Climate, leaves, and the legacy of two giants

Paleobotanical novices have no simple script to follow for using angiosperm fossil floras to test climatic hypotheses in the geological record. Many methods and approaches have been used, none of which can be verified with iron-clad independent methods. This is the current nature of the field. In this issue of New Phytologist, Peppe et al. (pp. 724–739) advance the latest cycle of recalibration of taxon-free leaf-climate methodology, using an expanded set of modern sites. The research is energized by nearly 100 calibration sites and the adoption of ‘digital leaf physiognomy’. Thus, three upgrades have occurred: an analytic method for data capture, a geographic expansion, and a move to multiple linear regression. The global calibration, compared to previous applications of digital leaf physiognomy (Royer et al., 2005), was achieved by adding some of Jack A. Wolfe’s (1993) worldwide sites to earlier datasets, plus c. 30 new sites collected by the authors.

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For almost a century, the most common means for reconstructing Cenozoic paleotemperature was via leaf fossils from clastic sediments. The simple correlation between the proportion of species with nonentire (toothed/serrated) margins in a fossil flora and the mean annual temperature (MAT), was used as an estimate of paleo-MAT. Angiosperm paleobotanists were in the driver’s seat with respect to estimates of paleoaltitude (via temperature lapse rates with elevation), paleogeographic reconstructions, and predicted response to climate change. However, as methods of deriving temperatures from oxygen isotopes, mammal and reptile climatic limitations, paleo-circulation patterns, and even phytoplankton distributions were refined and re-calibrated, discrepancies showed up between the MAT predicted by paleobotanists and other, leaf-margin independent, evidence. Previously complacent to use established techniques to reconstruct paleoclimate, paleobotanists sought to reconcile the discrepancies by refining the paleobotanical methods.

Cycles of improved approximations by calibration → complacency → reinvestigation → recalibration, etc. have been in motion since Wolfe (1978) first quantified the method of taxon-free temperature estimation in the 1970s. In fact, his first data were based on those from a half-century earlier: those of Bailey & Sinnott (1915, 1916). Initially, Wolfe’s intention was to free paleoclimate estimates from a dependency on taxonomic identification of each leaf, which could be only as accurate as the individual making the taxonomic determination. Motivated by frustration with small samples and single characters, Wolfe (1993, 1995) subsequently created the first multi-site, multi-character database for evaluating morphological correlation of leaves with climate. Both database and analysis are referred to as CLAMP (Climate Leaf Analysis Multivariate Program). The assumption was that, because leaves are under intense selection to perform optimally, all dicotyledonous angiosperm species from a similar climate regime will tend to converge on a unified solution to the triple problems of capturing sunlight, regulating temperature, and conserving water.

Wolfe acknowledged that leaves of some species may not be easily molded by their environment (Hickey & Wolfe, 1975; Wolfe, 1993). Instead, he specified that large numbers of woody dicot species (> 20) be used to calibrate models and to reconstruct paleotemperatures (Wolfe, 1995). However, the method was so alluringly simple, that some researchers, including Wolfe, were tempted to reconstruct paleotemperature based on small numbers of species: the species available in fossil floras were all they had! Controversy continued over whether the best reconstructions of paleoclimate could be achieved with a combination of leaf characters, or whether a univariate method was sufficient. The large number of subjectively scored characters in the CLAMP database was proposed as one reason that the simple character of nonentire vs entire leaf margins predicted MAT with greater accuracy than the combination of characters of CLAMP. In addition, when global CLAMP data were tested against regional data, be they local, hemispheric, or continental, the regional correlations were more precise than global correlations (e.g. Teodoridis et al., 2011). In this issue of New Phytologist, Peppe et al. attribute high regional correlations to phylogenetic history, although this might well be due to ecological similarity of available habitats. Few researchers have sought to change the basic approach: correlation of leaf characters in modern climate space is used to predict paleotemperature using fossil leaves (Spicer et al., 2009). When estimates from fossil floras do not agree entirely, all estimates are reported (e.g. Roth-Nebelsick et al., 2004).

