Paleotemperature Estimation Using Leaf-Margin Analysis: Is Australia Different?

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Australia has numerous fossil floras suitable for paleoclimatic analysis, with potential to improve understanding of Southern Hemisphere climatic evolution. Leaf-margin analysis (LMA) is a widely used method that applies present-day correlations between the proportion of woody dicot species with untoothed leaves and mean annual temperature to estimate paleotemperatures from fossil megafloras. Australia's unique history and vegetation imply that its leaf-margin correlation might differ from other regions; these possible differences are investigated here to improve paleoclimatic interpretations.

Australian rainforest vegetation shows nearly the same regression slope as recorded in East Asia and the Americas, indicating a globally convergent evolutionary response of leaf form to temperature. However, Australian sites tend to have fewer toothed species at localities with the same temperature as Asian and American sites. The following factors, singly or in combination, may account for this difference: (1) Australia's Cenozoic movement into lower latitudes, insulation from global cooling, and isolation from high-latitude cold-tolerant vegetation sources; (2) lack of high mountains as sources and refuges for cold-adapted taxa; (3) Pleistocene extinctions of cold-adapted taxa; and (4) the near absence of a cold-climate forest ecospace in Australia today.

Application of Australian LMA to Australian Cenozoic floras resulted in cooler temperature estimates than other LMA regressions. However, Australian paleotemperature estimates should account for the relative importance of cold-deciduous taxa. The timing and magnitudes of the extinctions of cold-adapted lineages are not known, and the most conservative approach is to use Australian LMA as a minimum and non-Australian LMA as a maximum temperature estimate.

INTRODUCTION

There is considerable interest in quantitative estimates of terrestrial paleoclimates, including paleotemperatures.

Apart from the value of placing evolutionary events and geological processes into a climatic framework (e.g., Upchurch and Wolfe, 1987; Gregory and Chase, 1992; Hunt and Poole, 2003), paleoclimate estimates offer tests of sensitivity studies using computer climate modeling (e.g., Sewall et al., 2000; Shellito et al., 2003). Australia, the focus of this study, lay at high Southern latitudes during the early Paleogene (Veevers et al., 1991) and is a valuable testing ground for climate modeling studies, which are most sensitive to forcing factors at high latitudes (Peters and Sloan, 2000; Shellito et al., 2003). Paleontological data long have indicated that the middle Eocene and late early Miocene of southeastern Australia were much warmer than today (e.g., Christophel, 1981; Greenwood, 1994; Kershaw et al., 1994; Macphail et al., 1994). Quantitative estimates derived from proxies for Australian paleoclimate are needed to improve understanding of these unusual time intervals, which are better known on other continents.

Terrestrial paleoclimates can be estimated from fossil floras using correlations between leaf physiognomic (size and shape) attributes and climate variables in living forests. A number of variations on the leaf-physiognomic approach have been demonstrated (e.g., Wolfe, 1993; Wing and Greenwood, 1993; Greenwood, 1994; Gregory and McIntosh, 1996; Jacobs, 2002), but a method known as leaf-margin analysis (LMA) was the first to be quantified as an estimate of mean annual temperature (MAT) and remains the most widely used (e.g., Wolfe, 1971, 1978, 1979; Greenwood and Wing, 1995; Wing et al., 2000; Greenwood et al., 2003; Hunt and Poole, 2003). Leaf-margin analysis is based on the strong positive relationship between MAT and the proportion of woody dicot species in a floral sample that has entire (untoothed) leaf margins (leaf-margin proportion, LMP). This trend was observed first among floras worldwide from areas without severe cold or moisture limitations (Bailey and Sinnott, 1915, 1916); it was quantified later, as a linear regression, for East Asian mesic vegetation (Wolfe, 1971, 1979; Wing and Greenwood, 1993). A leaf-margin analysis consists of inverting the regression for application to fossil floras, where the propor-

tion of untoothed species, the independent variable, is known, and MAT, the dependent variable, is unknown.

The adaptive value of leaf teeth, or their absence, is not well understood. Givnish (1979) argued that because evergreen leaves tend to be thicker than deciduous leaves, and flow resistance decreases as leaves become thicker, more growth will occur in the intercostal area, smoothing leaf margins. Other explanations, to date, include differential hydrodynamic expansion near the major veins of rapidly expanding, deciduous leaves with low vein density (Mosbrugger and Roth, 1996); teeth as sites of spring photosynthesis in young deciduous leaves (Baker-Brosh and Peet, 1997); and enhanced transpiration at leaf margins (Canny, 1990), which may compensate for reduced sap flow in cool environments (Wilf, 1997).

Margin type is not the only leaf character that is climatically informative, so Wolfe (1993) developed a multivariate database and analytical procedure known as CLAMP (climate leaf analysis multivariate program). This technique incorporated a broader geographical coverage than the original LMA, used additional leaf characters, and considered a number of climate variables in a correspondence analysis. In addition, a number of derivative methods have been proposed based on the CLAMP dataset (e.g., Gregory and Chase, 1992; Wing and Greenwood, 1993; Gregory-Wodzicki, 2000). However, leaf-margin type is the most significant character in every multivariate model used to estimate temperature (Wolfe, 1993; Wing and Greenwood, 1993; Wilf, 1997; Gregory-Wodzicki, 2000). Thus, understanding regional or hemispherical variation in the LMA regression is fundamental to paleotemperature analysis, whether multivariate or univariate methods are used. In addition, because the reproducibility of leaf-margin analysis, based on a single unambiguous character, mitigates observational errors in scoring multiple characters (Wilf, 1997), tests on living floras have generated MAT estimates from LMA that are generally as good as or better than multivariate approaches (Burnham, 1997; Wilf, 1997; Wiemann et al., 1998; Gregory-Wodzicki, 2000).

Accurate paleoclimate estimates may be derived best using modern calibration data that match, as closely as possible, the climatic response of leaf physiognomy in the fossil floras studied (Wolfe, 1993; Wing and Greenwood, 1993; Jordan, 1997; Greenwood and Wing, 1995; Stranks and England, 1997; Gregory-Wodzicki, 2000; Jacobs, 2002). Regional climate history, past and present edaphic conditions, and regional peculiarities of plant phylogenetic history may all shift leaf-climate relationships. For example, extreme cold and dryness, as found in subalpine sites, or poor soils may force relatively high leaf-margin proportions (Bailey and Sinnott, 1915, 1916; Webb, 1968), and the foliage of some plant lineages is obligately toothed or untoothed (Wolfe, 1993; Wing and Greenwood, 1993; Gregory and McIntosh, 1996). Examples of possible historical and phylogenetic effects include the predominance of families in the Australian flora that characteristically bear untoothed leaves, such as Myrtaceae, and the strong representation in North American floras of deciduous tree species with toothed leaves.

With regard to regional effects, of particular interest here is that separate LMA regressions initially were presented for the Northern and Southern hemispheres (Wolfe, 1979; Upchurch and Wolfe, 1987). The Southern Hemisphere scale was described as a 4% increase in entire-margined species for an increase of 1°C of MAT, compared to 3% for the Northern Hemisphere (Wolfe, 1979; Upchurch and Wolfe, 1987). This difference was attributed to ". . . the almost total absence of deciduous plants in the southern hemisphere . . . " and the anecdotally recognized, but unquantified correlation of toothed margins and deciduousness (Upchurch and Wolfe, 1987, p. 35). Unfortunately, no data were ever presented to support the Southern Hemisphere scale; consequently, the relative representations of deciduous taxa in various regions of the Southern Hemisphere remain unquantified.

Subsequent research has demonstrated substantially the same relationship between leaf-margin proportion and MAT in East Asia and the Americas, including South America (Wilf, 1997; Wiemann et al., 1998; Gregory-Wodzicki, 2000; Burnham et al., 2001; Kowalski, 2002). One data set of 30 sites from tropical South America showed, for a given temperature, leaf-margin proportion somewhat above (corresponding to about +3°C), but in general agreement with, other data sets (Kowalski, 2002). The exception was a group of cold sites from high elevations, for which toothed species were comparatively rare. As stated by Kowalski (2000), this appears to result from the unusual selective environment of Neotropical cloud forests, which are associated typically with thick, small, untoothed leaves (e.g., Leigh, 1999; Velázquez-Rosas et al., 2002). In addition, Kowalski's (2002) results must be regarded as preliminary because 17% of the species in her data set were not scored for margin state due to unavailability of herbarium specimens.

