CLIMATE RECONSTRUCTION FROM LEAF SIZE AND SHAPE: NEW DEVELOPMENTS AND CHALLENGES

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ABSTRACT.—Leaf physiognomy (size and shape) in fossils is commonly used to reconstruct terrestrial paleoclimate. Physiognomic leaf-climate methods are underpinned mostly by the covariation between toothed margins and mean annual temperature (MAT) and between leaf size and mean annual precipitation. Digital leaf physiognomy, a multivariate method based largely on variables that are functionally linked to climate and that can be measured by computer algorithm, minimizes many of the deficiencies present in other approaches. Nevertheless, the relationships between MAT and many physiognomic variables, especially tooth-related variables, are confounded by leaf thickness, leaf habit (deciduous vs. evergreen), and phylogenetic history. Until these factors are properly accounted for, a minimum error in MAT of ±4 °C for digital leaf physiognomy and ±5 °C for other methods should be assumed.

INTRODUCTION

PLANTS ARE sessile, and their leaves have a high surface-to-volume ratio. These characteristics help explain why plants—and especially leaves—often are sensitive indicators of climate. The practice of inferring climate from fossil plants has a rich history extending over a millennium (Sun, 2005). This review focuses on the subclass of plant-climate methods that uses leaf physiognomy (size and shape). Physiognomic-based methods have been practiced for almost a century (Bailey and Sinnott, 1915), and are widely applied today to quantitatively reconstruct terrestrial climates for the Cretaceous and Cenozoic (Wolfe, 1993, and references therein; see also compilation in Little et al., 2010). Because there already are excellent reviews on physiognomic methods (e.g., Chaloner and Creber, 1990; Parrish, 1998; Greenwood, 2007; Jordan, 2011), I will emphasize herein new developments and challenges related to the functional significance of leaf teeth, a leaf-climate method called digital leaf physiognomy, and the confounding effects of local water availability, leaf habit (deciduous vs. evergreen), and phylogenetic history.

LEAF-MARGIN ANALYSIS AND THE ADAPTIVE SIGNIFICANCE OF LEAF TEETH

A striking correlation exists between mean annual temperature (MAT) and the percentage of woody flowering plants (exclusive of monocots) with no teeth along their leaf margins (e.g., Greenwood, 2005a; Peppe et al., 2011). This correlation has been calibrated in most regions of the world (Table 1), and the relationship typically is statistically significant and convergent across regions (but see "factors that confound leaf-margin analysis" section below). The correlation was first noted over a century ago (Brenner, 1902; Bailey and Sinnott, 1915, 1916), and when inverted to infer MAT, it is called leaf-margin analysis (Wolfe and Hopkins, 1967; Wolfe, 1971), the most widely used leaf-climate method. To emphasize this point, Little et al. (2010) compiled 351 references that discuss leaf teeth and climate, the majority of which focus on the calibration or application of leaf-margin analysis.

Despite the popularity of leaf-margin analysis, comparatively little is known about its adaptive significance. Why do leaves have teeth and why are teeth more common in cold climates?

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Herbivory

Brown and Lawton (1991) hypothesized that leaf teeth may physically deter insect folivory, but subsequent experiments provided little support (Rivero-Lynch et al., 1996). Because insect folivory scales with MAT (e.g., Adams et al., 2011; Garibaldi et al., 2011) and thus could drive a correlation between margin type (toothed vs. untoothed) and MAT, this topic warrants further work. Spines on leaves may deter mammalian feeding (Givnish, 1979), but by convention, indentations with no vasculature, which includes spines, are not considered teeth when scoring for leaf-climate methods (Wolfe, 1993).

Convective cooling

The physical shape of toothed leaves should thin their boundary layer and promote cooler leaf temperatures, but experiments with metal models are inconclusive (Vogel, 1970; Gottschlich and Smith, 1982). If this functional link was strong, it would select against untoothed species in warm climates, which is opposite to what is observed.

Pulse in early season gas exchange

There is a long history of hypothesizing a link between leaf teeth and transpiration (Bailey and Sinnott, 1916; Canny, 1990; Wolfe, 1993; Roth et al., 1995), mostly because teeth are highly vascularized and have a high perimeter:area ratio (thinner boundary layer). This link, therefore, may be related to the temperature hypothesis just discussed via transpirational cooling. Alternatively, enhanced transpiration may serve to accelerate the delivery of nutrients to leaves (Cramer et al., 2009). Royer and Wilf (2006) measured photosynthesis and transpiration in toothed and untoothed leaf margins of 60 woody species native to Pennsylvania and North Carolina. Toothed species often had higher gas-exchange rates in their teeth than leaf interior, and this pattern was most pronounced in the Pennsylvania (colder) flora and was restricted to the first ~30 days of the growing season. Leaves emerging later in the growing season showed no tooth effects, even when they were young. Untoothed species showed little difference in gas exchange between the margin and interior, even early in the growing season (Royer and Wilf, 2006). These results are consistent with the earlier work of Baker-Brosh and Peet (1997), who used radiocarbon dosing to infer higher rates of photosynthesis in teeth relative to the leaf interior for eight tree species in North Carolina. Their spike in gas-exchange activity was also restricted to the beginning of the growing season and was not observed in the four untoothed species. In a related study, Mora and Jahren (2003) used isotope tracers to discern a pulse in ecosystem-wide transpiration early in the growing season for three forests in the southeastern United States; however, their methodology did not differentiate toothed from untoothed species.

What causes the drop in tooth transpiration after the first few weeks of the growing season? Hydathodes are fixed pores common in teeth (Feild et al., 2005), and probably are responsible for considerable water loss (via guttation) in leaves early in the growing season (Mauseth, 1988; Feild et al., 2005). Crucially, in some species, wax occludes these pores by the time the leaf is fully expanded (Mortlock, 1952; Stevens, 1956; Takeda et al., 1991). This pattern is consistent with the idea that teeth serve an important role early in the growing season, and once this window passes, wax plugs help to prevent unwanted water loss.

