Foliar Physiognomic Record of Climatic Conditions during Dormancy: Climate Leaf Analysis Multivariate Program (CLAMP) and the Cold Month Mean Temperature

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ABSTRACT

The extent to which the leaves of woody dicots encode in their physiognomy the climatic conditions that exist during dormancy was tested by sampling 20 sites along an approximately west-east transect across European Russia, the Crimean Peninsula, Western Siberia, and central Eastern Siberia. This transect encompassed the most extreme mean annual temperature range recorded in the modern world where vegetation exists. Climate Leaf Analysis Multivariate Program (CLAMP) revealed little change in calibration of the warm month mean temperature compared with the PHYSG3AR data set derived from less extreme sites primarily in North America and Japan, but significant change with respect to the cold month mean temperature (CMMT) calibration. Although CLAMP underestimated the CMMT by up to 9°C in the coldest sites, the addition of the transect sites improved CLAMP's performance at low temperatures. This suggests that winter cold is encoded in foliar physiognomy even though the leaves are functional only during the late spring and summer months. This increase in performance was, however, at the cost of decreasing precision. Precipitation predictive capabilities were only slightly affected, but calibration of key climatic variables such as enthalpy, used in determining palaeoaltitude, remained more or less unchanged after the inclusion of the cold transect samples.

Introduction

Climate Leaf Analysis Multivariate Program (CLAMP) is a multivariate statistical technique for determining, quantitatively, a range of paleoclimate parameters using the physiognomy of fossil leaves of woody dicotyledonous flowering plants (Wolfe 1993; Wolfe and Spicer 1999; Spicer 2000). The relationship between angiosperm foliar physiognomy and climate appears to have evolved early in flowering plant history, and CLAMP has been used successfully to explore paleoclimates as old as the early Late Cretaceous (Herman and Spicer 1996; Herman et al. 2002; Kennedy et al. 2002; Spicer et al. 2002). For paleotemperatures, CLAMP complements the marine oxygen isotope record in that it provides air temperature estimates over land; moreover, CLAMP temperature estimates are consistent with those for nearby sea surface waters

derived from oxygen isotopes (Kennedy et al. 2002). Clearly, CLAMP can provide climate data only within the climatic tolerance window of woody dicots; however, fortunately in the modern world, that window encompasses a temperature range that is probably greater than many that have existed during the past 100 m.yr. The present-day equator-to-pole temperature gradient, for example, is steeper than at any time from the beginning of the Late Cretaceous until the end of the Pliocene, yet equatorial temperatures have remained largely unchanged (Skelton et al. 2003). Despite the current relatively harsh global climate, woody dicots exist in all but the most cold and dry climate regimes. What appears to limit CLAMP's application is not the present-day vegetational adaptation to climate but the range of climates represented in the CLAMP calibration data sets.

At the heart of the CLAMP technique are the modern-day vegetation reference data. These are used to define and calibrate the relationships between foliar physiognomy and a range of climate
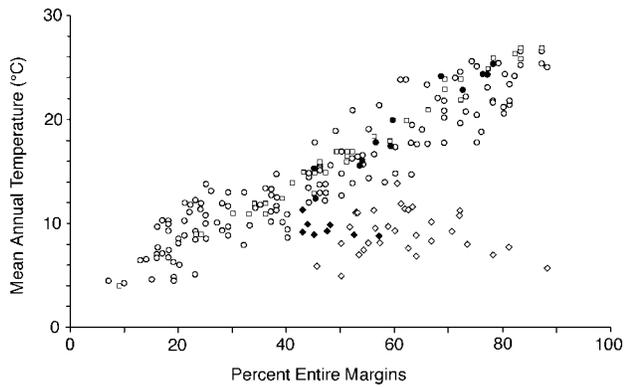
Figure 1. Percentage of woody dicot taxa with entire (nontoothed) leaves plotted against mean annual temperature for several suites of vegetation sites. Note that the Climate Leaf Analysis Multivariate Program (CLAMP) data set, data from the humid forests of Southeast Asia, and samples from Bolivia, all fall along the same trend. The New Zealand sites, however, behave differently and show very little direct correlation between margin type and temperature. *Open circles* = CLAMP PHYSG3BR data set; *filled circles* = Bolivian data set of Gregory-Wodzicki (2000); *open squares* = data from southeastern Asia, Wolfe 1979; *open diamonds* = data from New Zealand (Kennedy 1998); *filled diamonds* = New Zealand data from Stranks (1996).

