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RESEARCH PAPER

Land surface skin temperature captures thermal environments of C_3 and C_4 grasses

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ABSTRACT

Aim Numerous studies have documented ecological sorting of C_3 and C_4 grasses along air temperature gradients. However, phylogenetically structured analyses suggest that closely related C_3 and C_4 grasses (in the same PACMAD clade: Panicoideae, Arundinoideae, Chloridoideae, Micrairoideae, Aristidoideae and Danthonioideae) occur in environments with similar air temperature, challenging our understanding of how the photosynthetic pathway influences grass biogeography. To better understand thermal differences between C_3 and C_4 grass lineages, we analysed the surface radiative temperature as an alternative measure that is more closely aligned with plant microclimate.

Location Hawaiian Islands, USA.

Methods We used the MODIS land surface temperature (LST) product, a satellite-based measurement of radiative temperature. We compared LST with mean annual air temperature (MAT) for locations where C_3 and C_4 grass species were collected. We also utilized other satellite products, like MODIS tree cover, as a proxy for relative habitat openness where these grasses occur.

Results Comparisons of C_3 lineages [in BEP (Bambusoideae, Ehrhartoideae and Pooideae) and PACMAD clades] and C_4 lineages (PACMAD clade only) illustrate the differing thermal environments for each group. C_4 taxa are found in the environments with the highest MAT, followed by C_3 PACMAD species. By contrast, C_3 PACMAD species are found in the environments with the coolest LST, and the LST values for C_3 BEP species are substantially higher than their MAT values. The difference in LST between C_3 and C_4 PACMADs is larger than the difference in MAT between these groups.

Main conclusions Though LST has been used infrequently in ecology and biogeography, it is intimately related to water and energy balance and ecosystem structure, and should more accurately capture plant temperatures and microclimates than MAT. Our results provide support for a pronounced thermal difference in the environments of closely related C_3 and C_4 grass taxa, and show that C_3 PACMADs occur in the coolest and least variable thermal environments, probably due to the greater tree cover of these habitats.

Keywords
BEP, C_3, C_4, clade, distribution, land surface temperature, niche, PACMAD, photosynthetic pathway.

INTRODUCTION AND SCIENTIFIC CONTEXT

Grasses are some of the most ecologically successful plants on earth. Grasslands and savannas cover *c.* 30% of earth's ice-free surface, and grasses provide much of the food for humanity. The photosynthetic pathway composition (C_3/C_4 fraction) of grasses is a fundamental physiological and biogeographical distinction in tropical, subtropical and temperate savannas and grasslands. Of the *c.* 11,000 grass species on earth, some 4500 use the C_4 pathway and the remainder are C_3 (Kellogg, 2001). Although

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they account for less than 2% of vascular plant species, C_4 grasses are estimated to cover some 19 million km^2 and to account for 20–25% of terrestrial productivity (Still *et al.*, 2003). The ecological and biogeographical importance of C_4 grasses is a fairly recent phenomenon in earth's history. Although the age of grasses is still controversial, with estimates ranging from *c.* 90 to 125 Ma (Vicentini *et al.*, 2008; Prasad *et al.*, 2011), recent phylogenetic evidence suggests that most C_4 grasses originated *c.* 30 Ma, coincident with and probably driven by the Oligocene decline in CO_2 concentrations (Christin *et al.*, 2008, 2011). It wasn't until the late Miocene (c. 5–8 Ma), however, that C_4 grasses became ecologically important on several continents (Cerling *et al.*, 1997; Tipple & Pagani, 2007). The explanations for this dramatic C_4 expansion range from lowered atmospheric CO_2 (Cerling *et al.*, 1997) to increased fire and enhanced climatic seasonality and aridity (Keeley & Rundel, 2003; Sage, 2004; Beerling & Osborne, 2006; Tipple & Pagani, 2007; Bond *et al.*, 2008). Explaining the Miocene–Pliocene C_4 expansion is a central challenge for fields from biogeography to palaeoecology (Edwards *et al.*, 2010), and partly motivates our attempt to better characterize modern C_4 grass environments.

A comprehensive review of C_4 biogeography concluded that the principal climatic determinants of ecological success for C_4 grasses are growing season air temperature and irradiance, with higher temperatures and light favouring growth of C_4 over C_3 grasses (Sage *et al.*, 1999). The primary physiological explanation for controls on C_3/C_4 distributions by temperature and light is the quantum yield model (Ehleringer, 1978; Ehleringer *et al.*, 1997). The quantum yield is the ratio of moles of CO_2 assimilated by a leaf to moles of absorbed photosynthetically active radiation (APAR) during conditions when light limits photosynthesis (Ehleringer & Björkman, 1977; Hattersley, 1983; Collatz *et al.*, 1998). Ehleringer (1978) hypothesized that temperature-driven differences in quantum yields determine competitive success, as higher yields should increase growth and reproductive success. The quantum yield in C_3 plants decreases with increasing leaf temperature at a constant CO_2 concentration, and increases with CO_2 at a given leaf temperature, essentially reflecting the influence of these factors on photorespiration (Ehleringer & Björkman, 1977; Pearcy & Ehleringer, 1984; Collatz *et al.*, 1998; Long, 1999; Sage, 2004). By comparison, the quantum yield of C_4 plants is relatively constant across a range of temperatures and CO_2 levels due to the C_4 carbon-concentrating mechanism. The point at which the quantum yield of C_3 grasses equals the quantum yield of C_4 grasses is defined as the 'crossover temperature' (Ehleringer *et al.*, 1997; Collatz *et al.*, 1998). At temperatures below this cutoff C_3 grasses should have a higher capacity to fix carbon, while C_4 grasses should have higher capacities at temperatures above this cutoff. Empirical crossover temperatures for C_4 monocots versus C_3 leaves vary from 16 °C to 24 °C (Ehleringer *et al.*, 1997). Based on empirical evidence and photosynthesis modelling, Collatz *et al.* (1998) developed threshold climate criteria: C_4 grasses should be more productive and dominate grasslands and savanna herbaceous layers where the minimum monthly mean air temperature is 22 °C or higher for at least 1 month when at least 25 mm of precipitation falls in that month.