Together, these studies suggest that leaf teeth boost gas exchange during the first few weeks of the growing season, and that the effect is more pronounced in colder climates. Toothed species therefore ramp up carbon production rates sooner and/or faster than if they lacked teeth. This is true both because teeth often mature more quickly than the leaf interior (Billings, 1905; Bailey and Sinnott, 1916; Baker-Brosh and Peet, 1997; Feild et al., 2005) and therefore start fixing carbon sooner (Baker-Brosh and Peet, 1997; Royer and Wilf, 2006), and because teeth increase sap flow (Royer and Wilf, 2006), delivering nutrients to young, expanding leaves at a faster pace (Cramer et al., 2009). This ‘carbon pump’ may be increasingly adaptive in colder climates, where the time-window for growth is more limiting. However, there is a water cost to teeth, and in warmer climates, this cost may outweigh the diminishing benefit of maximizing an increasingly longer growing season (Wing et al., 2000; Royer and Wilf, 2006). The balance between photosynthesis and transpiration can thus explain (at least in part) the observed pattern between leaf teeth and MAT.

Release of excess root pressure

When Feild et al. (2005) experimentally plugged tooth hydathodes in the herbaceous basal angiosperm *Chloranthus japonicus*, the intercellular spaces flooded and photosynthesis was inhibited. The authors hypothesized that teeth may serve as a release valve for excess sap (guttation fluid), especially when positive root pressure is high. Toothed species thus are better equipped to maintain rapid sap flow with less risk to damage from high root pressure (Feild et al., 2005). In this regard, the root-pressure hypothesis shares features with the earlyseason gas-exchange hypothesis, namely heightened sap flow rates. The link with MAT is less direct, but may be related to the ability of root pressure to expedite leaf expansion and to refill (repair) freeze-thaw embolisms (Feild et al., 2005).

Some species produce toothed leaves as juveniles but untoothed leaves as adults (see Richards, 1996). This pattern is compatible with the root-pressure hypothesis because low-statured juveniles are especially prone to root pressure damage. The pattern is also compatible with the early season gas-exchange hypothesis because there is often a large premium for rapid growth in juveniles.

Leaf thickness

Givnish (1978, 1979) hypothesized that thin leaves are mechanistically linked to teeth. He argues that any point on a thin leaf is likely to be supported by less volume of vascular tissue than on a thick leaf, and that to support their flimsier leaf tissue, thin leaves often have large, parallel, secondary veins. As a result, regions along the leaf margin between secondary veins may have insufficient hydraulic or structural support for growth, creating a wavy or serrated margin. Using a model, Roth et al. (1995) demonstrated that this effect is most pronounced in leaves that lack a marginal vein and have secondary veins extending all the way to their margin.

A correlation between leaf thickness and margin type has long been noted (e.g., Bailey and Sinnott, 1916), but Givnish's hypothesis (1978, 1979) has been difficult to test owing to the lack of large data sets. Recently, Royer et al. (2012) found support for the hypothesis: in a broad survey of 667 species, untoothed species were 57% thicker on average than toothed species ($P < 0.001$). Leaf mass per area, which correlates closely with leaf thickness (Niinemets, 1999; Royer et al., 2012), was also significantly higher in untoothed species (66%; $P < 0.001$) (Royer et al., 2012). These data provide new, quantitative support for the leaf thickness hypothesis.

Leaf habit (deciduous vs. evergreen)

Baker-Brosh and Peet (1997) proposed that toothed species are linked to the deciduous habit because rapid leaf expansion, driven by a tooth-related pulse in gas-exchange activity, is most adaptive in canopies that are leafless during the off-season. In closed, evergreen-dominated canopies with less light, the photosynthetic benefit associated with rapid leaf expansion is diminished. Similarly, Peppe et al. (2011) speculated that because deciduous species flush their leaves all at once, any tooth-driven increase in sap flow is more pronounced than in toothed evergreen species. Both of these related proposals are compatible with the early season gas-exchange hypothesis.

Alternatively, leaf habit and margin type may be linked via the leaf economic spectrum (Royer et al., 2005). This spectrum is composed of leaf traits that are inter-correlated within and across most species, and is largely independent of biome type, climate, and phylogenetic history (Wright et al., 2004). Together, these traits are functionally related as to how quickly (or slowly) a plant is consuming nutrient resources. A "slow-return" specialist typically has low photosynthetic and respiration rates, low nitrogen and phosphorus concentrations (because less maintenance of the photosynthetic machinery is needed), a long leaf lifespan to pay back fixed construction costs, and a high leaf dry-mass-per-area in order to build a leaf that can better resist damage over its longer life. Leaf habit is linked to leaf lifespan, a core leaf economic variable. Teeth may also be related to the leaf economics spectrum if the early season gas-exchange hypothesis is valid, because the pulse in early season required by the hypothesis may be best facilitated by "fast-return" specialists. Indeed, Royer et al. (2012) established that toothed species correlate significantly with traits associated with the fast-return end of the leaf economics spectrum, including high leaf nitrogen content, low leaf mass-per-area, the deciduous habit, and ring-porous wood. These data support the view that the leaf economics spectrum serves as a functional bridge between leaf-margin type and leaf habit. Further, the spectrum may be a bridge between leaf-margin type and leaf thickness because plants with thin leaves (low leaf mass-per-area) are also likely to be fast-return specialists.

Support for a coordination between leaf habit and margin type comes largely from qualitative observations (Bailey and Sinnott, 1916; Givnish, 1979) and limited quantitative data sets (Wolfe, 1971, 1993; Jordan, 1997). In a more extensive survey of woody dicot species from 29 Asian and

Central and North American sites, Peppe et al. (2011) found additional support: within sites, evergreen species are more proportionately untoothed than deciduous species. The leaf-habit effect is also more pronounced at colder sites, and the ability of leaf margins to predict MAT is weaker in evergreen species (i.e., the regression slope between percent untoothed and MAT is flatter). In an expanded survey of 3006 species, Royer et al. (2012) found that 57% of all deciduous species were toothed while only 22% of evergreen species were toothed, a highly significant difference ($P < 0.001$).

FACTORS THAT CONFOUND LEAF-MARGIN ANALYSIS

Leaf thickness and leaf habit

Both leaf thickness and leaf habit are linked to margin type (see previous subsections), but neither correlate very strongly with MAT (Givnish, 2002; Wright et al., 2004, 2005; Royer et al., 2012). Thus, leaf thickness and habit can confound the leaf-margin analysis signal, but they have little primacy in explaining the underlying leaf-climate correlation. To provide one example that highlights this point, eastern Australian floras approach 100% evergreen, and for a given MAT, contain proportionately fewer toothed species than most other regions (i.e., a shift in the y-intercept); however, the slope between percent untoothed and MAT is similar to that observed elsewhere in the world (Greenwood et al., 2004).