Preliminary studies of Australian mesic vegetation produced a poor correlation between LMP and MAT, with a significantly different regression slope and intercept from East Asia (Upchurch and Wolfe, 1987; Greenwood and Christophel, 1990; Greenwood, 1992, 2001). However, the analyses of Australian LMA included a majority of sites where the margin type either was not known for some species (Greenwood and Christophel, 1990; Greenwood, 2001), or was based on forest-floor litter collections from a small number of sites (Greenwood, 1992). Jordan (1997) found that both LMA and multiple-regression models consistently over-estimated MAT for modern southeastern Australian and New Zealand vegetation, and Kennedy (1998) found no relationship between leaf-margin proportion and MAT for New Zealand vegetation. However, New Zealand is a small and isolated landmass with an unique biogeographic history, and its forest cover exists within a limited range of MAT (5°–15°C). The New Zealand flora suffered major extinctions of plant lineages during the Neogene and Pleistocene (Lee et al., 2001). It is perhaps not surprising that the relationship of leaf physiognomy with climate in modern New Zealand might be different from the continental floras of Australia and the Americas.

This paper addresses the issue of regional effects on leaf physiognomy by re-examining the relationship of leaf-margin proportion to temperature for Australian vegetation. The possible influence of soil type also is considered because of the prevalence of nutrient-poor soils in many Australian ecosystems (Beadle, 1966). Based on a revised correlation for Australia, new temperature estimates for a series of Australian Paleogene floras are presented and

compared to results derived from the same floras using other calibrations. Factors are highlighted that might contribute to observed deviations in the Australian correlation, and general recommendations are presented for paleoclimatic estimation from Australian fossil floras.

MATERIALS AND METHODS

Extant Vegetation Database

In marked contrast to North America and Asia, the Australian flora is depauperate in deciduous trees and shrubs. The primary Australian woody vegetation is sclerophyllous and evergreen, and the dominant tree genera are *Eucalyptus, sensu lato* (Myrtaceae), and *Acacia* (Mimosaceae), all of which have entire leaf margins (Crisp et al., 1999). Along the east coast, there are also areas of mesic forest lacking (or at least not dominated by) *Eucalyptus* that often are termed rainforest in the Australian literature, but are termed vine forests under Webb's structural-physiognomic classification (Webb, 1959, 1968; Webb et al., 1984; Greenwood, 1996; Appendix 1). The Australian usage of rainforest is much broader than elsewhere, as it encompasses all forests where; (1) markedly sclerophyllous trees and shrubs (e.g., *Eucalyptus*) are either absent or uncommon; (2) the canopy is closed at least during the wettest part of the year; (3) life forms, or synusiae, characteristic of true rain forest are present; and (4) the dominant species are either species characteristic of true Australian rain forest (Webb, 1959, 1968; Greenwood, 1996), or are closely related to them. The greatest diversity of deciduous tree species in Australia is not found in temperate forests, but rather is found in the seasonally dry tropical vine forest and vine thickets (Webb, 1959, 1968; Appendix 1). Webb et al. (1984) produced a comprehensive survey of sites throughout the climatic range of rainforest (or vine forest) within Australia. These forests are dominated by trees and shrubs with broad laminae (length:width < 4.0), whereas *Eucalyptus* species are markedly sclerophyllous and typically stenophyllous (length:width ≫ 4.0). Structurally, the rainforests differ also from the sclerophyllous forests by having closed canopies (i.e., >70% projected foliage cover), a significant presence of woody vines, and other synusiae characteristic of true rain forests (Webb, 1959, 1968; Greenwood, 1996; Richards, 1996). The Webb et al. (1984) forest surveys varied in size from about 0.25 hectare to several hectares, but the authors reported an intention to provide a representative floristic inventory of the vegetation type in each locale. Some data were based on the mapping of all woody plants with a stem diameter at breast height > 15 cm, whereas others were surveyed using transects and included woody vines.

Most plant families are found both in the Australian sclerophyllous forests and rainforests (e.g., Myrtaceae), and many genera have either species or closely related genera in both biomes (Webb et al., 1984; Crisp et al., 1999). Nonetheless, the physiognomic-structural transition between sclerophyllous forests and rainforest is marked, and serves to highlight discrete ecophysiological strategies (Webb, 1959, 1968). The tropical and subtropical rainforests are often highly species rich and diverse (Appendix 1), and typically lack dominants in their canopy. The seasonally dry tropical deciduous vine-forest-
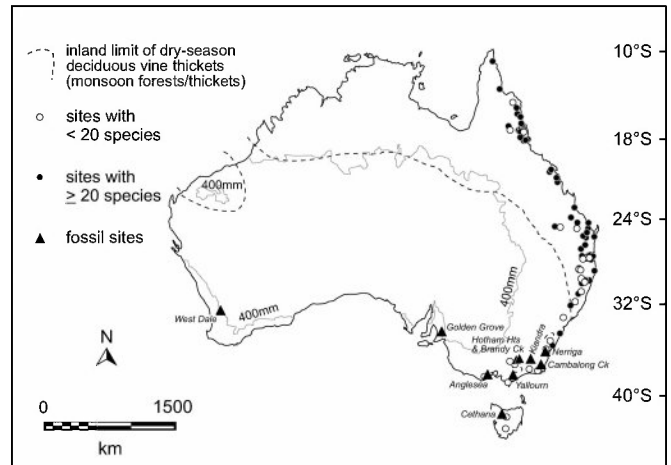

FIGURE 1—Locations of sites for which floral list data (Webb et al., 1984; Appendix 1) were compiled, superimposed on a map showing the limits of tropical rainforest and deciduous tropical woodlands in Australia, and Australian fossil sites discussed in the text. The ≥ 400 mm isohyet is indicated, demarking the limit of tree-dominated vegetation.

thicket sites in the Webb et al. (1984) database contain significant numbers of obligately or facultatively deciduous species (e.g., *Brachychiton* spp. and *Ficus virens*). A small number of sites from southeastern Australia contain emergent *Eucalyptus* spp. and/or *Acacia* spp. in the canopy; these sites are likely to be successional in response to forest fires. The cool-temperate rainforest sites, from southeastern Australia and Tasmania, typically have low woody-dicot diversity (<10 spp./ hectare) and are dominated by toothed broadleaved evergreen species, such as *Nothofagus cunninghamii, N. moorei* (Nothofagaceae), and *Atherosperma moschatum* (Atherospermataceae).

Australia's rainforests floristically and physiognomically reflect the predominant vegetation types of much of the Australian continent for much of the Cenozoic (Christophel and Greenwood, 1989; Kershaw et al., 1994; Greenwood et al., 2003). In contrast, the sclerophyllous forests were probably occupied a minor part of the landscape until perhaps the late Neogene, when markedly seasonal rainfall regimes became dominant (e.g., Gallagher et al., 2003). The sclerophyllous forests are adapted to low soil phosphorous and frequent wildfires, as well as seasonal drought or low annual rainfall (Beadle, 1966; Hill, 1998). For these reasons, the Webb et al. (1984) database of rainforest sites was selected here to assess LMA for Australia.

Sampling and Measurement

Data presented here are culled from floral lists by Webb et al. (1984) for over 600 rainforest sites. These are predominantly located towards the relatively wet east and northern coasts as well as the southeast of Australia; approximately two thirds of the continent is arid and lacks forest cover (Fig. 1). The subset of 113 sites that is used here have complete locality data and for which the leaf-margin types of all species could be determined (Fig. 1). This approach improves upon earlier analyses that used all sites (Greenwood and Christophel, 1990; Greenwood, 2001). Here, only woody dicot species from these floral

lists were scored for leaf-margin type, consistent with standard practice for paleoclimatic calibration data (e.g., Wolfe, 1993). Climate values for the sites were extrapolated using the BIOCLIM module (Busby, 1991) within the ANUCLIM version 5.0 software (Houlder et al., 1999), based on geographic data (Appendices 1 and 2). BIOCLIM uses a mathematical climate surface of present-day Australian climate, based on standard meteorological decadal means, and a digital elevation model.