The crossover temperature model simplifies the physiological differences between C_3 and C_4 plants by only considering light-limited conditions when grasslands often experience saturating irradiance (Collatz *et al.*, 1998). However, modelled crossover temperature ranges for both light-limited and light-saturated conditions are similar (*c.* 21–24 °C; Still *et al.*, 2003). Differences in light utilization across a range of conditions are broadly captured by the concept of light-use efficiency (LUE), which describes the conversion efficiency between canopy APAR and growth (Monteith, 1977; Ruimy *et al.*, 1999). Even when considering different light environments, C_4 grasses should have higher LUE than C_3 grasses when air temperatures exceed 21 °C (Still *et al.*, 2003, 2004, 2009).

Thus, the crossover temperature model remains useful for predicting C_4 distributions. While it has been applied at continental (Still & Powell, 2010) and global (Collatz *et al.*, 1998; Still *et al.*, 2003) scales to predict distributions of C_4 vegetation, this model is not always successful at capturing finer-scale distributions. For example, Auerswald *et al.* (2009) showed that this model worked at regional scales (hundreds of km^2), but not at smaller scales (tens of km^2). Although the biochemical rationale for temperature and light controls on C_3/C_4 distributions is strong, other factors also influence C_3/C_4 distributions.

C_4 grasses exhibit a higher water-use efficiency (WUE) than C_3 grasses because of lower stomatal conductance, producing a higher carbon gain per unit of water loss (Pearcy & Ehleringer, 1984; Sage, 2004; Mantlana *et al.*, 2008). This should provide a competitive advantage for C_4 over C_3 grasses in water-limited environments. Indeed, measurements document much higher transpiration water losses in a C_3 grass, particularly during conditions of variable sunlight (Knapp, 1993). A growth chamber study showed that the higher WUE of a C_4 grass enabled it to grow for a longer time and to postpone the onset of water stress, compared with a C_3 grass (Kalapos *et al.*, 1996). At larger scales, studies have inferred an important role for precipitation and its seasonal distribution on relative C_4 grass productivity (Paruelo & Lauenroth, 1996; Epstein *et al.*, 1997; Winslow *et al.*, 2003; Murphy & Bowman, 2007; von Fischer *et al.*, 2008).

Other research provides more evidence for strong moisture control on C_3/C_4 biogeography. Edwards & Still (2008) studied ecological sorting of C_3 and C_4 sister grass taxa in the PACMAD (Panicoideae, Arundinoideae, Chloridoideae, Micrairoideae, Aristidoideae and Danthonioideae) clade using phylogenetic comparative methods, and found that the primary advantage of the C_4 pathway was in conferring higher drought tolerance, rather than higher temperature acclimation. However, most previous studies compared C_4 grasses with C_3 grasses from a different evolutionary clade (BEP; Bambusoideae, Ehrhartoideae and Pooideae). This work realigned the focus of comparative C_3–C_4 studies around sister taxa from the same PACMAD clade, whereas most previous studies compared C_4 grasses with C_3 grasses from a different evolutionary clade (BEP). Importantly, results from this phylogenetically structured comparison challenged the notion of distinct temperature niches that were thought to result from the differing biochemistry of each photosynthetic pathway.

The importance of higher WUE in C_4 species was further supported by experimental work documenting large differences in WUE between closely related C_3 and C_4 sister taxa (Taylor *et al.*, 2009), and in distribution models of C_3 and C_4 grass taxa in Hawaii (Pau *et al.*, 2013). Edwards & Smith (2010) used a global sampling of grasses and found that the evolution of C_4 taxa from their C_3 progenitors was generally accompanied by a shift from wetter (closed-canopy tropical forests) to drier (open tropical savannas), but not necessarily warmer, climate niches. These findings challenge our fundamental understanding of how temperature influences the evolution of grasses and the responses of grasses to global change. The lack of inferred temperature niche differentiation between closely related C_3 and C_4 sister grass taxa is puzzling given the strongly contrasting microclimates of these habitats: shaded and moist tropical forest understories where mean annual precipitation (MAP) typically exceeds 1500 mm (C_3 taxa), and tropical and subtropical savanna and open grassland habitats with lower MAP and higher insolation for C_4 taxa. At similar latitudes, open grassland and savanna environments are almost always hotter, drier and brighter than adjacent closed canopy forest environments (especially forest understorey environments where any grasses would grow). These physical differences should strongly affect vegetation function, with open-environment C_4 grasses adapted to different conditions than closed forest C_3 PACMAD grasses.

