*Rhamnus caroliniana*	0
Crataegus columbiana	0	*Rhamnus purshiana*	1
Crataegus douglasii	0	*Rhizophora mangle*	1
Crossopetalum rhacoma	1	*Rhododendron catawbiense*	1
Cupania glabra	0	*Rhododendron macrophyllum*	1
Cyrilla racemiflora	1	*Rhododendron maximum*	1
Dalea spinosa	1	*Rhus integrifolia*	0.5
Diospyros texana	1	*Rhus kearneyi*	1
Diospyros virginiana	1	*Rhus lanceolata*	1
Dipholis salicifolia	1	*Rhus laurina*	1
Dodonaea viscosa	1	*Rhus microphylla*	1
Drypetes diversifolia	1	*Rhus ovata*	0.5
Drypetes lateriflora	1	*Rhus_copallina*	1
Ehretia anacua	0.5	*Rhus glabra*	0
Elliottia racemosa	1	*Rhus typhina*	0
Erythrina herbacea	1	*Robinia kelseyi*	1
Erythrina flabelliformis	1	*Robinia viscosa*	1
Esenbeckia berlandieri	1	*Robinia neomexicana*	1
Eugenia axillaris	1	*Robinia pseudoacacia*	1
Eugenia confusa	1	*Salix alaxensis*	1
Eugenia rhombea	1	*Salix bonplandiana*	0
Euonymus atropurpureus	0	*Salix fluviatilis*	0
Euonymus occidentalis	1	*Salix laevigata*	0
Exostema caribaeum	1	*Salix lasiandra*	0
Exothea paniculata	1	*Salix pellita*	1

Appendix A (*continued*)

Species	Type	Species	Type
Eysenhardtia polystachya	1	*Salix petiolaris*	0
Eysenhardtia texana	1	*Salix pyrifolia*	1
Fagus grandifolia	0	*Salix taxifolia*	0
Ficus aurea	1	*Salix amygdaloides*	0
Ficus citrifolia	1	*Salix bebbiana*	1
Forestiera acuminata	1	*Salix caroliniana*	0
Forestiera angustifolia	1	*Salix exigua*	1
Forestiera phillyreoides	1	*Salix floridana*	0
Forestiera segregata	1	*Salix geyeriana*	0
Franklinia alatamaha	0	*Salix hindsiana*	0
Fraxinus americana	0	*Salix hookeriana*	0
Fraxinus anomala	0	*Salix lasiolepis*	1
Fraxinus berlandieriana	0	*Salix lucida*	0
Fraxinus caroliana	0	*Salix mackenzieana*	0
Fraxinus cuspidata	0	*Salix nigra*	0
Fraxinus dipetala	0	*Salix scouleriana*	1
Fraxinus gooddingii	0	*Salix sericea*	1
Fraxinus greggii	0	*Salix sessilifolia*	1
Fraxinus latifolia	0	*Salix sitchensis*	1
Fraxinus nigra	0	*Sambucus velutina*	0
Fraxinus papillosa	0	*Sambucus callicarpa*	0
Fraxinus pennsylvanica	0	*Sambucus canadensis*	0
Fraxinus profunda	0	*Sambucus glauca*	0
Fraxinus quadrangulata	0	*Sambucus melanocarpa*	0
Fraxinus texensis	0	*Sapindus drummondii*	1
Fraxinus velutina	0	*Sapindus saponaria*	1
Fremontodendron californicum	0	*Sassafras albidum*	1
		Schaefferia frutescens	1
Fremontodendron mexicanum	0	*Schoepfia chrysophylloides*	1
		Shepherdia argentea	1
Farrya elliptica	0	*Simarouba glauca*	1
Genipa clusiifolia	1	*Sophora affinis*	1
Gleditsia aquatica	1	*Sophora secundiflora*	1
Gleditsia triacanthos	0	*Sorbus americana*	0
Gordonia lasianthus	0	*Sorbus decora*	0
Guaiacum angustifolium	1	*Sorbus scopulina*	0
Guaiacum sanctum	1	*Sorbus sitchensis*	0
Guapira discolor	1	*Staphylea bolanderi*	0
Guettarda elliptica	1	*Staphylea trifolia*	0
Guettarda scabra	1	*Stewartia malacodendron*	0
Gyminda latifolia	1	*Stewartia ovata*	1
Gymnanthes lucida	0.5	*Styrax americana*	0
Gymnocladus dioicus	1	*Styrax grandifolia*	1
Halesia carolina	0	*Suriana maritima*	1
Halesia diptera	0	*Swietenia mahagoni*	1
Halesia parviflora	0	*Symplocos tinctoria*	1
Hamamelis virginiana	0	*Taxus floridana*	1
Hamelia patens	1	*Tetrazygia bicolor*	1
Helietta parvifolia	0.5	*Tilia caroliniana*	0
Hippomane mancinella	0	*Tilia heterophylla*	0
Hypelate trifoliata	1	*Tilia americana*	0
Ilex krugiana	1	*Toxicodendron vernix*	1
Ilex laevigata	1	*Trema lamarckiana*	0
Ilex ambigua	0	*Trema micrantha*	0
Ilex amelanchier	1	*Ulmus crassifolia*	0
Ilex cassine	0	*Ulmus thomasii*	0
Ilex coriacea	0	*Ulmus alata*	0
Ilex decididua	0	*Ulmus amerericana*	0
Ilex longipes	0	*Ulmus rubra*	0

Appendix A (*continued*)

Species	Type	Species	Type
Ilex Montana	0	*Ulmus serotina*	0
Ilex myrtifolia	1	*Umbellularia californica*	1
Ilex opaca	0	*Ungnadia speciosa*	0
Ilex verticillata	0	*Vaccinium arboreum*	1
Ilex vomitoria	0	*Vauquelinia californica*	0
Illicium parviflorum	1	*Vauquelinia pauciflora*	0
Illicium floridanum	1	*Viburnum lentago*	0
Jacquinia keyensis	1	*Viburnum trilobum*	0
Juglans californica	0	*Viburnum nudum*	1
Juglans hindsii	0	*Viburnum obovatum*	1
Juglans microcarpa	0.5	*Viburnum prunifolium*	0
Juglans cinerea	0	*Viburnum rufidulum*	0
Juglans major	0	*Ximenia americana*	1
Juglans nigra	0	*Zanthoxylum americanum*	1
Kalmia latifolia	1	*Zanthoxylum clava-herculis*	0
Koeberlinia spinosa	1		
Krugiodendron ferreum	1	*Zanthoxylum coriaceum*	1
Laguncularia racemosa	1	*Zanthoxylum fagara*	0
Larrea divaricata	1	*Zanthoxylum flavum*	1
Leitneria_floridana	1	*Zanthoxylum hirsutum*	0
Leucaena pulverulenta	1		
Leucaena retusa	1		

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