Another important consideration is that leaf thickness and leaf habit are auto-correlated: deciduous leaves tend to be thinner than evergreen leaves (e.g., Royer et al., 2012). This raises an important issue about causality: is margin type functionally linked to leaf habit, with the correlation to thickness merely secondary, or is it the other way around, with margin type more functionally linked to leaf thickness? Using logistic regression, Royer et al. (2012) demonstrated that leaf-margin type correlates significantly with MAT, leaf thickness, and leaf habit, even after accounting for the influence of other two variables. Leaf-margin type, therefore, is controlled independently by all three factors. This raises a legitimate concern for paleoclimate reconstruction if thickness and habit are not accounted for. One way forward is to include, as an additional variable in leaf-climate methods, a proxy for leaf mass-per-area based on petiole dimensions (Royer et al., 2007; see also Jordan, 2011), because leaf mass-per-area is functionally linked to both thickness and habit. A preliminary analysis by Royer et al. (2012) found that, indeed, including this petiole information improves the precision of both leaf-margin analysis and digital leaf physiognomy, a multivariate method described later in this paper.

Abundance of available water

Local water availability can confound the relationship between leaf-margin type and MAT. In brief, at a given MAT, toothed species are more common in physiologically wet environments. This includes freshwater-margin (Brenner, 1902; Wolfe, 1971, 1977; Burnham et al., 2001; Kowalski, 2002; Greenwood, 2005b; Royer et al., 2009a; Steart et al., 2010; Peppe et al., 2011) and shady understory environments (Brenner, 1902; Xu et al., 2008). In contrast, at a given MAT, untoothed species are proportionately more abundant in saline (Bailey and Sinnott, 1915, 1916; Greenwood, 2005b; Royer et al., 2009a) and arctic/alpine environments (Bailey and Sinnott, 1915, 1916; Wolfe, 1993).

The freshwater-margin effect has received the most attention, in part because the majority of fossil plants are preserved in freshwater environments, but efforts to calibrate leaf-climate relationships with extant foliage sometime focus on other, locally drier environments (who wants to get their feet wet?). The magnitude of the effect, quantified by sampling across local water gradients, is typically no more than 4°C (Burnham et al., 2001; Peppe et al., 2011). Kowalski and Dilcher (2003) report a bias up to 10°C, but this is not representative of most regions (Peppe et al., 2011). With strategic sampling of calibration floras, the bias can be minimized. Wolfe (1993), for example, sampled the full range of microenvironments at each calibration site and, as a result, discerned only a weak water availability effect (see also Peppe et al., 2011). Paradoxically, mean annual precipitation only weakly correlates to leaf-margin type (Wolfe, 1993; Peppe et al., 2011; Royer et al., 2012; but see Jacobs, 1999). Presumably, this is because many factors beyond total rainfall determine local water availability (temperature, humidity, slope, soil type, groundwater flow, etc.).

The selection against toothed species in physiologically dry environments provides strong support for the early season gas-exchange and root-pressure hypotheses. With both hypotheses, transpirational water loss plays a critical role. At a given MAT, as water becomes more limiting, teeth become more expensive and thus less common; also, in drier environments, the risks of excess root pressure are diminished.

Height within canopy

Bailey and Sinnott (1916) concluded from qualitative analyses that the sensitivity of leaf margins to MAT is less for subcanopy plants (herbs and shrubs) than for canopy trees. They surmised that this lack of sensitivity is due to more uniform environmental conditions (e.g., humidity, temperature) across latitude in the subcanopy. The root-pressure hypothesis also may provide a functional explanation because low-statured plants are more susceptible to root-pressure damage (Feild et al., 2005). In the first follow-up study to Bailey and Sinnott (1916), Royer et al. (2012) found strong support for the hypothesis: leaf margins in herbaceous species are not sensitive to MAT (n = 235 species; slope = -0.018; P = 0.40; based on logistic regression), trees are highly sensitive (n = 878; slope = 0.22; $P < 0.001$), and shrubs intermediate (n = 582; slope = 0.06; $P < 0.001$). The confounding effect of herbs largely can be ignored because herbs rarely enter the fossil record (e.g., Spicer, 1981), but the difference in sensitivity between shrubs and trees is more problematic because distinguishing between these growth forms in fossils can be difficult. The fact that most extant calibrations for leaf-climate methods include both shrubs and trees helps, because the statistical error for MAT estimation includes some component of the growth-form effect.

Seasonality

Axelrod and Bailey (1969) proposed that mean annual range in temperature (MART), not MAT, is a primary driver controlling leaf-margin type. Because the proportion of untoothed species can be linked to the length of season when growth is possible (Royer and Wilf, 2006), this proposal warrants scrutiny. For example, if two sites have different MATs but experience no frost or drought, how will their percentages of untoothed species compare?

Most field data do not support Axelrod and Bailey's (1969) hypothesis (Wolfe, 1971, 1979, 1993). For example, in the 144 site calibration of Wolfe (1995), percent untoothed correlates significantly to MAT, even after accounting for MART with partial correlation (r = 0.81, $P < 0.001$), but it does not correlate at all to MART after accounting for MAT (r = -0.001, P = 0.99). Wolfe's data come mostly from northern temperate regions, whereas Peppe et al. (2011) include more sites from Australasia and South America, allowing additional testing of geographical differences. For their 69 sites that include leaf-habit information, the partial correlation between MART and percent untoothed is significant (r = -0.40, $P < 0.001$; controlling for MAT). However, in these same data, MART correlates significantly with leaf habit (r = -0.75, $P < 0.001$), and if both MAT and leaf habit are controlled for, the partial correlation between MART and percent untoothed reverses slope and is not significant (r = 0.16, P = 0.20).

Together, these point to only a limited role for MART. The same holds true for other growing-season-related variables, such as growing season length, growing degree-days, and growing season degree-days: they correlate more weakly with percent untoothed than does MAT (Royer et al., 2005; Peppe et al., 2011). Although not fully understood, MAT is capturing information important for teeth, perhaps during times outside the growing season, that growing-season variables simply do not.