The amount of tree cover will affect shading and grass LUE, net radiation and soil moisture and temperature. For instance, Cerling *et al.* (2011) report soil surface temperature data for savannas and grasslands in Africa. They document much higher maximum soil surface temperatures in open, grassy environments (*c.* 30–60 °C) compared with woody, shaded habitats (*c.* 25–48 °C) over an annual cycle, and note that grassy open environments experienced 130 days with maximum soil surface temperatures exceeding 45 °C. Such hot soils emit tremendous long-wave radiation fluxes, some of which are absorbed by adjacent and overlying grasses. Thus, large temperature gradients can exist in the first few metres above grassland canopies.

We hypothesize that a reason for the lack of a temperature niche difference between C_3 and C_4 sister taxa is that air temperature (T_{air}) climatology datasets fail to capture true thermal differences between these environments. T_{air} datasets can be strongly affected by interpolation errors, particularly in sparsely sampled tropical and subtropical regions where most C_4 grasses occur (Peterson *et al.*, 2000; Hijmans *et al.*, 2005; Vancutsem *et al.*, 2010). Another concern with the use of T_{air} is that the more relevant quantity is the temperature of the object or surface of interest (referred to as 'skin temperature,' or T_{skin}). Because any object's thermodynamic temperature can deviate frequently from air temperature (Jones, 1992; Campbell & Norman, 1998), using T_{air} is insufficient for a range of scientific questions – rather, it is of equal or greater importance to measure T_{skin}. Because numerous biological processes and environmental attributes depend nonlinearly on temperature, substantial errors can occur when using T_{air} instead of T_{skin}.

Thus, T_{air} datasets may not adequately capture variations in microclimate and actual plant temperatures, which are critical for biochemical differences to be manifest (Berry & Björkman, 1980). Indeed, Edwards & Smith (2010) discuss the importance of differences in leaf temperature in the evolution and niche partitioning between understorey (C_3) and open environment (C_4) PACMAD grass taxa. Resolving temperature controls on tropical grass distributions, particularly for C_3 and C_4 sister taxa, ideally requires measurements of leaf temperature collected across a variety of spatial and temporal scales in differing habitats. Satellite remote sensing provides new environmental information, such as the percentage of a pixel covered by trees, along with T_{skin} measurements more closely related to vegetation canopy temperature than T_{air}, and that do not suffer from the inaccuracies imposed by spatial interpolation of sparse data. We suggest that satellite T_{skin} datasets are currently as close as we can get to relatively fine-scale mapping of vegetation temperatures across large tropical and subtropical regions.

Our goal in this research is to advance basic knowledge of C_3/C_4 grass biogeography by more accurately capturing their thermal environments. We hypothesize that C_3 and C_4 sister grass taxa inhabit distinct thermal environments that are driven by differences in tree cover. We examine how functional differences imposed by photosynthetic pathway and evolutionary history influence C_3 and C_4 grass distributions in the Hawaiian Islands by combining herbarium, climate and satellite datasets. Using the same data, we previously demonstrated that land surface temperature (LST) and tree cover were two of the most important variables in modelling distributions of C_3 and C_4 grasses (Pau *et al.*, 2013). While that work discussed the potential importance of LST, in this current paper we focus on its general potential for questions in ecology and biogeography, and in particular its application for assessing differences in thermal niches. We examine LST and tree cover in more depth and explain the biophysical relevance of these environmental characteristics.

RESEARCH METHODS

Grass species locality and climate normal datasets

The Hawaiian Islands are ideal for studying distributions and niches of C_3 and C_4 grasses due to: (1) extremely large climatic gradients in a small area [MAP across the islands varies from 200 to > 6000 mm, and mean annual temperature (MAT) varies from approximately 11–25 °C; Giambelluca *et al.*, 1986; Juvik & Juvik, 1998]; (2) the presence of a diversity of grass lineages, and an existing database of grass species occurrence. Previous work in Hawaii has shown significant correlations of C_4 grass distributions with temperature and precipitation (Rundel, 1980). We utilized the same dataset on species collection localities across the Hawaiian Islands from Edwards & Still (2008), and also the gridded climate normal datasets (250-m resolution) from Giambelluca *et al.* (1986). The Hawaiian grass flora is of moderate size (*c.* 200 species) and is almost entirely non-native, as humans introduced over 75% of the grass species in the last

100–150 years (Wagner *et al.*, 1999); the most commonly encountered grasses are invasive and found across all of the major islands. Because the current grass community in Hawaii has largely assembled in the last *c.* 150 years, grass distributions should primarily result from ecological sorting along modern climate gradients, where the niche of a given species is the result of intrinsic ecological preferences and relative competitive ability, and not of insular biogeographical processes (Edwards & Still, 2008). Thus, although confined to a relatively small area, our results should be broadly relevant for grasses in other regions of the world.

We further characterized the C_4 species in this database by biochemical subtypes, each representing a different decarboxylation type (NAD-ME, NADP-ME and PCK; Kanai & Edwards, 1999). Grasses with these subtypes have distinct functional characteristics and often inhabit differing climates (e.g. Ellis *et al.*, 1980; Schulze *et al.*, 1996; Taub, 2000). NADP-ME monocots typically have higher quantum yields (*c.* 10%) than do NAD-ME monocots (Ehleringer *et al.*, 1997). The subtypes can have characteristic leaf anatomies, nitrogen use efficiency, carbon isotope fractionation, responses of WUE to drought (Ghannoum *et al.*, 2002, 2005) and leaf chlorophyll $a:b$ ratios (Watson & Dallwitz, 1992).