The 113 sites closely approximate the complete climatic range of rainforest environments in Australia. The sites' range of MAT is 3.3°C to 24.9°C, mean annual range of temperature (MART) was 3.5°C to 12.5°C, and their range of mean annual precipitation (MAP) is 691 to 3686 mm/yr (Appendix 1). The MART throughout Australia today is low compared to most of North America (Fig. 2). The majority of sites have a summer peak of rainfall; however, some temperate sites have a winter precipitation peak that includes occasional snowfalls.

Leaf-margin type (toothed, untoothed, or both) for all species was obtained from published taxonomic descriptions in the *Flora of Australia* series (see Crisp et al., 1999) or from Hyland et al. (1999). A tooth was defined as a vascularized extension of the leaf margin with a corresponding sinus incised less than one quarter the distance to the midvein (Wilf, 1997; Ash et al., 1999). Facultatively toothed species were scored as half-toothed (score of 0.5; Wolfe, 1993). Because species richness influences the degree of error in estimates based on LMA (Upchurch and Wolfe, 1987; Wilf, 1997; Burnham et al., 2001), the database was subdivided into 2 subsets for analysis: all 113 sites, and 74 sites, each of which contains at least 20 species of woody dicots. In Australia, mesic forests at low MAT ($< 10°C$) are species poor, typically with fewer than ten species of woody dicots per site (Appendix 1). Consequently, the removal of depauperate sites also deleted the coldest sites from analysis, changing the minimum MAT from 3.3 to 10.8°C. However, a broad range of temperature remained, from 10.8 to 24.9°C, and MAP was in a comparable range (717 to 3193 mm/yr) to the full data set.

Webb et al. (1984) included limited data on soil characteristics for the majority of sites (Appendix 1). The sites were classified into one of nine soil categories, based primarily on the parent rock (e.g., basalt, acid volcanic, basic volcanic, limestone, sandstone, granite, or metamorphic), if known, and the manner of pedogenesis (e.g., *ex situ* soils, such as alluvium, versus *in situ* soils). To analyze these data for possible correlations of soil type with leaf-margin proportion, soils were grouped into fertile and infertile categories, according to the definitions of Webb (1968). The fertile category includes eutrophic to mesotrophic soils with high-to-medium mineral-nutrient status (68 sites), and the infertile category includes oligotrophic soils deficient in some minerals important for plant growth, particularly phosphorus (34 sites).

RESULTS

Leaf Margins and MAT

Analysis using least squares linear regression shows that leaf-margin proportion (LMP) is correlated signifi-

cantly with MAT using all sites. The correlation also is significant for the subset of sites with at least 20 species:

(1) All 113 sites

$$MAT = 22.0 \cdot LMP + 1.32, \qquad \sigma = +3.0°C$$

$$(r^2 = 57.3\%, \qquad F = 147, \qquad p < 10^{-21})$$

(2) 74 sites ≥ 20 species

$$MAT = 27.0 \cdot LMP - 2.12, \qquad \sigma = \pm 2.2°C$$

$$(r^2 = 63.0\%, \qquad F = 122, \qquad p < 10^{-16})$$

The standard errors for equations (1) and (2) are similar to those derived from equivalent databases from other geographical areas; for example, the error from LMA based on the CLAMP database is $\pm 3.4°C$, and with the coldest sites removed it is $\pm 2.1°C$ (Wilf, 1997).

The regressions for the 74 Australian sites with ≥ 20 species each (used in equation 2) versus the sites in the East Asian data set (Wolfe, 1979) showed a statistically significant difference in slope ($p \ll 0.001$, slope equality test of Sokal and Rohlf, 1995, p. 495). This was the most severe test because the difference in slope is greater for East Asia than for the other datasets (Fig. 3). In practice, this is not critical because the difference in slope for East Asia only amounts to 0.7° C of difference in temperature increase per 20% of LMP, less than half the amount originally suggested (Wolfe, 1979; Upchurch and Wolfe, 1987), and this value is negative, and less in absolute value, for the other data sets besides East Asia. Thus, the response of leaf-margin proportion to temperature is similar in Australia to elsewhere, as seen in the slope of the regression, but Australian vegetation is depleted in toothed species at all temperatures, as seen in the intercept (Fig. 3). Regarding the observation that the relationship between leaf-margin proportion and MAT in the Southern Hemisphere is different from the Northern Hemisphere (Upchurch and Wolfe, 1987), there is a major difference in the intercept but a negligible difference in the slope (Fig. 3). For South America, the only other large area of the Southern Hemisphere that has been examined, no significant difference has emerged (e.g., Gregory-Wodzicki, 2000).

Leaf Margins and Other Climate Variables

Results from univariate regression analyses of selected climatic variables (Appendix 2) on leaf-margin proportion are shown in Figures 4 and 5. Matching the results from other regions (e.g., Wing and Greenwood, 1993; Wilf, 1997), the strongest influences on LMP were temperature variables (Fig. 4), and no variable had a higher correlation coefficient than MAT. All of the temperature variables were correlated strongly with MAT, and when MAT is held constant, the highest coefficient of partial correlation with LMP was -0.24, for maximum temperature of the warmest quarter. The highest-scoring variables all relate to the thermal load experienced by plants, such as seasonal temperature extremes. The majority of sites were mesic (MAP >800 mm/yr); however, seasonal variation (as either precipitation seasonality or totals for driest, wettest, coldest, and warmest quarters; Fig. 5) was significant between sites. Nonetheless, correlations of LMP with precipitation variables were not significant ($p > 0.05$).
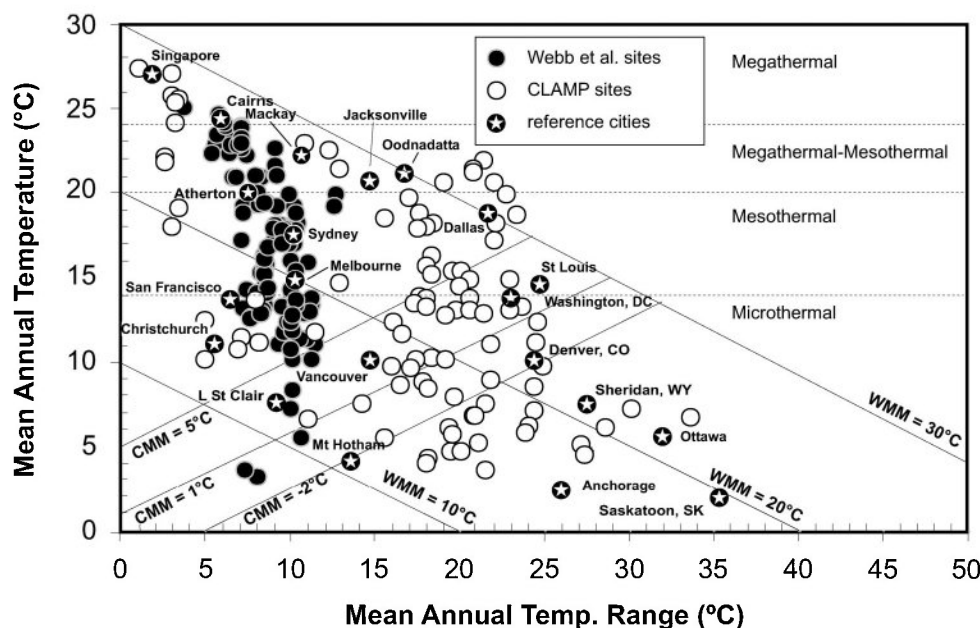
FIGURE 2—Bivariate plot of mean annual range of temperature (MART) versus mean annual temperature (MAT) for all sites in the Australian LMA calibration data set and sites from the CLAMP database for comparison (data from Wolfe, 1993, 1995). MART=the range from coldest month mean temperature (CMM) and warmest month mean temperature (WMM). Several North American and Australian cities are plotted for reference (from data compilation of Greenwood and Wing, 1995, and sources cited therein).