Nutrient availability

There is some evidence that untoothed species are more common in nutrient-poor soils than fertile soils, but this has been studied only in eastern Australia (Webb, 1968; Greenwood et al., 2004). This effect is best linked to the early season gas-exchange hypothesis because nutrient-poor soils will select against fast-return specialists (vis-à-vis the leaf economics spectrum) (Wright et al., 2001; see also Jordan, 2011).

Phylogenetic history

A fundamental assumption with all physiognomic-based paleoclimate methods is their independence from phylogenetic factors. In other words, a given climate (and sufficient time) will inevitably select for the same leaf physiognomy, regardless of species composition. If correct, then fossils do not need to be formally identified and placed in an evolutionary framework (e.g., Bailey and Sinnott, 1916; Wolfe, 1971). Indeed, all that is required is that fossil specimens are confidently sorted into morphospecies. This contrasts with nearest living relative approaches (e.g., palms as a frost-free indicator), which fundamentally hinge on phylogenetic placement.

How robust is this assumption? At one extreme, even the most ardent supporter of physiognomic leaf-climate methods probably would not claim that the geographic distribution of toothed margins is completely independent of phylogenetic history. While there are many examples of genera that contain both toothed and untoothed species (e.g., *Ilex*, *Prunus*, *Quercus*, *Rhododendron*, *Rhus*, *Salix*, *Vaccinium*), many families—each spanning a large MAT range—are overwhelmingly toothed (e.g., Adoxaceae, Betulaceae, Juglandaceae, Vitaceae) or untoothed (e.g., Cornaceae, Fabaceae, Lauraceae, Myrtaceae, Rubiaceae). Clearly, phylogenetic history has some influence (Jordan, 1997, 2011). The key question is whether the influence is important enough to warrant modification (or discarding) of existing leaf-climate methods.

Little et al. (2010) quantified the influence of evolutionary history for plants at 17 North and Central American sites that previously were used to calibrate leaf-climate relationships (Royer et al., 2005). They observed a significant phylogenetic signal in the relationship between margin type and MAT ($n = 569$, $K = 0.51$, $P < 0.001$), a result consistent with other studies (Jones et al., 2009; Burnham and Tonkovich, 2011; Hinojosa et al., 2011). Moreover, a phylogenetic generalized least squares analysis confirms that including phylogenetic information improves the ability of MAT to predict margin type, but at the expense of a flatter regression slope and wider uncertainty bands. A significant signal between margin type and MAT remains, but it is diminished relative to the non-phylogenetic case.

Little et al. (2010) conclude that climate and evolutionary history jointly control margin type, and that physiognomic methods need to incorporate phylogenetic information. The methodology for this is not immediately obvious because phylogenetic analyses are species-based, while leaf-margin analysis is site-based.

Precision of leaf-margin analysis

Most fossil applications of leaf-margin analysis use the East Asian calibration of Wolfe (1979), which has a standard error of at least ±2°C (Wilf, 1997; Miller et al., 2006); this is a minimum error because the component related to the binomial sampling distribution is dependent on the percent untoothed value. The more globally distributed calibration of Peppe et al. (2011) indicates a larger error of at least ±5°C (see also Jordan, 1997, 2011). The loss of precision in the global model probably reflects a greater contribution by confounding variables. In other words, the East Asian calibration captures a wide range in MAT, but not in other factors that also impact leaf teeth.

There has been a push in the paleoclimate community to use calibrations from the same regions as the fossil sites (e.g., Jacobs and Deino, 1996; Gregory-Wodzicki, 2000; Kowalski, 2002; Hinojosa et al., 2006; Uhl et al., 2007; Su et al., 2010). The tacit assumption with this strategy is that it reduces the error related to evolutionary history. This is problematic not only because regional species composition changes over time, but because no accommodation for other confounding factors are made (Jordan, 2011; Peppe et al., 2011). Following the call of Little et al. (2010), quantitative corrections for these factors are needed. For example, leaf mass per area, as already discussed, is linked to both leaf thickness and leaf habit and can be inferred from petiole dimensions (Royer et al., 2007). Alternatively, more robust and complete assessments of model error are needed. Presently, a minimum error of ±5°C should be assumed. An exception to this would be a sequence of fossil sites from one region spanning a short interval of time where confounding factors are presumably less influential; in this case, and if using an appropriate regional calibration, errors associated with the relative change in MAT should be closer to ±2°C.

LEAF-AREA ANALYSIS

Leaf size typically scales with available moisture (Givnish, 1984, and references therein; Wolfe, 1993; Richards, 1996; Wilf et al., 1998; Jacobs, 1999; Malhado et al., 2009; see also Table 1). Larger leaves will be warmer than smaller leaves because of their thicker boundary layer (e.g., Raschke, 1960; Vogel, 1970; Gates, 1980). Givnish and colleagues (Givnish and Vermeij, 1976; Givnish, 1978, 1979) proposed that because warmer leaf temperatures increase transpiration more dramatically than photosynthesis, large leaves become prohibitively expensive in dry environments. Alternatively, Scoffoni et al. (2011) demonstrated that because small leaves tend to have a higher density of major veins (due to allometric scaling), they should be less vulnerable to hydraulic disruption (e.g., embolisms). As a result, small leaves better tolerate drought.

Leaf-area analysis harnesses these relationships to reconstruct mean annual precipitation (MAP) from site-mean leaf area (Wilf et al., 1998). Estimates from leaf-area analysis tend not to be very precise, ranging from approximately ±50 cm (Wilf et al., 1998) to ±100 cm or more (Peppe et al., 2011). Multiple reasons underlie this imprecision. First, at many sites, MAP may reflect water availability poorly, which can be affected by temperature, soil and groundwater characteristics, wind speed, etc. As discussed above, a relatively weak coordination between MAP and water availability probably explains the poor correlation between MAP and the percentage of untoothed species. Temperature in particular may be an important confounding factor because it directly affects both Givnish's cost-benefit model and the vein-density hypothesis. The presence of comparatively small leaves at some warm but wet sites bears out this prediction (Peppe et al., 2011). However, except in Australasia (Webb, 1968; Greenwood, 1992; Peppe et al., 2011; Carpenter et al., 2012) the overall relationship between MAT and leaf size is weak, even after accounting for the covariation with MAP (Peppe et al., 2011). Also, small leaves are common at infertile sites, irrespective of water availability (e.g., Webb, 1968; Givnish, 1978, 1984). According to the cost-benefit model, this is caused by a reduction in photosynthetic capacity, which diminishes the photosynthetic benefit of any warming due to larger leaves.