Satellite datasets of land surface temperature and percentage tree cover

Satellites from NASA's Earth Observing System routinely measure reflectance from earth's surface and atmosphere, allowing us to examine fundamental ecosystem processes at a global scale. NASA's Moderate Resolution Imaging Spectroradiometer (MODIS) measures the radiative skin temperature (T_{skin}) of the land surface, which enables scientists to capture new information on how T_{skin} varies with ecosystem distribution and function. This quantity, the MODIS LST product, is produced daily with near global coverage at 1-km resolution. Combining data from the Terra and Aqua satellites, LST can be measured globally four times each day at *c.* 10:30, 13:30, 22:30 and 01:30 local solar time (depending on pixel longitude location) in clear-sky conditions (Wan, 1999).

While LST (or any T_{skin} measurement) is related to near-surface air temperature (T_{air}), it is also affected by radiative exchanges or latent and sensible heating, and is related to soil moisture status, vapour pressure deficit (VPD) and plant stress. T_{skin} is coupled to surface water and energy balances (Anderson *et al.*, 2007; Karnieli *et al.*, 2010), and differs from near-surface T_{air} in fundamental ways (Norman & Becker, 1995; Jin & Dickinson, 2010; Vancutsem *et al.*, 2010). Comparisons of T_{skin} and T_{air} typically show contrasting patterns for night and day, with differences in magnitude, phase, response to sky conditions and biome type (Jin & Dickinson, 2010). While LST and T_{air} can be very similar, particularly at night, LST captures other aspects of the environment that are important for ecological questions, and is more closely related to vegetation surface temperature and microclimate than T_{air}.

For this research, we used 8-day, 1-km daytime LST data collected at 10:30 local time (MOD11A2 from Terra) as a proxy for daytime vegetation canopy temperatures and microclimates. The Terra LST record is longer than the Aqua record, so we focused on the Terra dataset. Only collections within grassland vegetation classes were compared with 1-km MODIS LST data. The Hawaii GAP Analysis land-cover dataset, created based on 30-m resolution Landsat imagery from 1999–2003 and edited using ancillary data (US Geological Survey, Gap Analysis Program (GAP) August 2011, National Land Cover, Version 2), was used to screen out collections outside of grassland classes. This was done because some proportion of the coarser 1-km MODIS LST pixels might contain non-grasslands, thus affecting our surface temperature estimations for grasses. We further screened grass collections on the island of Hawaii, which as the youngest island in the chain has the most exposed lava. We removed collections that fell within 1 km of visible lava fields using high-resolution imagery from Google Earth. This screening was done to minimize the possibility of including pixels that contain lava and thus would have very low albedo and very high LST values. This illustrates the challenge of capturing environmental data using relatively coarse-scale satellite imagery with often very heterogeneous pixels for small-scale point collection localities, which have some uncertainty with regard to their location.

To quantify aspects of habitat openness and tree cover for our grass localities, we utilized the MODIS Vegetation Continuous Fields (VCF) product (MOD44B, collection 4, version 3), which includes layers that represent percentage tree cover at 0.5 km for the year 2005 (the most recent compositing period available). This product is based on the work of DeFries *et al.* (1999) and Hansen *et al.* (2003), who established an approach to image classification in which each pixel on the land surface is characterized in terms of percentage vegetation cover. The MODIS tree cover product is technically not the percentage crown cover, or total ground area under tree crowns, as is usually assumed. Rather, it is the mean percentage canopy cover per grid cell, i.e. the amount of skylight obstructed by tree canopies, and thus it rarely exceeds 80% even in what would be taken as closed-canopy forests (Hansen *et al.*, 2003). In other words, the mean percentage canopy cover values presented here are underestimations (by *c.* 25%) of the actual crown covers that would shade understorey grasses and affect their light, temperature and moisture conditions. Although we screened points for grassland classes, the 0.5-km grid cells of the tree cover product encompassing some of the grassland cover pixels (at 30 m) will necessarily include non-grass vegetation (i.e. tree cover for our points will not always be 0%).

Statistical analyses

Statistical analyses were conducted using R software version 2.15.2 (R Core Team, 2012). To assess which variables are most important in a classification tree of C_3 PACMAD and C_4 taxa, we used the 'tree' routine in R and the following explanatory environmental variables: MAT, MAP, LST, tree cover and elevation.