variables. These reference sets consist of numerical scores describing the physiognomy, or architecture, of woody dicot leaves growing under known climatic regimes. Thirty-one different character states describe the degree of leaf lamina dissection, margin features, and the size, shape, apex, and base

form of leaves from at least 20 species of woody dicots within areas of stable vegetation growing within a kilometer or so, and at the same altitude as, meteorological stations. The full range of foliar morphological variation present in the vegetation is captured and scored. The early CLAMP calibration data set was largely restricted to North America, and this geographical bias is still present in the two most widely used reference sets: PHYSG3AR and PHYSG3BR (http://tabitha.open.ac.uk/spicer/CLAMP/Clampset1.html). The main difference between these two sets is that PHYSG3AR contains data from vegetation growing under so-called alpine conditions where cold is a significant growth limiter for part of the year. The plants experience physiological drought because the groundwater is frozen. Leaf size tends to be small under these circumstances, and in extreme cases, the reduced leaf size can lead to a loss of other characters such as teeth on the leaf margin. As a consequence, these leaves can display some features of leaves exposed to drought under warm regimes, and the temperatures predicted by CLAMP can be erroneously warm (Wolfe 1993).

Despite the North American bias of the CLAMP reference data sets, the calibration they provide appears valid for Europe, Asia, Central America, and South America. However, leaf data from genetically isolated regions such as New Zealand do not show the same type of relationship with climate as those from areas where gene flow is less restricted (Kennedy et al. 2002). Figure 1 shows this in terms of the simple correlation that exists between leaf margin form and temperature, but similar anomalous behavior can be seen in other characters. New Zea-

Table 1. Climate Parameters Normally Used in Climate Leaf Analysis Multivariate Program (CLAMP)

Climate parameter investigated by CLAMP	Abbreviation	SD of residuals[a]
Mean annual temperature (°C)	MAT	1.7
Warm month mean temperature (°C)	WMMT	1.8
Cold month mean temperature (°C)	CMMT	2.6
Length of the growing season (mo)	GROWSEAS	.9
Growing season precipitation (mm)	GSP	326.5
Mean monthly growing season precipitation (mm)	MMGSP	37.1
Precipitation during the three wettest months (mm)	3-WET	13.9
Precipitation during the three driest months (mm)	3-DRY	91.5
Relative humidity (%)	RH	8.1
Specific humidity (g/kg)	SH	1.0
Enthalpy (kJ/kg)	ENTHALPY	3.8

Note.   Abbreviations used in this article and the standard deviations of the residuals about the regression line of observed climate data against the CLAMP climate parameter vector score using the PHYSG3AR data set.
[a] Reflects standard deviation of residuals about the regression line between the observed value and the climate parameter vector score.
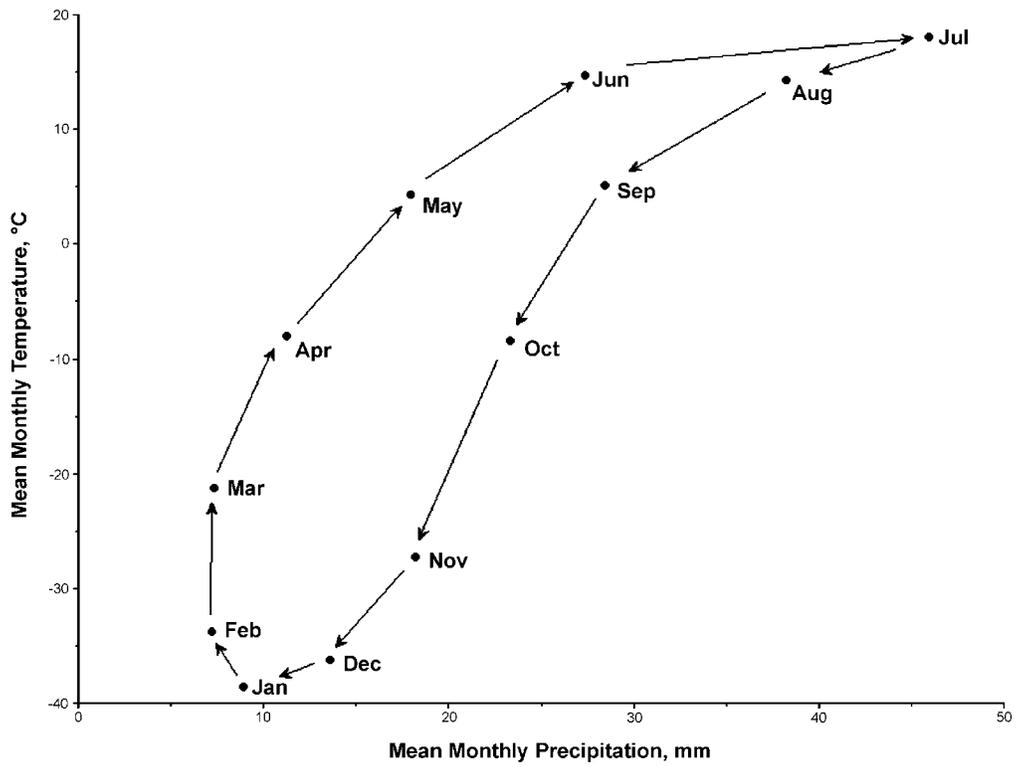
Figure 2. Plot of mean monthly precipitation against mean monthly temperature for Viluisk, central Eastern Siberia
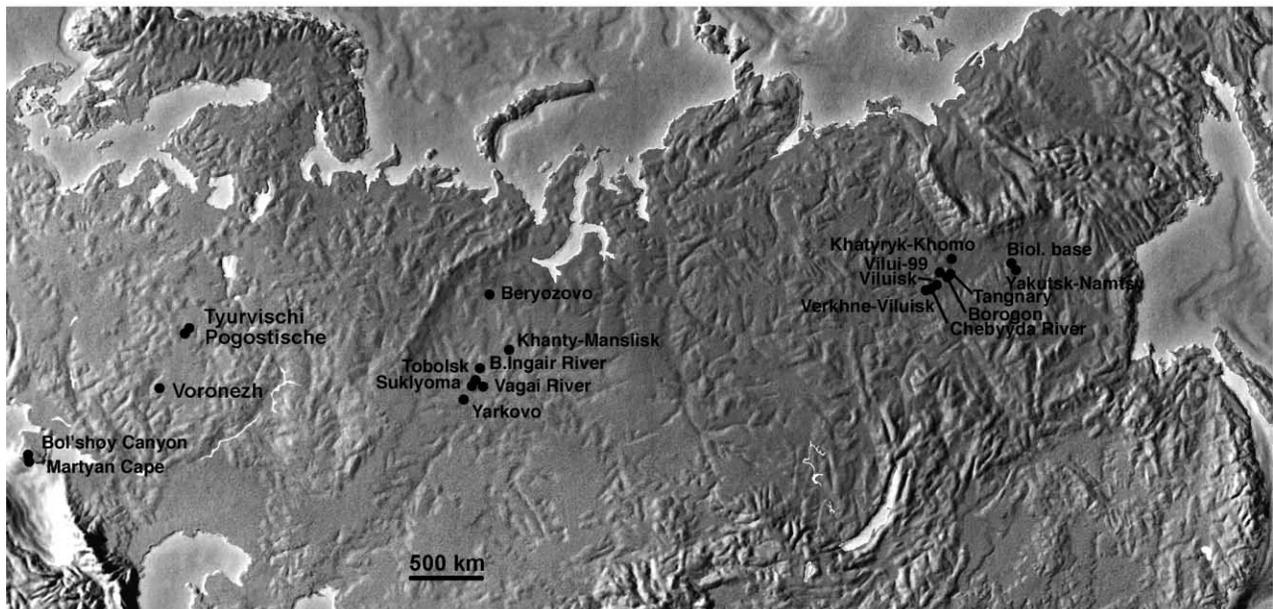