A novel approach was employed to solve the problem of subjectively-scored character states (Huff et al., 2003; Royer et al., 2005). By digitally capturing the shape and size of leaves from geographic areas distinct from those originally used by Wolfe, algorithms of shape capture programs could be tested and applied to characters more objectively. ‘Digital leaf physiognomy’ was capable of placing different
leaf tooth attributes on a continuum, rather than leaving them to the scoring decisions that a weary researcher might make. Further, this approach highlighted the presumed physiological advantages that specific traits conferred and included only those traits. For example subtle, irregularly-spaced teeth may serve a leaf less effectively under transpirational dynamics than large, regular teeth, and accordingly they would be scored differently. Reducing the total number of characters scored, combined with standardizing the measurements, should have made it possible to create credible paleotemperature estimates. However, the differences between nonleaf generated paleotemperatures (Markwick, 1998; Zachos et al., 2001; Fricke & Wing, 2004) and those from leaves have not been erased.

Similar efforts to reconstruct precipitation from fossil leaves have run parallel to MAT methods (e.g. Wilf, 1997). Predictions of precipitation from fossil leaves have been more readily acknowledged as approximations, perhaps because of the clear tradeoffs for leaves in investments among photosynthesis, herbivore defense, desiccation resistance, and leaf construction. Models to approach the tradeoffs through the leaf economics spectrum have been proposed (Royer et al., 2007), with a surprising correlation between the petiole width of a leaf and the leaf mass per area ($M_A$). This however did not solve the precipitation conundrum.

The oldest method for climate reconstruction from leaves is the ‘nearest-living relative’ method and it has also been upgraded and quantified to create comparable terminology and methods (Mosbrugger & Utescher, 1997; Roth-Nebelsick et al., 2004). One drawback is that the method is slow and difficult because each fossil species must be confidently identified, which is tricky without attachment of leaves to stems, details of surface features like glands or hairs, or presence of reproductive parts. Another is that the method is rooted in the concept that species of closely related plant lineages share climatic tolerances. While this might be true, it is also true that speciation often occurs by the very separation in space that a climatic barrier would provide. Most angiosperm paleobotanists are, in practice, working with a combination of methodologies, using one to illuminate the others. For example, the freezing tolerances of palm species are well-defined, with only a few species capable of surviving freezing temperatures (Larcher & Winter, 1981). The presence of a palm in a fossil flora immediately suggests a relatively high mean annual temperature and a relatively long growing season (Walther et al., 2007). This type of observation is added to a taxon-free analysis to exclude extremes.

These methods stand on the shoulders of Jack A. Wolfe, an individual with the foresight to voucher his intensive worldwide collections, at a time when such vouchering was only conceivable for herbarium-quality specimens. At the same time that Wolfe gathered data on the relationship between leaf form and climate, Alwyn H. Gentry was
amassing data on woody plant density and species composition worldwide. Gentry censused and collected modern plant biodiversity data from 226 sites in temperate and tropical forests using 0.1-ha transects. Had communication between these two relentless, empirical botanists occurred, what discussions might have ensued? To our knowledge, they were not in communication, even though they were both known to haunt the world’s herbaria. Gentry’s phenomenal drive to capture the world’s plant biodiversity ran parallel to Wolfe’s search for the perfect correlation between leaf form and climate. Both were deeply involved in angiosperm phylogenetics, although neither made phylogeny the centerpiece of their work (Hickey & Wolfe, 1975; Gentry, 1990). Three sites from Gentry’s data made it into the data set used by Peppe et al., an addition that seems long overdue. However, the data used by Peppe et al. include 17 sites with 20 or fewer species, which could have been exchanged for more of the sites from Gentry’s data (Phillips & Miller, 2002).

Another splash was made recently by Little et al. (2010), who demonstrated that climate-leaf analysis can be influenced by ‘nonrandom phylogenetic signal’. Their work, using explicitly phylogenetic models, demonstrates that the ancestry of plant species influences the presence and abundance of teeth. Similarly, significant phylogenetic effects on leaf veins were found by Walls (2011), almost simultaneously. Expectations based on adaptive convergence would predict exactly the opposite pattern. Notable among the sites used to evaluate the phylogenetic signal, but more importantly will suggest specific means for reducing or removing the nonenvironmental signal.

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References


Letters

Can publication bias affect ecological research? A case study on soil respiration under elevated CO2

Literature surveys are a prerequisite to enhance scientific knowledge as they allow us to separate systemic from idiosyncratic mechanisms and processes, and thus provide insight at a higher level than can be gained from individual studies. In ecological research, statistical synthesis of literature surveys is a prerequisite to enhance scientific knowledge as they allow us to separate systemic from idiosyncratic mechanisms and processes, and thus provide insight at a higher level than can be gained from individual studies. In ecological research, statistical synthesis of literature surveys is a prerequisite to enhance scientific knowledge.

References


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