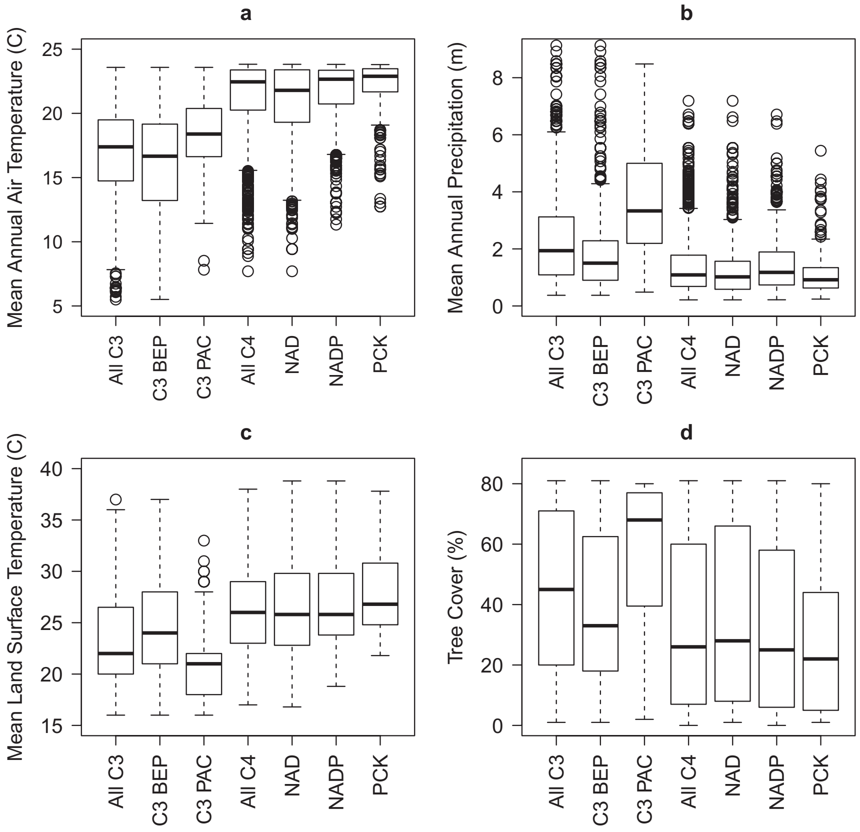

Figure 1 Boxplots of (a) mean annual air temperature (MAT, °C), (b) mean annual precipitation (MAP, mm), (c) Moderate-Resolution Imaging Spectroradiometer (MODIS) 10-year mean clear sky land surface temperature (LST, °C) from the 1030 Terra overpass, and (d) MODIS tree cover (%) for the various C_3 and C_4 grass taxa categories. The thick horizontal line is the median value, upper and lower parts of the box represent the interquartile values (25th and 75th percentiles), whiskers extend to 1.5 times the interquartile range from the upper and lower interquartiles, and open circles represent outliers. BEP refers to C_3 species in the BEP grass clade, and PAC refers to C_3 species in the PACMAD grass clade. NAD, NADP-ME and PCK refer to C_4 species with the different decarboxylation subtypes.

Table 1 Mean (± SD) values of environmental variable for sampling locations of C_3 and C_4 grasses, along with subcategories within each photosynthetic pathway type.

Environmental variable	C_3 ($n = 595$)	C_3 BEP ($n = 411$)	C_3 PACMAD ($n = 184$)	C_4 ($n = 1204$)	C_4 NADP-ME ($n = 662$)	C_4 NAD-ME ($n = 373$)	C_4 PCK ($n = 169$)
MAT (°C)	16.8 (0.1)	16.0 (0.1)	18.4 (0.2)	21.4 (0.1)	21.7 (0.1)	20.8 (0.1)	22.1 (0.1)
LST (°C)	23.4 (4.5)	24.5 (4.5)	20.9 (3.1)	26.1 (3.8)	26.0 (3.9)	25.4 (4)	26.9 (3.7)
MAP (mm)	2468 (54)	1961 (55)	3700 (108)	1385 (21)	1442 (28)	1327 (43)	1141 (46)
Tree cover (%)	44.2 (26.6)	38.8 (25.4)	57.3 (24.9)	34.1 (27.4)	33.1 (27.4)	36.3 (27.9)	26.8 (24)

MAT, mean annual air temperature; LST, mean land surface temperature; MAP, mean annual precipitation; BEP, grass clade containing only C_3 species; PACMAD, grass clade containing both C_3 and C_4 species. NAD, NADP-ME and PCK are different carboxylation subtypes.

RESULTS AND DISCUSSION

Across groupings, C_3 PACMAD taxa are found in environments with higher MAT than C_3 BEP taxa, while C_4 taxa occur in the environments with the highest MAT (Fig. 1a, Table 1). Similarly, rankings of annual mean daytime maximum air temperature are similar to MAT patterns shown in Fig. 1(a), but the magnitudes are elevated (not shown). Figure 1(b) shows MAP for the grass groupings. C_3 PACMAD taxa occur in by far the wettest environments, as shown previously (Edwards & Still, 2008). C_4 grasses with the NAD-ME and PCK subtypes occur in drier climates than NADP-ME grasses (Fig. 1a,b and Table 1), in agreement with earlier studies (Vogel *et al.*, 1986; Schulze *et al.*, 1996; Taub, 2000; Ghannoum *et al.*, 2001). However, C_4 subtypes are associated with specific grass subfamilies, and the traits that determine distributions and certain physiological and functional differences are probably not due solely to decarboxylation type, but to other evolutionary aspects of the subfamilies (Hattersley & Watson, 1992; Taub, 2000; Cabido *et al.*, 2008; Taylor *et al.*, 2009).

Patterns of mean LST across groupings both support and contrast with the MAP and MAT results. We also examined seasonal (May–October or November–April) measures of air temperature, precipitation and LST; differences among grass groupings are maintained (not shown), so we focus here on annual averages of these climate variables. Daily maximum air temperatures were also examined: they have same relative rankings as MAT, but are elevated by *c.* 3–5 °C. LST values are elevated in all cases compared with MAT, and the differences and orderings among grass groups differ from those for MAT (Fig. 1c). MAT for C_4 environments is 21.3 °C and for C_3 PACMADs is 18.3 °C; by contrast, the LST offset between C_4 and C_3 PACMAD species is larger (26.2 °C and 21.4 °C, respectively; Table 1). We believe LST better reflects the true thermal niches of these grasses: the mean LST value for C_3 PACMAD taxa is considerably depressed compared with either C_4 taxa or C_3 BEP grasses. In other words, approximately 90% of C_3 PACMAD grass collections occur where LST is below the mean LST (*c.* 26 °C) for C_4 taxa. Thus, C_3 PACMAD grasses rarely experience the extreme thermal environments experienced by both C_4 and C_3 BEP grass species.