Influence of Soil Type

The regression of LMP against MAT, contrasting fertile and infertile soil sites with at least 20 species each (Fig. 4A), showed that the significance of the correlation was higher for fertile sites ($n = 46$) relative to that calculated using all sites ($n = 23$; i.e., r^2 fertile sites = 73% [$p < 0.001$], r^2 infertile sites = 61% [$p < 0.001$] versus r^2 all sites $\geq$ 20 spp. = 63% [$p < 10^{-16}$]). On visual inspection, neither the slope nor the intercept of the regression line for solely infertile or solely fertile sites are shifted markedly relative to those for all sites with at least 20 species

FIGURE 3—Bivariate plot of mean annual temperature versus proportion of woody dicot species with untoothed leaf margins for the Australian data set of this study (subset with $\geq$20 species per site) and other databases. Other data from Wolfe (1979, 1995) and Gregory-Wodzicki (2000). LMA East Asia (Wolfe, 1979; Wing and Greenwood, 1993) slope = 30.6; LMA derived from CLAMP 'coldest sites removed' (Wilf, 1997, p. 380) slope = 24.4; LMA from Bolivia (Gregory-Wodzicki, 2000) slope = 24.9.

(Fig. 4). This result suggests that the primary effect of differences in soil fertility is to increase the variance in LMP between sites that otherwise have similar environmental characteristics. However, based on ANCOVA, the infertile soils had significantly higher LMP than fertile soils ($F_{1,66} = 5.55, p = 0.021$, MAT covariate), indicating that infertile soils generally support vegetation with a higher proportion of untoothed species than do fertile soils with the same MAT.

AUSTRALIAN PALEOGENE TEMPERATURES

A series of paleotemperature estimates is presented in Table 1 for ten Paleocene through Miocene floras, each containing at least 20 species, from southeastern and southwestern Australia. Hunt and Poole's (2003) estimate for the middle Eocene Dragon Glacier flora from King George Island, off the Antarctic Peninsula, also is included; this flora is dominated reportedly by deciduous dicots and contains many of the taxa typical of Australian Paleogene megafloras. Results using Australian LMA are compared to previous multiple regression analyses (Greenwood and Wing, 1995), and to results from East Asian (Wing and Greenwood, 1993) and Bolivian (Gregory-Wodzicki, 2000) calibrations.

All of the Cenozoic MAT estimates are lower using Australian LMA (equation 2) than for either East Asian or Bolivian LMA calibrations (Table 1). The greatest differences are for the warmest estimates (e.g., Brandy Creek, Golden Grove, Hotham Heights, and Nerriga), which differ by more than 3°C between Australian LMA (equation 2) and the East Asian LMA (Wolfe, 1978; Wing and Greenwood, 1993). In no case do the standard errors of the estimates from East Asian and Australian LMA overlap, although overlap occurs for the coolest floras between the Austra-
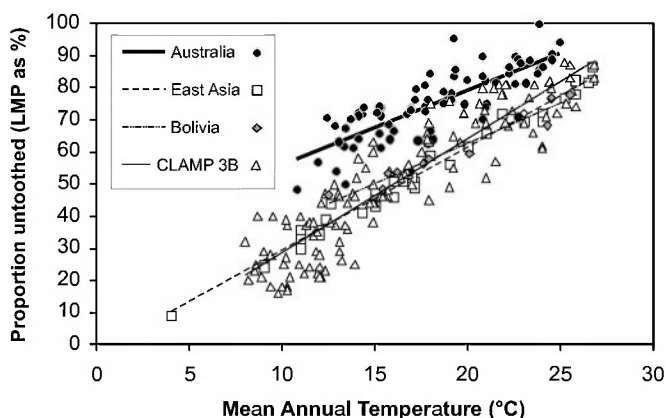
A

B

C

D

E

F

FIGURE 4—Bivariate plots of selected temperature variables (Appendix 2) versus proportion of woody dicot species with untoothed leaf margins for the Australian data set of this study (subset with ≥20 species per site). (A) MAT versus LMP, Australian data subdivided into fertile soil sites ○, and infertile soil sites △. (B) Temperature seasonality. (C) Minimum temperature of the coldest period. (D) Maximum temperature of the warmest quarter. (E) Mean temperature of the coldest quarter. (F) Mean temperature of the warmest quarter.

lian LMA and the Bolivian LMA. This result is consistent with the differences among the intercepts and slopes of the respective regression equations (Fig. 3). All of the estimates derived from the East Asian LMA for the early and middle Eocene sites also analyzed by Greenwood and Wing (1995) are consistently cooler using the Australian LMA, but they are close to and overlap within the errors for the estimates using the 1995 multiple linear regression equation.

The four revised Eocene estimates, although lower than calculated by Greenwood and Wing (1995), all indicate much warmer conditions at their paleolatitudes than are found at similar elevations and latitudes today (Greenwood et al., 2003). In addition, the revised Eocene estimates remove the appearance of a warmer Southern than Northern Hemisphere during the Eocene that was reported earlier (Greenwood and Wing, 1995).

The overall temporal pattern of the revised MAT esti-

A — plot with axes: Mean Annual Precip. (mm) (x-axis, 0–4000) vs Proportion untoothed (LMP as %) (y-axis, 0–100).
$$y = 0.003\,x + 69.089$$
$$r^2 = 0.04,\ p = 0.107$$

B — plot with axes: Precip. Seasonality (x-axis, 0–100) vs Proportion untoothed (LMP as %) (y-axis, 0–100).
$$y = 0.281\,x + 57.833$$
$$r^2 = 0.32,\ p = 1.5 \times 10^{-7}$$

C — plot with axes: Precip. Driest Qtr. (mm) (x-axis, 0–400) vs Proportion untoothed (LMP as %) (y-axis, 0–100).
$$y = -0.055\,x + 85.491$$
$$r^2 = 0.15,\ p = 0.0007$$

D — plot with axes: Precip. Wettest Qtr. (mm) (x-axis, 0–2000) vs Proportion untoothed (LMP as %) (y-axis, 0–100).
$$y = 0.010\,x + 66.018$$
$$r^2 = 0.14,\ p = 0.0013$$

E — plot with axes: Precip. Coldest Qtr. (mm) (x-axis, 0–500) vs Proportion untoothed (LMP as %) (y-axis, 0–100).
$$y = -0.038\,x + 84.314$$
$$r^2 = 0.14,\ p = 0.0013$$