Most users of leaf-area analysis urge caution in its interpretation (e.g., Wilf et al., 1998; Burnham et al., 2005; Peppe et al., 2011). At a minimum, estimates should be compared with other rainfall proxies. One silver lining, at least relative to leaf-margin analysis, is that evolutionary history appears to affect leaf size less than margin type (Jones et al., 2009; Little et al., 2010).

MULTIVARIATE APPROACHES

CLAMP

It is clear that multiple factors affect margin type and leaf size, not just MAT and MAP. Conversely, MAT and MAP affect many physiognomic characters, not just margin type and leaf size (e.g., Davis and Taylor, 1980). In principle, estimating MAT and MAP from multiple characters should be more robust than from single characters. It is in this spirit that Jack Wolfe developed CLAMP (climate leaf analysis multivariate program) (Wolfe, 1990, 1993, 1995; Spicer, 2012; see also Table 1). CLAMP uses 31 leaf characters related to margin type, size, base shape, apex shape, and overall shape. Site means of the characters are calculated and analyzed in a principle-axes framework (canonical correspondence analysis is the most popular) to estimate MAT, humidity, enthalpy, and variables related to thermal and moisture seasonality.

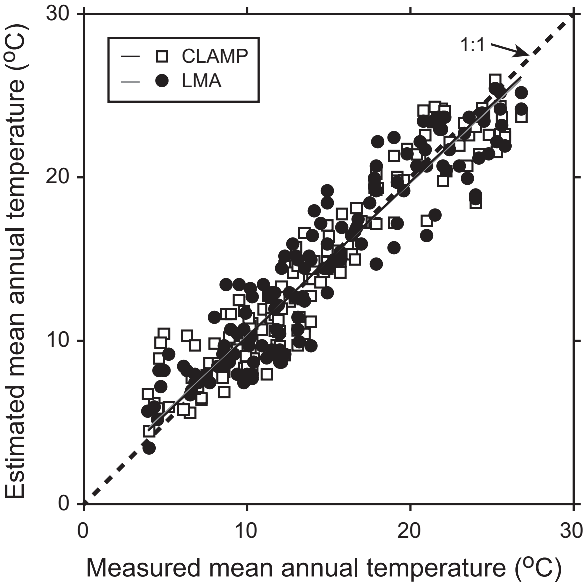

FIGURE *1*.—Comparison between CLAMP and leaf-margin analysis (LMA) in estimating mean annual temperature at 144 extant sites. Tested sites come from the CLAMP calibration (Wolfe, 1993; Spicer, 2012). Both CLAMP and LMA are calibrated directly to the 144 sites; regression equation for LMA: mean annual temperature = 0.204 × (percent untoothed) + 4.6. Dashed line is 1:1 line. Standardized major axes for both approaches are very similar (CLAMP: slope = 0.95; r^2 = 0.90; LMA: slope = 0.93; r^2 = 0.87; P = 0.72 for test of common slope).

Despite the use of multiple variables, estimates of MAT and MAP from CLAMP are no better than those from leaf-margin analysis and leaf-area analysis (Wilf, 1997; Wiemann et al., 1998; Wilf et al., 1998, 1999; Jacobs, 1999; Gregory-Wodzicki, 2000; Kowalski, 2002; Kowalski and Dilcher, 2003; Royer et al., 2005; Dilcher et al., 2009; Smith et al., 2009). The equivalence between methods is seen by comparing estimates of MAT for 144 extent sites used in the CLAMP calibration (Figure 1). Both methods show similar scatter relative to actual MAT (P = 0.95 for paired-sample t-test), implying that CLAMP shares the same minimum error as leaf-margin analysis (±5°C). The lack of improvement with CLAMP probably is related to imprecise definitions of some character states, quantitative biases associated with the leaf-size categories, the coarseness of a category-based system, lack of functional links between some character states and climate, and using canonical correspondence analysis in a predictive framework (Jordan, 1997; Wilf, 1997; Wiemann et al., 1998; Wilf et al., 1998, 1999; Green, 2006; Peppe et al., 2010).

Digital leaf physiognomy

CLAMP workers have partly addressed some of these concerns (Spicer et al., 2004, 2005, 2009, 2011; Spicer and Yang, 2010; Teodoridis et al., 2010; Jacques et al., 2011), but many are not resolvable given the framework of CLAMP (e.g., reliance on categorical variables, inclusion of characters not functionally linked to climate). Recognizing these deficiencies, Huff et al. (2003) proposed a new leaf-climate approach called digital leaf physiognomy (see Table 1), which preserves the key advantage of CLAMP—that it is multivariate—while avoiding or minimizing its deficiencies. In digital leaf physiognomy, variables related to leaf size, tooth size and number, and leaf dissection are measured quantitatively from digital images. Most variables are continuous and are measured by computer algorithm; as a result, measurements are more accurate and repeatable than in CLAMP (e.g., Peppe et al., 2010). Computing power has expanded immensely in the two decades since CLAMP was first developed, and there are now many software packages to measure leaf physiognomy (e.g., Abramoff et al., 2004; Bakr, 2005; Krieger et al., 2007; Bylesjö et al., 2008; Weight et al., 2008; Backhaus et al., 2010). Because most characters in digital leaf physiognomy are continuous, they should have more predictive power than their categorical counterparts. To provide one extreme example, leaf-margin analysis and CLAMP cannot readily distinguish between a leaf with one tooth or 100 teeth, but digital leaf physiognomy can.

A second key advance in digital leaf physiognomy is that most variables can be functionally linked to climate. For example, any hypothesis that provides a mechanistic basis for leaf-margin analysis would likely predict that tooth size and abundance increases in colder climates. That is, not only are toothed species more proportionately abundant in cold climates, but their teeth are larger and more frequent. Both qualitative (Bailey and Sinnott, 1916; Wolfe, 1993) and quantitative analyses (Huff et al., 2003; Royer et al., 2005; Peppe et al., 2011) support this view. This covariation between tooth characters and MAT sometimes is observed even within species (Royer et al., 2005, 2008, 2009b). For *Acer rubrum* (red maple), a reciprocal garden experiment demonstrated that tooth traits can even respond plastically to a change in MAT (Figure 2) (Royer et al., 2009b). This result highlights that not only are tooth size and number functionally linked to climate, but they can respond quickly to climate change, a real advantage for paleobotanists applying digital leaf physiognomy to fossils.