Differences between MAT and LST for the grass categories also imply differences in the amount of atmospheric moisture in the environment these grasses operate in during photosynthesis and transpiration. The difference in VPD (in kPa) between closely related PACMAD C_3 and C_4 sister grass taxa will be larger when using LST as a leaf temperature proxy in place of air temperature, as saturation vapour pressure increases nonlinearly with temperature. The VPD difference for C_3 and C_4 PACMAD taxa calculated with LST is more than twice that calculated with MAT (0.92 kPa versus 0.42 kPa). Including VPD differences bolsters our ability to characterize other aspects of differences in the moisture niche between closely related C_3 and C_4 grass taxa.

The LST range for C_3 PACMAD taxa environments is compressed compared with the environmental ranges for either C_3 BEP or C_4 grass species (interquartile ranges of 4 °C for C_3 PACMAD compared with 7 °C and 6 °C for C_3 BEP and C_4 taxa, respectively; Fig. 1c). The compression of LST ranges for C_3 PACMAD taxa is probably driven by the higher tree cover of the habitats in which these taxa occur. Higher tree cover should correlate to higher cooling latent heat fluxes during the day (Gates, 1968), and thus lower maximum daytime skin temperatures; similarly, such environments should have higher nighttime water vapour concentrations in the atmosphere above the vegetation, which would enhance the nighttime greenhouse effect and thus raise the nighttime minimum skin temperatures. This echoes Mildrexler *et al.* (2011), who surveyed global biomes and showed that forests on earth never exceed a maximum annual LST of *c.* 38 °C.

The preference of C_3 PACMAD taxa for habitats with higher tree cover and higher MAP was inferred by Edwards & Smith (2010) using a much larger grass collection locality dataset and climate datasets; our data extend their findings with the use of remotely sensed measurements of T_{skin} and tree cover. The percentages of tree canopy cover for the various grass type collection localities are shown in Fig. 1(d) and given in Table 1. As expected, the patterns of tree canopy cover across grass categories largely reflect MAP patterns, with C_3 PACMAD grasses growing in the most forested locations, followed by C_3 BEP grasses and C_4 grasses. C_3 PACMAD grasses are growing in environments where the mean *crown* cover (i.e. total ground area under tree crowns) is not 57% but 71% (see Research Methods). Within the subtypes, NAD-ME taxa are found in the most forested sites and PCK in the least forested.

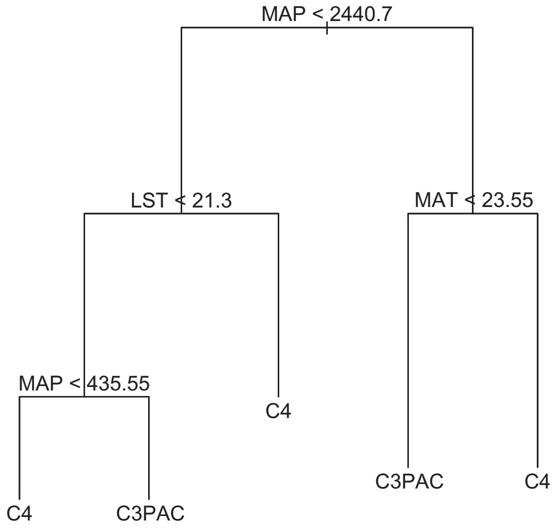

Figure 2 Decision tree for classifying C_3 PACMAD versus C_4 taxa. Environmental predictor variables are mean annual air temperature (MAT, °C), land surface temperature (LST, °C) and mean annual precipitation (MAP, mm).

Another interesting difference is that C_3 BEP grasses are generally found in the coolest (higher-elevation) MAT environments, but in much warmer LST environments (Fig. 1c). Indeed, the LST values for C_3 BEP grasses approach those values for C_4 grasses, though they are still lower (Table 1). This result is surprising, but it probably follows from a key difference between LST and MAT. Whereas air temperature typically declines with elevation following moist and dry adiabatic lapse rates (varying from –4 to –10 °C km^{-1}), LST should in some cases increase with elevation as it is closely related to net radiation, which increases with surface insolation as atmospheric thickness declines with elevation. Since many of the C_3 BEP collection localities are at medium to high elevations (median elevation 1338 m), which can often be above the Hawaiian Islands' trade wind inversion which caps cloud cover (Juvik & Juvik, 1998; Cao *et al.*, 2007), these grass taxa should on average experience greater insolation and thus higher LST. Grass canopies often grow in a warmer microclimate near the soil surface. Grasses often experience high leaf temperatures as their leaf boundary layer and canopy aerodynamic conductances to heat and water vapour are much lower than for taller and rougher woody vegetation, reducing net energy dissipation by sensible and latent heat exchanges and uncoupling them from overlying air (Campbell & Norman, 1998; Bonan, 2008).