F — plot with axes: Precip. Warmest Qtr. (mm) (x-axis, 0–2000) vs Proportion untoothed (LMP as %) (y-axis, 0–100).
$$y = 0.011\,x + 67.015$$
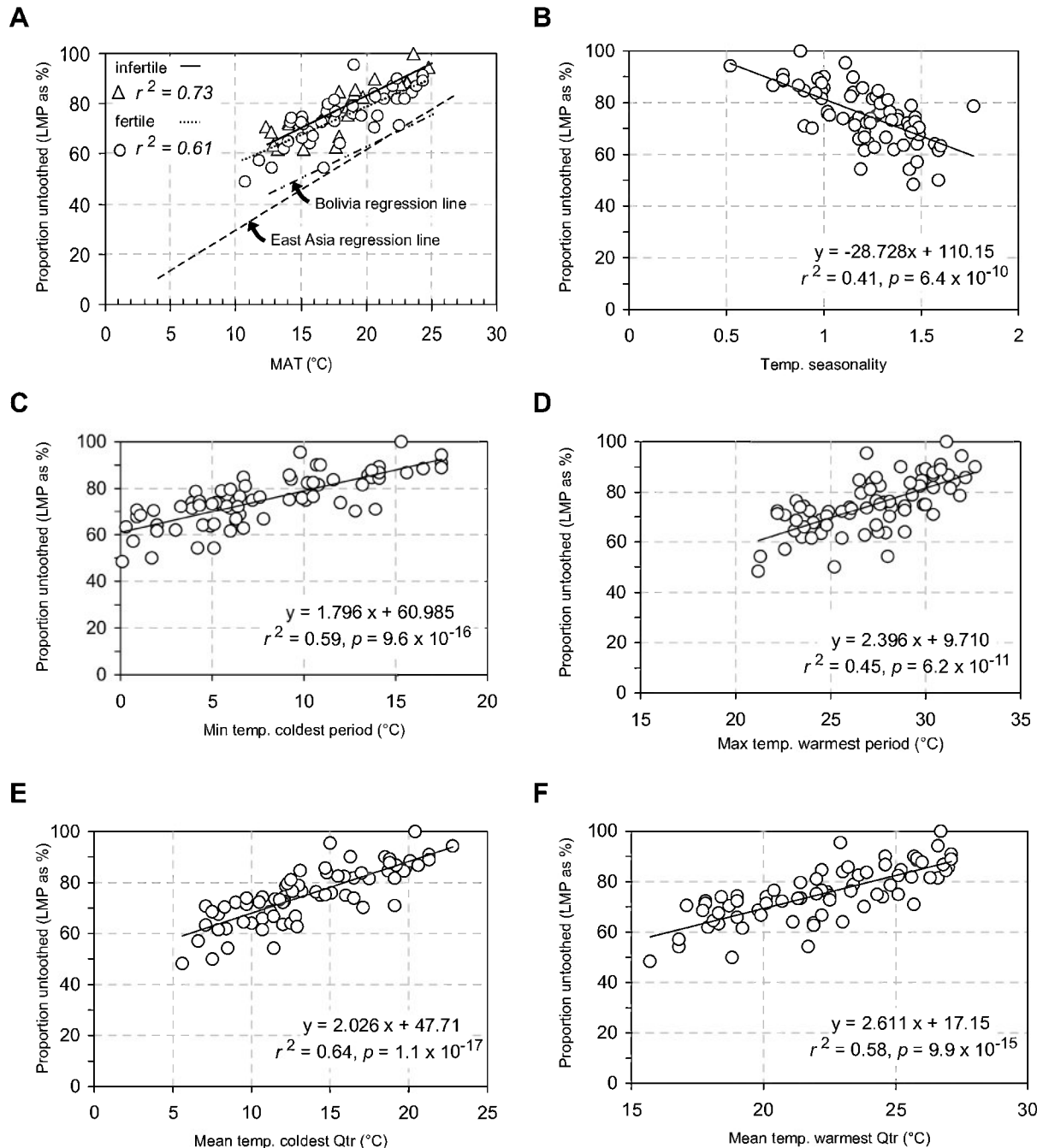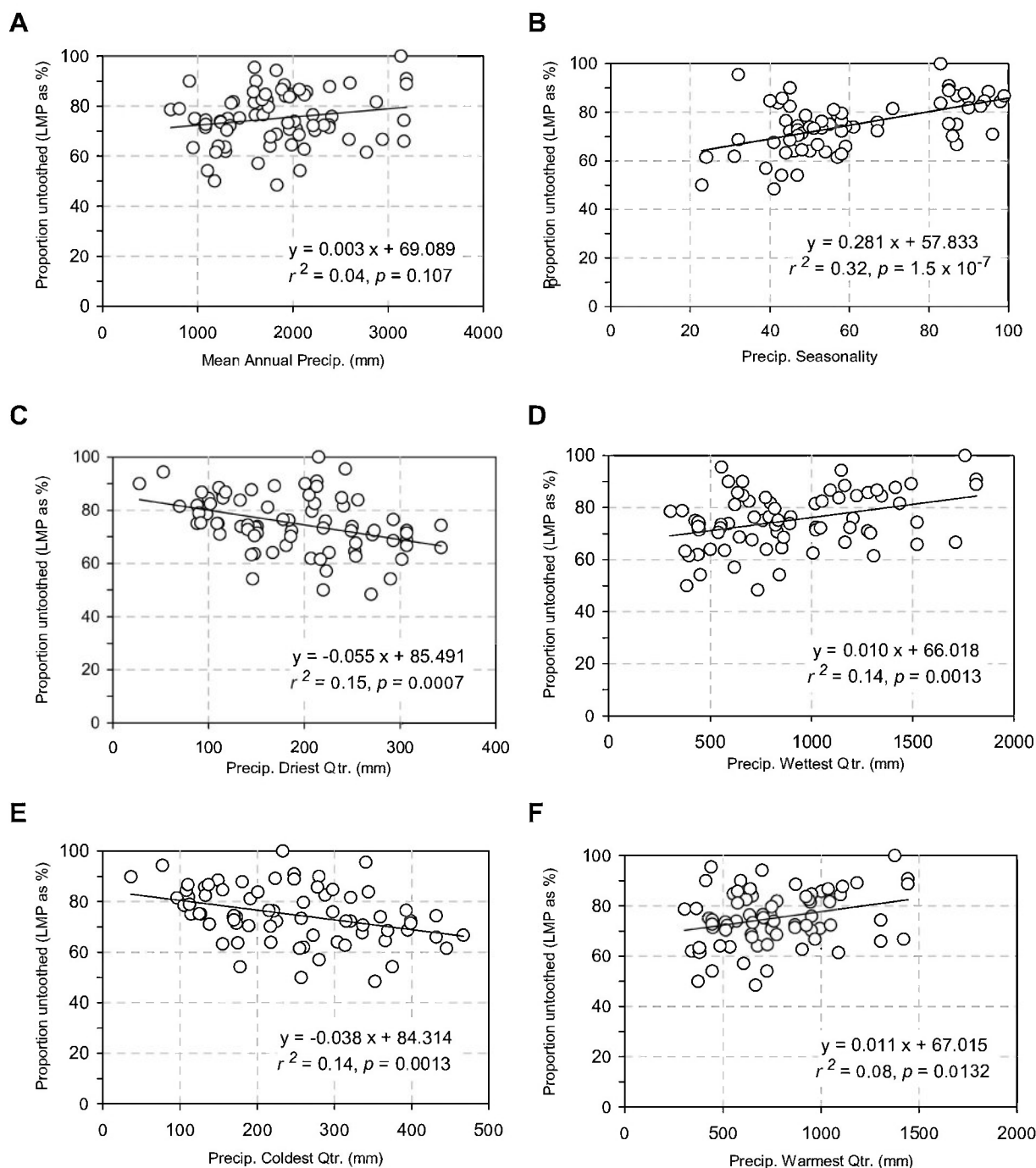$$r^2 = 0.08,\ p = 0.0132$$

FIGURE 5—Bivariate plots of selected precipitation variables (Appendix 2) versus proportion of woody dicot species with untoothed leaf margins for the Australia (this study; $\geq$20 species per site subset). (A) mean annual precipitation. (B) Precipitation seasonality. (C) Precipitation of the driest quarter. (D) precipitation of the wettest quarter. (E) Precipitation of the coldest quarter. (F) Precipitation of the warmest quarter.

mates is consistent with other paleoclimatic proxy data that indicate warm episodes during the early Eocene and early Miocene, but cooler conditions during the early Oligocene. However, the cold MAT of 4.2°C that is estimated here for the early Oligocene Cethana flora is problematic and underscores the importance of evaluating multiple proxies. Carpenter et al. (1994) reported a diverse flora from Cethana, including cycads and araucarian conifers, that is consistent with an ecotone in the modern Austra-

lian flora between sclerophyllous wet forest and temperate rainforest and an MAT of 10–14°C. These values lie at the upper end of the estimate derived using the East Asian LMA. The unexpectedly low estimated MAT for the Oligocene Cethana flora possibly is due to the diversity of toothed sclerophyllous taxa, such as *Banksieaephyllum* spp. (Proteaceae), a result that contradicts Jordan's (1997) hypothesis that LMA for Australian sites will be confounded by the predominance of obligately entire-margined

TABLE 1—Estimates of MAT for southern Australian and Antarctic Paleocene to Miocene macrofloras, contrasting Australian LMA, East Asian LMA, and Bolivian LMA. Details of all floras are given in Greenwood and Christophel (2003) and Hunt and Poole (2003). Notes: (1) multiple linear regression estimates from Greenwood and Wing (1995); (2) using LMA equations: East Asia MAT = 30.6·LMP + 1.141 (Wolfe, 1979; Wing and Greenwood, 1993), Bolivia MAT = 37.9·LMP − 3.83 (Gregory-Wodzicki, 2000), Australia MAT = 27.0·LMP − 2.12 (equation 2); (3) a minimum error of the estimate calculated as $\sigma_{[LMA]}$ = slope*$\sqrt{((LMP^*(1 - LMP))/r)}$, from Wilf (1997); (4) LMP scored from curated collections (University of Adelaide, Victoria University and Melbourne University); (5) LMP scored from a publication (descriptions and/or illustrations of named taxa); (6) estimates and data from Greenwood et al. (2003); (7) estimates and data from Hunt and Poole (2003).