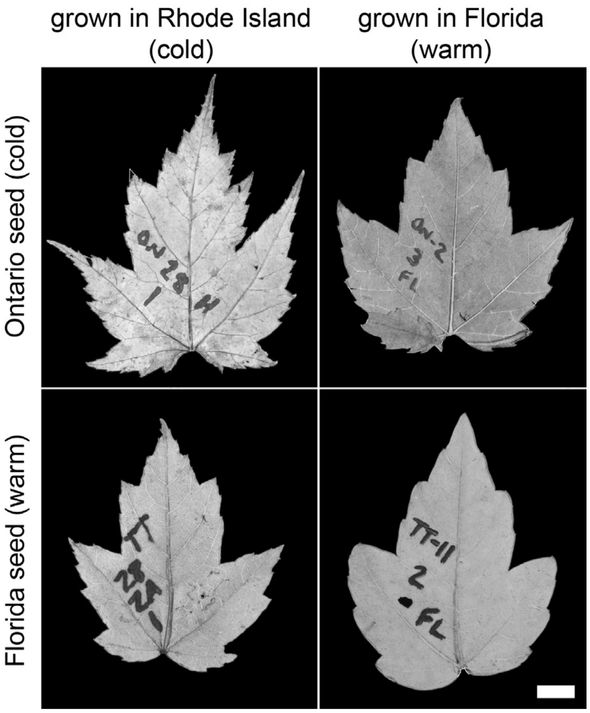

FIGURE 2.—Representative leaves of *Acer rubrum* (red maple) from a reciprocal common garden experiment. Leaves from each row share the same seed source while leaves from each column share the same growth environment. Leaves sharing the same seed source are less toothy when grown in a warmer environment (Florida), indicating that variables used by digital leaf physiognomy show phenotypic plasticity. Scale bar = 1 cm. Images modified from Royer et al. (2009b).

Calibration of digital leaf physiognomy reveals a reduction in the standard error of ~1°C relative to leaf-margin analysis (Peppe et al., 2011); this calibration only uses variables that can be measured on leaf fragments (e.g., number of teeth:leaf perimeter ratio). For MAP, the improvement relative to leaf-area analysis is more modest. More importantly, estimates of MAT for fossil floras, and to a more limited degree, MAP, appear substantially more accurate using digital

TABLE *1*.—A selection of studies that calibrate leaf-climate methods with extant vegetation. LMA = leaf-margin analysis; LAA = leaf-area analysis; CLAMP = climate leaf analysis multivariate program. Leaf size information from CLAMP is not appropriate for LAA because of its consistent underprediction of leaf area (Peppe et al., 2010). For more complete information on CLAMP and digital leaf physiognomy sites, consult Spicer (2011) and Royer and Peppe (2012), respectively. [a]Includes herbaceous taxa.

Region	Study
North America	LMA: Wolfe, 1993; Adams et al., 2008; Peppe et al., 2011 LAA: Peppe et al., 2011 CLAMP: Wolfe, 1993 Digital leaf physiognomy: Peppe et al., 2011
Central America	LMA: Wolfe, 1993; Wilf, 1997; Peppe et al., 2011 LAA: Wilf, 1997; Peppe et al., 2011 Digital leaf physiognomy: Peppe et al., 2011
South America	LMA: Halloy and Mark, 1996[a]; Wilf, 1997; Kowalski, 2002; Aizen and Ezcurra, 2008; Hinojosa et al., 2011; Peppe et al., 2011 LAA: Halloy and Mark, 1996[a]; Wilf et al., 1998; Kowalski, 2002; Peppe et al., 2011 CLAMP: Kowalski, 2002; Hinojosa et al., 2006 Digital leaf physiognomy: Peppe et al., 2011
Asia	LMA: Wolfe, 1979, 1993; Su et al., 2010; Peppe et al., 2011 LAA: Peppe et al., 2011 CLAMP: Wolfe, 1993; Spicer et al., 2004; Jacques et al., 2011 Digital leaf physiognomy: Peppe et al., 2011
Europe	LMA: Halloy and Mark, 1996[a]; Traiser et al., 2005; Peppe et al., 2011 LAA: Halloy and Mark, 1996[a]; Peppe et al., 2011 Digital leaf physiognomy: Peppe et al., 2011
Africa	LMA: Midgley et al., 1995; Steart et al., 2010 LAA: Wilf et al., 1998; Jacobs, 1999 CLAMP: Steart et al., 2010
Australasia	LMA: Halloy and Mark, 1996[a]; Jordan, 1997; Greenwood et al., 2004 LAA: Halloy and Mark, 1996[a] CLAMP: Wolfe, 1993; Stranks and England, 1997 Digital leaf physiognomy: Peppe et al., 2011

leaf physiognomy than with univariate techniques (see section on "fossil applications").

Factors that confound CLAMP and digital leaf physiognomy

Although CLAMP and digital leaf physiognomy are multivariate methods, margin type and leaf size still explain most of the variance in MAT and MAP (Wolfe, 1993; Peppe et al., 2011). As such, factors that confound leaf-margin analysis and leaf-area analysis also confound CLAMP and digital leaf physiognomy. Compared to the presence/absence of teeth, the additional tooth-related characters in digital leaf physiognomy are equally affected by leaf habit (Peppe et al., 2011), but less so by local water availability (Royer et al., 2005; Peppe et al., 2011). As with leaf-margin analysis, the correlations of physiognomic characters to growing season indices (growing season length, growing degree-days, etc.) are no better than with MAT, again suggesting a strong functional link between physiognomy and MAT. All trait-MAT relationships contain a significant phylogenetic signal, but the new traits in digital leaf physiognomy generally are less affected than is margin type (Little et al., 2010). Together, these results suggest that digital leaf physiognomy should be somewhat less sensitive to phylogenetic and water availability factors.

A change in the concentration of atmospheric CO_2 potentially could affect leaf physiognomy because it would alter the balance of carbon uptake and water loss (e.g., Givnish, 1979). This may be particularly true with leaf teeth if the early season gas-exchange hypothesis is valid. However, based on growth-chamber experiments, CLAMP characters appear largely insensitive to CO_2 (Gregory, 1996). Thomas and Bazzaz (1996) found an increase in leaf perimeter/area at high CO_2, but they used the heteroblastic herb *Taraxacum officinale* (dandelion) that may not be representative of most species. The CO_2 sensitivity of characters important for digital leaf physiognomy (tooth size, tooth number) is currently unknown.