The most important explanatory variables from our decision tree classification (C_3 PACMAD or C_4) are MAP, LST and MAT; altitude and tree cover were not important (Fig. 2). The misclassification error rate for this tree is extremely low (2 out of 2658 observations). Decision trees are very useful for classifications like this because they characterize interactions between predictor variables and distinguish variable thresholds (Franklin, 2009). At MAP values below 2440 mm (2086 of 2658 total observations), LST values above 21.3 °C are classified as C_4

(1866 observations); at lower LST values, only dry environments (MAP < 435 mm) are classified as C_4 (112 observations). At MAP values above the 2440 mm threshold (572 observations), the tree classifies MAT environments above 23.5 °C as C_4 (298 observations) and below that threshold as C_3 PACMAD. In summary, the classification places the majority of C_4 observations (82%) where MAP < 2440 mm and LST > 21.3 °C, while most C_3 PACMADs (72%) occur where MAP > 2440 mm and MAT < 23.5 °C. These classification results provide context for the differences and ordering of climate variables across grass groupings (i.e. MAT, MAP and LST averaged across all species collection localities within each grouping) shown in Fig. 1(a–d).

Figure S1(a,b) in the Supporting Information demonstrates how the spatial structure of MAT and LST differ across the Hawaiian Islands. Spatial patterns of MAT are smoothed in some areas by the need to interpolate across sparse weather station density, and vertical gradients reflect atmospheric lapse rates and rainfall patterns. By contrast, LST captures spatial patterns related to several factors, including the density and type of vegetation, surface albedo and net radiation, soil moisture availability and the partitioning of net radiation between sensible and latent heat fluxes. The difference between MAT and LST with elevation is especially pronounced on the island of Hawaii, with its greater topographic range and size. This island has the most lava cover, and the spatial patterns of LST also reflect this. MAT is plotted against LST for each grass grouping in Fig. S2(a–c) and the lack of a relationship is notable, as might be expected based on the differing aspects of temperature captured by each metric. There is no exact way to compare temperature metrics that are sampled at different times of the day, and maximum and minimum air temperatures are likely to occur at somewhat different times than maximum and minimum land surface temperatures.

These comparisons apply to the mean values for each climate or environmental variable within each category (C_3 BEP, C_3 PACMAD and C_4). However, it is desirable to compare less aggregated groupings to see if they conform to these broader patterns. Thus, we compared two sister genera, *Oplismenus* (C_3 PACMAD) and *Echinochloa* (C_4), that both occur at low elevations. *Oplismenus* taxa are found in wetter environments, with a MAP almost twice that for *Echinochloa* taxa. The average MAT for occurrence of *Oplismenus* taxa was 1.8 °C below that for *Echinochloa* taxa. By contrast, mean LST for *Oplismenus* species was slightly over 3 °C cooler than it was for *Echinochloa* species (Table 2), in agreement with the higher tree cover of *Oplismenus* habitats. The importance of tree cover for *Oplismenus* distributions was inferred by Pau *et al.* (2013).

A final comparison of MAT and LST across species is displayed in Fig. 3, which depicts a phylogeny for Hawaiian grass taxa (Edwards & Still, 2008) with mean values of MAT and LST illustrated at the species tips. C_3 BEP taxa are shown in light grey, C_3 PACMAD taxa are in red, and C_4 taxa are in black. The different patterning of LST versus MAT across this tree is apparent, as there is little correlation between the LST and MAT values of individual species. Within the PACMAD clade, in four of five cases, the differences in temperature niche between C_3 and C_4 PACMAD become exaggerated with LST compared with MAT. The one exception is in the C_3 PACMAD subfamily Danthonioideae, which had very low MAT values compared to other PACMAD subfamilies, but LST values are comparable. Interestingly, these are higher-elevation, open-habitat grasses.

Table 2 Mean (± SE) values of environmental variable for sampling locations of closely related C_3 (*Oplismenus*) and C_4 (*Echinochloa*) sister genera. All variables differ statistically between genera based on Welch's *t*-test, which does not assume equal variance ($P << 0.01$, $n = 56$).

Environmental variable	*Oplismenus* sp. (C_3)	*Echinochloa* sp. (C_4)
MAT (°C)	21.1 (0.2)	22.9 (0.1)
LST (°C)	24.2 (0.5)	27.3 (0.4)
MAP (mm)	2382 (171)	1223 (130)

MAT, mean annual air temperature; LST, mean land surface temperature; MAP, mean annual precipitation.

CONCLUSIONS

These results help to resolve the apparent paradox found in Edwards & Still (2008) and Edwards & Smith (2010), namely, that closely related C_3 and C_4 sister taxa apparently grow in similarly warm environments (i.e. there is no temperature niche differentiation), despite numerous previous ecological and physiological studies that demonstrated why and how C_4 grasses should be favoured in high-temperature and high-light environments compared with C_3 grasses. Our results suggest that the C_4 syndrome evolved at least partly in response to elevated leaf temperatures that occur in open, sunny environments. Of course, these analyses assume that modern relationships between climate and vegetation are similar to past ones. Interestingly, these data also suggest that the large inferred differences in temperature niche between BEP and PACMAD clades may be exaggerated based only on air temperature, and it is curious to consider why C_4 plants have never evolved in the BEP lineage. It is possible that the selection pressure is present but that certain pre-conditions that enable early C_4 evolution do not exist in these open-habitat BEP grasses (Christin *et al.*, 2013).