		r	LMP	MAT[1]	MAT[2] [E Asia]	MAT[2] [Bolivia]	MAT[2] [Aust]	σ [LMA Aust][3]
Early Miocene	Yallourn Clays[4]	27	0.71		22.9	23.1	17.1	2.36
Early Miocene	Kiandra[4]	20	0.72		23.2	23.5	17.3	2.71
Early Oligocene	Cethana[5]	30	0.23		8.3	5.0	4.2	2.09
Middle Eocene–Oligocene	West Dale[5]	29	0.60	17.9	19.6	19.0	14.2	2.46
Middle Eocene	Anglesea[4,6]	28	0.65	17.1	21.0	20.8	15.5	2.44
Middle Eocene	Golden Grove[4,6]	21	0.71	18.7	22.9	23.1	17.1	2.68
Middle Eocene	Dragon Glacier[7]	37	0.29		10.1	7.3	5.8	2.03
Early middle Eocene	Nerriga[4,6]	24	0.79	19.4	25.3	26.1	19.2	2.25
Early–middle Eocene	Brandy Ck[4,6]	28	0.75		24.1	24.6	18.2	2.21
Early–middle Eocene	Hotham Heights[4,6]	26	0.74		23.8	24.2	17.9	2.33
Late Paleocene	Cambalong Ck[4,6]	21	0.58		18.9	18.1	13.5	2.91

taxa. However, the compositions of the other floras in Table 1 are consistent with the MAT estimates presented here using Australian LMA (Greenwood et al., 2003; Greenwood and Christophel, 2004).

DISCUSSION

This study shows that the relationship between leaf-margin proportion and mean annual temperature is statistically significant for Australian rainforest vegetation. This result matches that shown for unstressed environments in other major regions around the world (Wolfe, 1979; Wilf, 1997; Gregory-Wodzicki, 2000), and the similar slopes support global evolutionary convergence of leaf physiognomy in response to the selection of temperature in mesic habitats. Leaf-margin characteristics appear to belong with a long list of other leaf traits, such as lifespan, nutrient content, thickness, and herbivore resistance, that show global convergence under similar selective pressures (e.g., Coley et al., 1985; Reich et al., 1997). However, the Australian correlation is weaker than for other analyses (e.g., LMA Australia r^2 = 63% versus LMA East Asia r^2 = 98%, LMA CLAMP 'coldest sites removed' r^2 = 84%, and LMA Bolivia r^2 = 89%), and the intercept differs so that fewer toothed species are present at a given temperature. The latter observation marks a true regional difference between Australia and other continents.

Hypotheses to explain the lack of toothed species include: (1) significant phylogenetic effects in Australia compared to other continents, such as a prevalence of taxa unable to develop marginal teeth; for example, the Australian flora is dominated by Myrtaceae, the majority of which are untoothed (Jordan, 1997); (2) additional factors in the physical environment confounding the relationship between leaf-margin proportion and MAT (e.g., low phosphorous, low annual temperature amplitude, high variability in rainfall); and (3) absence of historical factors favoring the evolution, survival, or migration to Australia of temperate deciduous lineages with high proportions of toothed species, or the loss of such lineages at some time during the Cenozoic.

Point (1) seems unlikely because sites dominated by obligately entire-margined genera, such as *Eucalyptus* in the Myrtaceae, were largely excluded in this study. Moreover, the closed forest formations studied here share many taxa with similar forests in Africa, South America, and East Asia (Crisp et al., 1999), and have done so for much of the Cenozoic (Vadala and Greenwood, 2001; Greenwood and Christophel, 2004).

Regarding point (2), the present analysis of the influence of other environmental factors, such as seasonality and rainfall, showed that they appear to have no significant effect in determining the Australian LMP versus MAT intercept, or at least, any effect is masked by the strong autocorrelation of the temperature variables and MAT (Figs. 4, 5). Analyses of sites with markedly infertile soils, and of solely fertile soil sites, did not shift the intercept or the line to approximate the other datasets (e.g., East Asia, North America; Fig. 4A), but did show that infertile sites were enriched in untoothed species relative to fertile soils sites, matching Webb's (1968) original observations. The analysis of the influence of soil was limited by the available data, and further analysis based on more detailed soil information may be warranted in Australia and elsewhere.

Regarding point (3), several preliminary observations are presented. First, a significant difference between the histories of the Australian and both the North and South American continents is Australia's lack since the Eocene of a land connection with high-latitude landmasses (i.e., a potential source of cold-adapted woody taxa). Webb (1968) noted a trend for decreasing diversity of deciduous tree species from the tropics to the subtropics, and almost all deciduous dicot species in the modern Australian flora are drought-deciduous tropical trees in families such as Meliaceae (e.g., *Toona*) and Sterculiaceae (e.g., *Brachychiton*). The sole tree species that is cold-season deciduous, *Nothofagus gunnii*, is restricted to Tasmania. Nonetheless, some Tasmanian Paleogene floras, such as Cethana, have a relatively high diversity of toothed taxa, such as *Nothofagus*. These higher-latitude sites may have supported some deciduous taxa, such as deciduous *Nothofagus* species, per-

haps in response either to short winter days or low temperatures (Greenwood et al., 2003; Greenwood and Christophel, 2004). Second, both North and South America have substantive high mountain ranges (the Rocky Mountains and Andes) that have acted as source areas for cold-adapted biota, whereas Australia has low relief now and had low relief for the whole of the Cenozoic (Taylor, 1994).

A further difference between the histories of the Australian and both the North and South American continents is that Australia was essentially insulated from Cenozoic global climate cooling by its northward drift into middle and low latitudes. Australia may have cooled as little as 5°C over the Paleogene and Neogene (Macphail et al., 1994; Greenwood et al., 2003). Additionally, late Cenozoic cold intervals appear to have acted to force regional extinctions in southeastern Australia, rather than to promote the *in situ* evolution of cold-adapted tree taxa (Kershaw et al., 1994). In significantly smaller New Zealand, extinction and floral turnover appear to have had dramatic effects on the composition of its flora (Lee et al., 2001).

A final factor for consideration regarding point (3) is that the present Australian climate, even at the highest latitudes and elevations, does not favor deciduous, cold-adapted trees. The cold-climate (i.e., winter-snow) tree flora is poorly adapted to extreme cold and is dominated by broad-leaved evergreen trees with untoothed leaves, such as the snow gum, *Eucalyptus pauciflora*, which does not tolerate sustained temperatures lower than $-23°C$, and typically experiences winter mean minima $>-5°C$ (Sakai and Larcher, 1987; Costin et al., 2000; Jobbágy and Jackson, 2000). According to Jobbágy and Jackson (2000), the altitudinal tree-line worldwide approximates a warm month mean temperature (WMMT) of 6.8–9.3°C, and in the Southern Hemisphere it corresponds to a cold month mean (CMMT) of $>-1.9°C$. The climatic limit at altitude for broadleaved evergreen trees is a CMMT approximately $-2°C$. Therefore, the climate space exclusively occupied by broadleaved cold-deciduous trees elsewhere in the world (i.e., WMMT $>10°C$ and CMMT $<-2.0°C$) is largely absent from present-day Australia. Southern Australia also appears to have lost significant diversity in the mesic microthermal to mesothermal forest types, with a markedly lower diversity today than in the Paleogene (Greenwood and Christophel, 2004), particularly for toothed taxa such as *Nothofagus*. Tasmania today has only two species of *Nothofagus*, one of which is deciduous (*N. gunnii*), the other evergreen (*N. cunninghamii*). Possibly as a result of the factors listed above, there is no pool of cold-adapted, toothed woody dicot species to fill the cool ecospace in today's relatively cold climate; hence, the modern flora is deficient in these elements relative to other continents. It is not known when the Australian flora lost its deciduous microthermal to mesothermal woody dicots, although some Paleocene and early Eocene high latitude floras may have represented deciduous forest (Greenwood et al., 2003; Greenwood and Christophel, 2004). From a practical perspective, the different intercept for Australian LMA (Fig. 3) means that previously published MAT estimates for Australian fossil leaf floras should be reevaluated (Table 1). For example, a flora with 80% non-toothed species will produce an estimate of ~25°C using East Asian LMA, but ~20°C using Australian LMA (equation 2). Multiple regression analysis shows some potential to lessen the discrepancy (Table 1). However, leaf-margin analysis based on modern Australian floras may not be suitable for some Paleogene floras that grew before significant extinctions of cold-adapted lineages occurred. Accordingly, paleotemperature estimates for the Cenozoic of Australia should take into account the relative importance of deciduous taxa. Some paleotemperature estimates may best be made using non-Australian LMA, derived from samples with a high representation of deciduous taxa. In other cases, Australian LMA may be more suitable. Until more is known about the timing and magnitudes of the extinctions of cold-adapted lineages, as well as the deciduousness or evergreenness of fossil leaf species, the most conservative approach is to use LMA based on Australia as a minimum temperature estimate and East Asian LMA as a maximum. Hunt and Poole (2003) applied this approach in a recent analysis of middle Eocene floras from King George Island, West Antarctica, noting that a Southern Hemisphere LMA was potentially inappropriate because the fossil floras were dominated by deciduous taxa.

