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Deriving temperature estimates from Southern Hemisphere leaves

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ABSTRACT

The percentage of woody dicots with entire-margined leaves in a flora is known to be positively correlated with mean annual temperature (Leaf Margin Analysis — LMA) but this relationship is not globally uniform. In particular the floras of Australia and New Zealand have been regarded as displaying a different physiognomic relationship to climate than floras seen in the Northern Hemisphere. This difference is more marked in New Zealand where the LMA relationship appears entirely absent. Here we amass data for both Northern and Southern hemispheres using standard protocols and show that regional variations in the leaf margin–mean annual temperature relationship are real but become less significant when other characters are included. Even New Zealand falls into line and most of the mean annual temperature signal in New Zealand floras is encoded in non-margin features. We introduce a new CLAMP (Climate Leaf Analysis Multivariate Program) calibration dataset for the Southern Hemisphere, comprising leaf physiognomic data from Argentina, Bolivia, South Africa, Australia, New Zealand and other Pacific Islands that offers comparable precision for climate prediction to similar datasets derived from the Northern Hemisphere.

1. Introduction

With the development of global palaeoclimate models, the value of quantitative palaeoclimate data for testing model reliability has stimulated new ways of producing quantitative climate reconstruction data from the fossil record. There are few quantitative palaeoclimate proxies applicable to terrestrial sediments. The use of leaf morphology is one of the most powerful, particularly because leaves respond directly to conditions in the atmosphere and fossil leaves can therefore be used as proxies for an array of climate parameters. Unfortunately, deriving a globally applicable foliar physiognomic climate reconstruction technique that provides accurate and precise results over geological timescales is no simple task. This is particularly so for the Southern Hemisphere where leaf form is often regarded as being poorly and/or differently correlated with climate compared to the Northern Hemisphere (Upchurch and Wolfe, 1987; Greenwood, 1992; Jordan, 1997; Stranks and England, 1997; Kennedy, 1998; Greenwood et al., 2004).

The most commonly used measure of climate for model validation is mean annual temperature (MAT), even though this is probably not a critical limiting measure for plant growth and distribution. Measures related to freezing such as the cold month mean temperature (CMMT), or potential heat stress such as the warm month mean temperature (WMMT) are likely to be climatic parameters that limit plant distribution. Nevertheless MAT can readily be compared both to climate model output and to measures provided by independent geochemical proxies such as those based on isotopes. MAT is also a key measure in determining the global mean surface temperature and latitudinal temperature gradients, a primary driver of the climate system. For this reason it is important to evaluate the capacity of leaf morphological proxies to reconstruct MAT both accurately and precisely.

The use of foliar physiognomic analysis as a tool for climate reconstruction assumes that leaf form is optimised through natural selection for maximising primary productivity and minimising structural investment, while managing water relations and radiation balance. Because this is such a basic evolutionary strategy the physiognomic approach is likely to be time-stable and has been successfully applied as far back as the early radiation of the angiosperms approximately 100 million years ago (e.g. Spicer and Herman, 2010, and references therein).

The term 'successfully' here needs qualification. Any proxy method can generate climate retrodictions but the critical issue is how well they reflect what the actual values were in the past (accuracy) and what the uncertainties are in those retrodictions (precision). The only way to evaluate accuracy for past climates is through consilience with

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other proxies (preferably based on independent methodologies) and for measures of precision we need to define carefully a standardised methodological framework so that calibration is consistent throughout the methodology and the statistics generated are therefore valid.

In this paper we discuss temperature estimation from two foliar physiognomic methods of analysis — the Climate Leaf Analysis Multivariate Program (CLAMP) and Leaf Margin Analysis (LMA). We investigate hemispheric disparities using a multivariate approach to foliar physiognomy at 90 locations throughout the Southern Hemisphere including newly collected data from New Zealand and Australia.

2. The universality of the foliar physiognomy/climate relationship

In the context of using standardised methodologies for collecting both physiognomic and climate data here we focus on two discussion points that are often associated with foliar physiognomic palaeoclimate proxies:

1. Is the relationship between leaf physiognomy and temperature the same in Northern and Southern hemispheres?
2. Is the relationship between leaf margin and temperature always the most dominant leaf character/climate relationship in these methodologies?

2.1. Is the relationship between leaf physiognomy and temperature the same in Northern and Southern hemispheres?

One of the most critical questions regarding the application of quantitative leaf morphology-based methods such as LMA and CLAMP concerns their global validity. For the most part, leaf physiognomic proxies have been developed in the Northern Hemisphere with Northern Hemisphere modern analogue datasets. The validity of their application to the Southern Hemisphere is questionable (e.g. Greenwood et al., 2004). It is clear that various LMA studies have shown important differences in regression statistics but because of the lack of standardisation regarding both the physiognomic and climate data the sources and magnitude of these differences have been unclear.