Despite its promise in biogeographical and ecological studies and its global coverage at relatively high spatial resolution, LST has been mostly unexploited in these fields. To date, LST has been utilized primarily in studies of drought monitoring, surface climate and hydrometeorology, phenology, carbon exchange and disturbance (Wan *et al.*, 2004; Mildrexler *et al.*, 2007). LST is intimately related to surface water and energy balances (Anderson *et al.*, 2007; Karnieli *et al.*, 2010). Pau *et al.* (2013) inferred an important role for LST in distribution modelling of C_3 and C_4 Hawaiian grasses, which is one of the few biogeographical studies to use this temperature metric. Researchers have also begun to utilize LST in studies of wildlife ecology. Albright *et al.* (2011) showed that heat wave indices based on LST better predicted avian community structure than

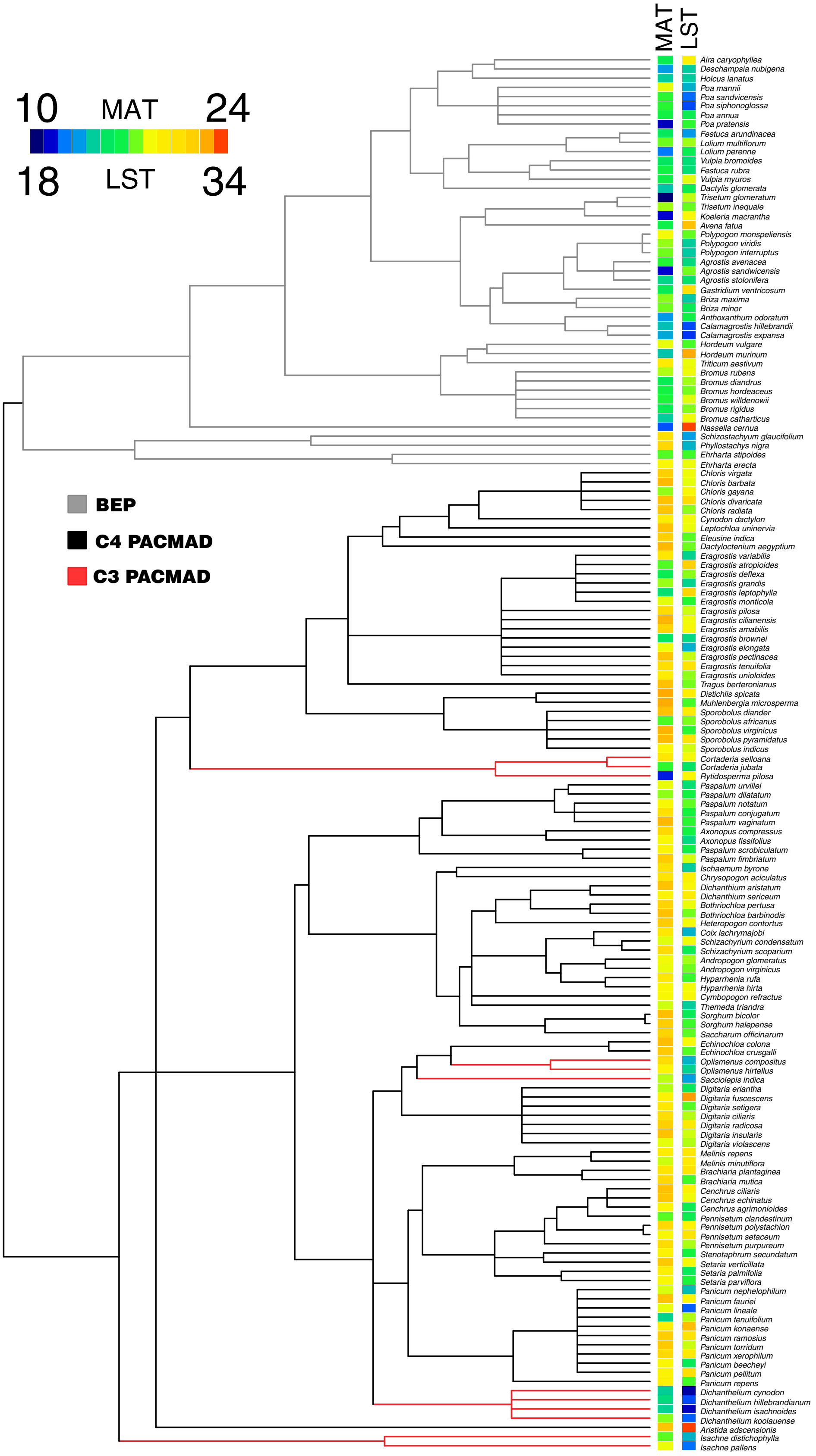

Figure 3 Phylogenetic tree of the grass flora of Hawaii, from Edwards & Still (2008). Mean values for each species of mean annual air temperature (MAT, °C) and mean land surface temperature (LST, °C) are mapped along the tips of the tree with taxon names given. C_3 BEP taxa are shown in light grey, C_3 PACMAD taxa are in red, and C_4 taxa are in black.

indices determined with interpolated T_{air}. Similarly, Moses *et al.* (2011) demonstrated that LST is the only environmental variable that correlates with survival of the desert kangaroo rat. Given these results and our findings, we suggest that LST can address a wide variety of biogeographical questions. The decade-plus MODIS LST record can also provide unprecedented information on the thermal regime in which most organisms live, including extremes related to drought and heat waves. Indeed, LST and other T_{skin} products are likely to be a superior measure of ecologically relevant temperatures, and should be considered in other investigations of environmental niches.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Figure S1 (a) Map of mean annual air temperature (°C) across the Hawaiian islands and (b) map of 10-year mean land surface temperature (°C) across the Hawaiian islands. Both maps are at 1 km resolution.

Figure S2 Plots of mean annual air temperature (°C) versus 10-year mean clear sky land surface temperature (°C) from the 1030 Terra MODIS overpass for the various grass categories: (a) C_3 BEP collection points, (b) C_3 PACMAD collection points, (c) C_4 collection points.

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