In summary, the response of leaf-margin proportion to climate, as seen in the slope of the regression, has yet to show a regional effect of any importance. Local conditions, especially environmental stresses, have accounted for all of the major deviations. Australia is different only in that there are fewer toothed species at a given temperature than elsewhere, but the amount of decrease in toothed species with temperature is not different from other regions. Investigations of leaf physiognomy in stressed environments, such as deserts, subalpine zones, and cloud forests, as well as in isolated areas, such as New Zealand, are important with regard to some fossil floras (e.g., Stranks and England, 1997; Gregory-Wodzicki, 2000). However, it is equally important not to conflate regional effects, which is a deviation that holds across environments within a wide area, with environmental effects on particular floras within a region that are probably convergent in many regions with the same environments (e.g., convergent physiognomies of deserts, subalpine zones, and cloud forests). For this reason, the division of leaf-climate space into three domains (Gregory-Wodzicki, 2000), which are a mixture of specialized environments, small landmasses, and continents, appears premature.

CONCLUSIONS

The statistically significant relationship between leaf-margin proportion and mean annual temperature is widespread globally in unstressed environments. The slope of the regression in Australia is virtually identical to that of East Asia, North America, and Bolivia. This indicates widespread convergence in the response of vegetation to temperature. However, the vertical intercept of the regression for the Australian database is higher than that of the majority of the other regional databases. Hence, woody dicot species with toothed leaf margins in Australia are a lower proportion of total species at a site than elsewhere at the same temperature.

Leaf-margin analysis, calibrated for Australian vegetation, can be used to estimate mean annual temperature for Australian Cenozoic leaf floras, with the error of the estimate similar to, but slightly greater than, that for LMA from other databases. The caveat for application is that

the Northern Hemisphere LMA may be more appropriate than the Australian LMA for Australian Cenozoic floras dominated by deciduous dicots. The most conservative approach is to use LMA based on Australia as a minimum temperature estimate and non-Australian LMA as a maximum (e.g., Hunt and Poole, 2003).

Multivariate approaches may help to compensate for regional differences in univariate leaf-climate relationships, including those related to historical events. However, previous applications of multivariate approaches, based on a global database lacking Australian sites, have not improved accuracy significantly for Australian vegetation (Greenwood and Wing, 1995; Jordan, 1997). An Australian multivariate database may be required to assess this point.

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APPENDIX 1

Site data for 113 Australian rainforest samples (from Webb et al., 1984), arranged in order of increasing site richness. The 20-species cutoff is indicated with a horizontal line (equation 2). The forest types follow the usage in the data set provided to us, which approximately follows Webb (1968) and Tracey (1982). A key is given at the end of this table. MAT = mean annual temperature; MAP = mean annual precipitation. Soil types (source regolith): fertile sites—A = alluvial, B = basalt, L = limestone, and V = basic volcanic; infertile sites—M = metamorphic, G = granite, R = acid volcanic, S = sand, and N = sandstone.

Site	Forest type	Elevation (m)	Latitude	Longitude	MAT (°C)	MAP (mm/yr)	Soil	Taxa	Non-entire	LMP (%)
436	MFF	1570	37°30	145°55	5.6	1655	—	3	1	33.3
435	MFF	1040	37°42	145°43	8.4	1589	—	4	2	50
428	SNVF	200	39°00	146°18	12.6	1139	A	5	2	40
431	MFF	25	38°46	143°37	13.2	1157	—	5	2	40
408	MFF	730	36°29	150°02	11.1	1203	—	5	3	60
427	SNVF	200	38°54	146°25	12.7	1104	A	5	3	60
483	SNVF	1000	29°18	152°06	13	951	M	5	3	60
204	MFF	800	35°27	149°52	11.1	1017	M	7	2	28.6
429	SNVF	200	39°01	146°20	12.6	1133	A	7	2	28.6
157	MFF	1400	31°10	152°20	10.2	1635	V	7	3	42.9
195	MFF	1400	31°58	151°30	10.2	1272	V	7	5	71.4
44	DVT	550	17°17	144°42	22.1	841	G	8	1	12.5
443	NMT	1500	41°47	146°34	3.3	1918	B	8	3	37.5
496	SNVF	50	37°27	149°50	14.3	923	M	8	3	37.5
440	MFF/NMT	1200	37°50	146°17	7.3	1580	—	10	5	50
254	NVF	1006	33°30	150°23	11.4	1213	A	10	6	60
471	MFF	1080	28°26	153°07	13.4	2072	B	11	3	27.3
162	CNVF	800	31°10	152°25	13.6	1738	V	11	7	63.6
458	ANVF	40	28°17	153°30	19.3	1785	A	13	1	7.7
206	SNVF*	400	37°35	149°10	11.8	1199	A	13	5	38.5
448	C/SNVF	1200	30°06	152°25	11.4	1330	G	13	9	69.2
561	LMVF	280	25°38	149°57	19.8	691	R	14	3	21.4
164	CNVF	800	31°10	152°25	13.6	1738	V	14	7	50
437	MFF/NMT	1350	42°40	146°30	3.7	1826	—	14	7	50
163	SNVF	950	31°10	152°25	12.7	1764	V	14	8	57.1
58	MVFFP	10	17°30	146°00	23.4	3686	A	15	1	6.7
498	MFF	1150	28°18	153°09	13.1	2044	B	15	6	40
161	SNVF*	400	31°12	152°25	15.9	1424	V	15	8	53.3
159	MFF	1400	31°10	152°20	10.2	1635	V	15	9	60
558	AMVF	300	25°40	152°03	19.1	938	M	16	3	18.8
182	ANVF	350	28°25	152°45	17.1	1140	V	16	5	31.3
454	CNVF	600	28°15	153°16	16.2	2462	R	16	9	56.3
7	ENVF	400	15°00	145°05	22.7	2014	M	17	1	5.9
456	MFF	925	28°16	153°10	14.4	1915	B	17	10	58.8
559	AMVF	300	25°40	152°02	19.1	931	A	19	4	21.1
165	CNVF	800	30°22	152°42	13.4	1985	B	19	6	31.6
445	MF/SNVF	1000	30°19	152°52	12.4	2413	M	19	10	52.6
482	SNVF	985	29°18	152°18	12.9	1123	M	19	12	63.2
45	DVT	550	17°05	144°25	22.5	914	L	20	2	10
388	SNVF*	40	25°28	153°05	20.8	1612	S	20	2	10
114	NVF	300	21°55	149°20	21	1316	V	20	5	25
410	MFF	820	32°20	151°25	13.4	1178	—	20	10	50
280	CMVF	40	18°04	145°41	23.8	2144	A	21	3	14.3
205	SNVF	400	35°41	150°10	13.3	1295	M	21	8	38.1
474	ENVF	5	29°32	153°33	19.2	1598	V	22	1	4.5
128	NVF	200	21°54	149°20	21.5	1375	V	22	4	18.2
160	CNVF	150	31°12	152°25	17.3	1287	A	22	8	36.4
90	ANVF	150	24°09	151°47	20.9	1240	—	23	6	26.1
243	CNVF	800	27°38	152°20	15.3	1081	B	23	6	26.1
193	CNVF	400	28°21	152°44	16.9	1104	B	24	11	45.8
212	MFF	1200	28°14	153°10	12.9	2075	B	24	11	45.8
194	CNVF	400	30°29	152°25	15.8	1216	B	25	9	36
450	CNVF	40	30°23	152°47	18.1	1761	B	25	9	36
113	MVF	250	15°28	145°16	23.3	1910	G	26	3	11.5
89	MVF	400	16°50	145°38	22.2	1984	M	26	4	15.4
411	MFF	750	32°20	151°26	13.8	1190	B	26	10	38.5
622	ENVF	40	17°14	145°48	23.8	3136	S	27	0	0
142	MVFFP	30	20°55	148°43	22.5	1596	A	27	5	18.5
47	SNVF	950	21°02	148°35	18	2943	G	27	9	33.3
560	ANVF	410	25°40	149°59	19.1	717	V	28	6	21.4
556	ANVF	190	25°28	152°07	19.8	971	A	28	7	25
158	MF/SNVF	1100	31°10	152°20	11.9	1636	V	28	12	42.9
93	CNVF	900	17°31	145°35	14.119.1	2411	B	29	7	24.1

APPENDIX 1

Continued.