To explore the applicability of LMA and CLAMP to the Southern Hemisphere we assembled datasets following the standardised field collecting protocols used in CLAMP, accompanied by high-resolution gridded climate data assembled from global station data for the 1961–1990 interval. Global, hemispheric and regional variations in leaf form/climate relationships can thus be investigated within a common leaf sampling and climatic framework. These datasets are composed of previously published sites, combined with newly collected material in the case of the Southern Hemisphere dataset.

2.2. Is the relationship between leaf margin and temperature always the most dominant leaf character/climate relationship in these methodologies?

There has been considerable debate as to the comparative usefulness of the univariate versus multivariate foliar physiognomic methods (Wolfe, 1979; Wing and Greenwood, 1993; Wolfe, 1993; Wilf, 1997; Wilf et al., 1998; Gregory-Wodzicki, 2000; Spicer et al., 2005; Spicer and Yang, 2010; Steart et al., 2010; Spicer et al., 2011). Univariate methods are attractive because of their simplicity. They are relatively straight-forward to score and to calculate, but are they always the most accurate and precise? Wilf (1997) stated that the CLAMP method does not improve temperature estimates produced using LMA because the temperature signal is dominated by the leaf margin character suite in the CLAMP dataset, masking any useful influence from other characters. We will test this assertion here.

3. Materials and methods

3.1. Leaf margin analysis (LMA)

3.1.1. Introduction: LMA

The first attempt to relate leaf form to temperature was that of Bailey and Sinnott (1915, 1916) who recognised that the leaf margin type in woody dicots is correlated with MAT, although they used no quantitative temperature observations in their work, using instead qualitative climate classifications such as ‘tropical’ and ‘warm temperate’.

Wolfe (1979) made use of the leaf margin/temperature relationship and established it as a quantitative palaeoclimate proxy. This quantitative approach is now commonly termed Leaf Margin Analysis (LMA). LMA utilises the positive correlation between observed temperature and the proportion of woody dicotyledonous species in a modern vegetation assemblage that have leaves with entire margins (E), and remains widely used. Regression equations produced using modern datasets of leaf margin and temperature information are then used to calculate mean annual temperature from the E value of the fossil assemblage. To-date the most widely applied palaeotemperature regression equation (MAT (°C) $= (E \times 0.306) + 1.141$) for this correlation is based on a Southeast Asian dataset (Wolfe, 1979; Wing and Greenwood, 1993). Several other LMA calibrations based on regional datasets and CLAMP datasets have also been applied (e.g. Wilf, 1997; Greenwood et al., 2003; Kowalski and Dilcher, 2003; Greenwood et al., 2004; Hinojosa and Villagrán, 2005; Miller et al., 2006).

Although still widely used, LMA suffers from a number of limitations. Wolfe (1979) emphasised that the technique did not perform well in dry or cold climates where water is limiting to growth. In these situations leaf size is small and water loss through marginal teeth would be disadvantageous (Bailey and Sinnott, 1915; Wolfe, 1993). Wolfe (1979) also noted that spinose margins adapted to deter browsing should be regarded as entire (untoothed).

The complication most detrimental to the routine use of LMA as a climate reconstruction tool is that there is no single globally applicable LMA regression and differences exist between Northern and Southern hemispheres (Wolfe, 1979; Upchurch and Wolfe, 1987). Wolfe's (1979) Northern Hemisphere LMA gradient, based on the monsoon-affected Southeast Asian vegetation, showed the approximate relationship between MAT (°C) and % entire margins (E) to be an increase in E of 3% for every 1 °C increase in MAT, with 60% E at the 20 °C isotherm. Wolfe employed only a few Southern Hemisphere floras but suggested that they indicated a margin/MAT relationship that was closer to 4% entire/1 °C for Southern Hemisphere floras.

In addition to hemispheric differences several workers have noted regional variations in LMA regressions (e.g. Greenwood, 1992; Greenwood et al., 2004; Steart et al., 2010) and these differences are often most strongly displayed in floras with high endemism. In the most extreme cases there appears to be no correlation at all between leaf margin (%E) and temperature, such as in Costa Rica (Dolph and Dilcher, 1980) and New Zealand (Stranks, 1996; Kennedy, 1998).

While many of these regional variations in LMA have been interpreted in terms of biogeographic history (Greenwood et al., 2004) and phylogeny (Little et al., 2010) part of the reason for the differences in LMA regressions can be attributed to different leaf sampling strategies, and to climate datasets collected over different time intervals and from stations with differing relationships (altitude, aspect, distance) to the vegetation sampled. This ‘calibration noise’ remains unquantified but can be broken down into that due to variation in collection methodology and that due to uncertainties in climate data.

3.1.2. Leaf data as a source of uncertainty in LMA

Flawed sampling strategies were embedded in foliar physiognomic research from the beginning. Bailey and Sinnott (1915) took their data from regional floras documented for taxonomic purposes and defined by political rather than phytogeographical boundaries, and which