FOSSIL APPLICATIONS

Taphonomic considerations

All physiognomic methods are affected by taphonomic processes. Recognition that fossil sites capture the original species composition of the immediate vicinity reasonably well, especially in swamp and overbank depositional settings (Spicer, 1981; Spicer and Wolfe, 1987; Burnham, 1989, 1993; Burnham et al., 1992; Greenwood, 1992, 2005b; Steart et al., 2006; Dilcher et al., 2009; Ricardi-Branco et al., 2009), boosts confidence that leaf-climate methods are providing meaningful climate estimates.

Fossil leaves are typically fragmented. Royer et al. (2005) demonstrated that errors with leaf-margin analysis increase by over 2°C when the distal half of leaves are removed. CLAMP and digital leaf physiognomy appear less sensitive to this effect (Wolfe, 1993; Royer et al., 2005), probably because multiple characters spread the risk of information loss.

Bailey and Sinnott (1916) speculated that the correlation between margin type and MAT should be strongest when based on individual trees, not species, because rare species would be less influential. Their premise has never been tested directly, but whatever the outcome, a specimen-based approach has limited value in fossil systems due to taphonomic factors. Most importantly, leaf litter reflects species abundance poorly because of variation in leaf production (e.g., evergreen vs. deciduous; large vs. small tree; tree with large vs. small leaves) and litter decomposition rates (e.g., evergreen vs. deciduous) (Spicer and Wolfe, 1987; Greenwood, 1992; Steart et al., 2006). As a result, leaf-margin analysis based on individual leaf counts from litter samples is not robust (Greenwood, 1992; Uhl et al., 2003).

Wolfe (1971) suggested that at least 30 species at a site are necessary to calculate a reliable MAT estimate; in practice, most paleobotanists adopt a benchmark between 20 and 30. However, for all but the most species-poor floras, the total number of species is less critical than the percent recovery. In diverse, extant floras with hundreds of species, 50 or more of the most-common species are necessary to calculate a reasonable MAT estimate (Burnham et al., 2001, 2005). In diverse fossil floras, sampling >30 species is advisable.

Comparison of paleoclimate estimates across methods

Numerous studies have compared paleoclimate estimates between physiognomic methods at single fossil sites, but there has been little effort to synthesize across studies. Figure 3 summarizes 180 MAT comparisons from 108 fossil sites and 27 studies. Most comparisons are between leaf margin-analysis and CLAMP (n = 84; Figure 3A, B), with a more minor component from digital leaf physiognomy (n = 10; Figure 3C). Additionally, and serving as an important cross-check, are estimates from nearest living relatives (n = 80) and isotopes (n = 6). There are no striking differences between leaf-margin analysis and CLAMP; nearly all estimates fall within a 10°C window (gray bands in Figure 3), which represents a reasonable minimum standard error for both methods (±5°C; see "precision of leaf-margin analysis" subsection).

Multiple studies have reported warmer MAT estimates based on nearest living relatives than with physiognomic approaches, and have suggested that physiognomic methods have a cool bias (e.g., Liang et al., 2003; but see Grimm and Denk, 2012, for a critique of the nearest living relative approach). My synthesis detects examples of this discrepancy (e.g., data plotting above the gray bands in Figures 3A, B), but the majority of comparisons fall within the 10°C band. In fact, some physiognomic estimates are warmer than that from nearest living relatives; this is true more for leaf-margin analysis than for CLAMP (27% vs. 17% of comparisons). Thus, there is a propensity for nearest living relative estimates to be warmer, but this is not overwhelmingly the case. A careful study of sites with the biggest differential between estimates may reveal the underlying cause.

Digital leaf physiognomy is the newest method, and has been applied to fossils the least often. Overall, the scatter in MAT comparisons is similar to that seen in other methods (compare Figure 3C to 3A, B). However, Peppe et al. (2011) argued that in light of other geological evidence, digital leaf physiognomy is considerably more accurate than leaf-margin analysis. For example, an estimate of 21.6°C for the late Cretaceous Fox