Site	Forest type	Elevation (m)	Latitude	Longitude	MAT (°C)	MAP (mm/yr)	Soil	Taxa	Non-entire	LMP (%)
263	SNVF	1000	28°13	153°17	14.1	2380	R	29	8	27.6
481	SNVF	1000	29°16	152°07	13	953	M	30	11	36.7
221	ENVF	100	28°17	153°35	19.2	1924	S	31	5	16.1
99	MVF	300	17°00	145°40	22.7	2035	A	31	9	29
465	CNVF	950	28°23	153°07	14.1	1987	B	31	11	35.5
447	CNV/MFF	1300	30°22	152°33	10.8	1832	B	31	16	51.6
312	MVF	40	18°16	145°59	23.7	2121	A	32	5	15.6
554	AMVF	190	25°27	152°06	19.8	967	V	32	8	25
203	CNVF	200	34°45	150°45	15.7	1827	B	32	10	31.3
609	MVFFP*	40	16°16	145°28	24.5	3193	A	33	3	9.1
115	NVF	300	21°35	149°12	20.9	1728	V	34	6	17.6
246	CNVF	600	26°42	153°34	17.1	2210	B	34	8	23.5
249	CNVF	600	26°32	152°34	16.9	1241	A	34	9	26.5
223	CNVF	800	28°13	153°17	15.2	3167	B	35	9	25.7
244	CNVF	800	27°38	152°20	15.3	1081	B	35	10	28.6
455	CNVF	900	28°15	152°29	14.3	1338	B	36	10	27.8
301	MVF	200	18°15	146°16	22.7	2599	G	37	4	10.8
183	SNVF	800	30°15	152°45	13.4	1766	—	37	12	32.4
96	CMVF	150	17°51	145°42	23.1	2876	A	38	7	18.4
102	CNVF	400	24°58	151°28	18.7	808	M	38	8	21.1
217	CNVF	200	26°16	152°55	19.1	1608	M	38	9	23.7
464	CNVF	250	28°22	152°49	17.7	1085	A	39	10	25.6
167	SNVF	1000	30°17	152°47	12.4	1964	M	41	12	29.3
264	CNVF	800	28°13	153°17	15.2	3167	B	41	14	34.1
463	ANVF	250	28°22	152°49	17.7	1085	B	44	12	27.3
32	ENVF	650	13°52	143°20	22.2	1883	A	45	6	13.3
331	CMVF	40	17°08	145°46	24	2069	A	45	6	13.3
224	SNVF	1000	28°13	153°17	14.1	2380	R	49	14	28.6
218	CNVF	400	26°45	152°45	17.8	1688	B	51	12	23.5
469	SNVF	750	28°24	153°16	15.3	2775	R	52	20	38.5
17	ENVF	150	11°32	142°47	24.9	1827	N	53	3	5.7
210	CNVF	400	28°12	153°11	17.2	1742	B	54	11	20.4
185	SNVF	800	31°24	152°10	13.7	1306	—	54	16	29.6
486	SNVF	910	30°21	152°46	12.8	2064	M	54	17	31.5
303	MVF	200	18°18	146°08	22.8	2388	G	57	7	12.3
214	ENVF	200	25°30	153°08	19.9	1676	S	57	10	17.5
295	CMVF	600	16°03	145°12	20.8	2232	A	57	17	29.8
168	SNVF	40	30°20	153°07	18	1713	N	59	9	15.3
92	SNVF	300	28°11	153°18	17.8	2119	R	59	22	37.3
211	CNVF	800	28°14	153°10	15.1	2326	B	65	18	27.7
171	CNVF	600	28°34	153°20	16	2589	B	66	22	33.3
466	CNVF	900	28°23	153°07	14.4	2016	B	69	18	26.1
213	ENVF	200	26°00	153°08	19.3	1586	S	70	10	14.3
453	CNVF	500	28°15	153°16	16.7	2213	B	72	20	27.8
209	CNVF	400	27°20	152°45	17.7	1351	B	74	14	18.9
607	CMVF	40	16°16	145°28	24.5	3193	V	81	9	11.1
170	NVF	250	30°18	153°05	16.9	1947	A	86	23	26.7
563	SNVF	1000	17°25	145°25	18.7	1438	R	101	25	24.8
593	CNVF	600	17°16	145°38	20.8	1965	B	172	28	16.3

Forest code	Webb-Tracey structural type	Approximate equivalents
NMT	Nanophyll mossy thicket	cool to warm temperate rainforest ± sclerophyll emergents and/or conifers
MFF	Microphyll fern forest	
SNVF	Simple notophyll vine forest	montane tropical to lower montane subtropical rainforest
CNVF	Complex notophyll vine forest	lower montane tropical to lowland subtropical rainforest
NVF	Notophyll vine forest	
LMVF	Low microphyll vine forest	semi-evergreen seasonal subtropical low forest
AMVF	Araucarian microphyll vine forest	semi-evergreen tropical low forest + araucarian emergents
ENVF	Evergreen notophyll vine forest	evergreen seasonal tropical forest ± sclerophyll emergents
ANVF	Araucarian notophyll vine forest	seasonal tropical forest + araucarian emergents
MVF	Mesophyll vine forest	tropical rainforest of Richards (1996), but including tropical ever-green seasonal forest by some definitions (Webb 1959; Greenwood 1996)
CMVF	Complex mesophyll vine forest	
MVFFP	Mesophyll vine forest + fan palms	
DVT	Deciduous vine thicket	low monsoon forest
MFF/NMT, MF/ SNVF, C/SNVF and CNV/MFF	Transitionary types	

APPENDIX 2

Climate variables assessed in this study (Figs. 4, 5), definitions from Houlder et al. (1999). Variables are listed in the order of r^2 (highest to lowest) in regression analysis with LMP.

Variable	Units	Definition (from Houlder et al., 1999)
Mean annual temperature (MAT)	°C	The arithmetic mean of the mean temperature (temp.). of each month, where the mean month temp. is the mean of each day (i.e., the mean temp. through each daily diurnal cycle)
Mean temperature of the coldest quarter (MeanTcoldQtr)	°C	The mean of the 3 successive months with the lowest mean temp.
Min. temp. coldest period (MinTcoldQtr)	°C	Mean minimum temp. for the coldest month
Mean temperature of the warmest quarter (MeanTwarmQtr)	°C	The mean of the 3 successive months with the highest mean temp.
Max. temp. warmest period (MaxTwarmQtr)	°C	Mean maximum temp. for the warmest month
Temperature seasonality	N/A	(temperature coefficient of variation) is the standard deviation of the weekly mean temperatures expressed as a % of the mean of those temperatures (in °K)
Precip. seasonality	N/A	(precipitation coefficient of variation) is the standard deviation of the weekly precip. estimates expressed as a % of the mean of those estimates (i.e., MAP)
Precipitation of the driest quarter (PrecipDriestQtr)	mm	The mean of the 3 successive months with the lowest precipitation
Precipitation of the wettest quarter (PrecipWetQtr)	mm	The mean of the 3 successive months with the highest precipitation
Precipitation of the coldest quarter (PrecipColdQtr)	mm	The mean of the 3 successive months with the lowest mean temp. (i.e., winter precip.)
Precipitation of the warmest quarter (PrecipWarmQtr)	mm	The mean of the 3 successive months with the highest mean temp. (i.e., summer precip.)
Mean annual precipitation (MAP)	mm/yr	The annual sum of each monthly mean precipitation