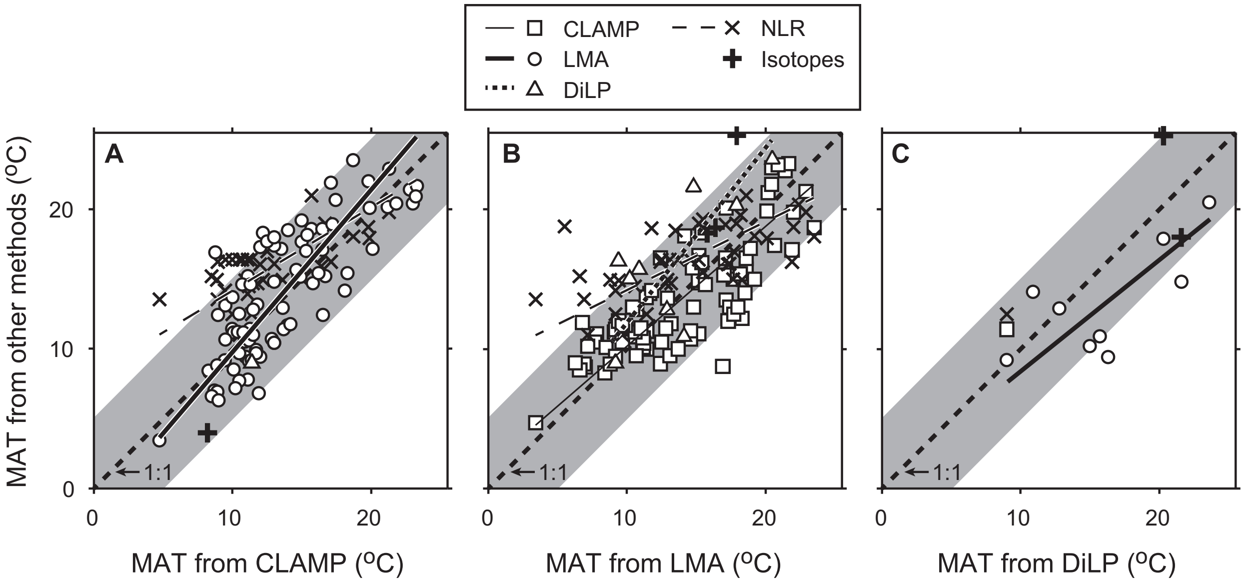

FIGURE 3.—Comparison across methods in estimating mean annual temperature (MAT) from fossil sites. Each panel compares MAT from a physiognomic method to other methods for the same sites. Some information is repeated but with the axes reversed, for example circles in panel A and squares in panel B. Gray envelope captures ±5 °C relative to the x-axis variable; dashed line is 1:1 line. CLAMP = climate leaf analysis multivariate program; LMA = leaf-margin analysis; DiLP = digital leaf physiognomy; NLR = nearest living relatives. Standardized major axes for all correlations composed of at least five sites are shown. CLAMP vs. LMA: slope = 1.16; r^2 = 0.65; CLAMP vs. NLR: slope = 0.60; r^2 = 0.43; LMA vs. CLAMP: slope = 0.86; r^2 = 0.65; LMA vs. DiLP: slope = 1.25; r^2 = 0.52; LMA vs. NLR: slope = 0.49; r^2 = 0.40; DiLP vs. LMA: slope = 0.80; r^2 = 0.52. Sources: Wolfe, 1960, 1994; Axelrod, 1966; MacGinitie, 1969, 1974; Wing and Greenwood, 1993; Greenwood and Wing, 1995; Davies-Vollum, 1997; Wolfe et al., 1998; Utescher et al., 2000; Carpenter et al., 2003; Kennedy, 2003; Liang et al., 2003; Fricke and Wing, 2004; Greenwood et al., 2005, 2010; Kvacek, 2007; Martinetto et al., 2007; Uhl et al., 2007; Zidianakis et al., 2007; Boyle et al., 2008; Smith et al., 2009; Teodoridis et al., 2010; Grein et al., 2011; Jacques et al., 2011; Peppe et al., 2011; Sunderlin et al., 2011.

Hills flora (North Dakota, USA) is close to the neighboring, isotope-based estimate of 18°C from Carpenter et al. (2003), and considerably warmer than the 14.8°C estimate from leaf-margin analysis. Similarly, estimates for three chronostratigraphic zones in the Paleocene Williston Basin flora (North Dakota, USA) are warmer than estimates from leaf-margin analysis (15.0–16.3°C vs. 9.4–10.9°C); in this case, a 10°C MAT for a mid-latitude site is incompatible with a coeval deep-sea temperature of 10°C and the presence of palms and crocodiles in the same basin (Peppe et al., 2011). The principle reason why digital leaf physiognomy yields warmer estimates at these sites is because many of the toothed species contain very few, reduced teeth. The incorporation of this additional information serves to warm MAT estimates relative to leaf-margin analysis. These case studies champion the value of using this new approach.

RECOMMENDATIONS

Teasing apart the relative roles of phylogenetic history, leaf habit, and leaf thickness is a high priority. These factors (when significant) need to be incorporated into leaf-climate methods. A proxy for leaf mass per area, which correlates strongly with thickness and, to a more limited degree, leaf habit, is available (Royer et al., 2007) and may improve the precision of physiognomic-based climate estimates (Royer et al., 2012; see also Jordan 2011). Incorporating phylogenetic information will be more difficult because leaf-climate methods are site-based, not species-based. Nevertheless, there may be room to develop solutions based on a modified phylogenetic least-squares approach or a hybrid physiognomic-nearest living relative approach.

An example that underscores the need for this additional information is the Southern Hemisphere, which has long been noted to contain a higher fraction of untoothed species at a given MAT (Bailey and Sinnott, 1916; Wolfe, 1971, 1979; Greenwood, 1992; Halloy and Mark, 1996; Jordan, 1997; Stranks and England, 1997; Greenwood et al., 2004; Hinojosa et al., 2006, 2011; Aizen and Ezcurra, 2008; Royer et al., 2009a; Steart et al., 2010). A similar offset is seen for many digital leaf physiognomy characters (Peppe et al., 2011). The reasons for this hemispheric divide are not clear. The leaf physiognomy of Southern Hemisphere species, especially in Australia, New Zealand, southern Africa, and southern South America, may be reflecting their Gondwanan heritage. On the other hand, many Southern Hemisphere floras are dominated by evergreen species with thick leaves. In the Peppe et al. (2011) data set, 98% of species in Southern Hemisphere sites are evergreen versus 25% at other sites, and site mean leaf habit correlates significantly with margin type, even after controlling for MAT ($r^2 = 0.54$, $n = 69$, $P < 0.001$). It is critical to disentangle how these factors affect leaf physiognomy (including their potential interaction) so that paleoclimate reconstructions can be updated.

An implicit assumption with current leaf-climate methods is that all teeth (with the exception of spines) relate to climate in the same way. Is it true? For example, do hydathodal (fixed pores on leaf surfaces), non-hydathodal, and nectary-bearing teeth all respond similarly to climate? If there are differences, can the different tooth types be reliably identified in fossils (e.g., glandular vs. non-glandular)? Complementing this issue, recent genetic work on tooth development (Tsukaya and Uchimiya, 1997; Groot and Meicenheimer, 2000; Nikovics et al., 2006; Reinhardt et al., 2007; Blein et al., 2008) may help illuminate the fundamental controls over margin type.

Physiognomic methods for reconstructing rainfall are weak and estimates should be viewed with caution. Improved methods would represent a key advance, but the strategy for achieving this is presently unclear.

Finally, all current methods are calibrated to woody flowering plants exclusive of monocots. Amongst extinct groups, Glasspool et al. (2004) applied existing CLAMP and leaf-margin analysis calibrations to Permian gigantopterids and calculated plausible climate estimates. However, given the lack of gigantopterid-specific calibrations, these estimates are highly provisional. Ferns can have very intricate leaf physiognomy, but almost nothing is known about how their physiognomy may relate to climate.

In this paper, I have focused primarily on the challenges facing physiognomic leaf-climate methods, but it is important to bear in mind the broader context of these methods: they have been applied to fossil assemblages for almost a century, and they remain one of the most robust and common ways to reconstruct terrestrial paleoclimates. Successful engagement with their current challenges will help to ensure their continued use.

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