Figure 3. Map of Eastern Europe and northern Asia shows the position of the cold transect vegetation sample sites reported on in this article.

Table 2. Mean Annual Summaries of Meteorological Data Relating to the Cold Transect Sites

Site no.	Site name	MAT (°C)	WMMT (°C)	CMMT (°C)	MART (°C) ★	Length of growing season (mo)	MAP (mm) ★	GSP (mm)	MMGSP (mm)	3-WET (mm)	3-DRY (mm)	RH (%)	SH (g/kg)	Enthalpy (kJ/kg)
1	Martian	12.3	23.3	1.9	21.4	6.6	577.0	250.0	36.0	241.0	66.0	66.9	6.5	30.6
2	B.Kanyon	10.2	20.0	.0	20.0	6.0	673.0	306.0	48.0	266.0	82.0	73.9	6.2	30.3
3	Voronezh	6.9	21.2	−9.5	27.8	5.4	510.0	273.0	48.0	207.0	73.0	72.9	5.2	29.7
4	Pogostische	4.4	18.7	−11.7	30.5	4.6	614.0	293.0	59.0	240.0	83.0	77.5	4.9	29.3
5	Tyurvischi	4.4	18.7	−11.7	30.5	4.6	614.0	293.0	59.0	240.0	83.0	77.5	4.9	29.3
6	Yarkovo	1.0	18.9	−19.0	37.9	4.0	464.0	224.0	56.0	218.0	49.0	75.1	4.2	28.8
7	Vagai	.7	19.0	−19.7	38.7	3.9	465.0	236.0	57.0	227.0	51.0	73.4	3.9	28.7
8	Suklyom River	.3	18.8	−20.2	39.0	3.7	470.0	226.0	58.0	221.0	48.0	74.7	4.1	28.7
9	Tobolsk	.3	18.8	−20.2	39.0	3.7	470.0	225.0	58.0	221.0	48.0	74.7	4.1	28.7
10	Bol'shoy Ingair	.3	18.8	−20.2	39.0	3.7	470.0	226.0	58.0	221.0	48.0	74.7	4.1	28.7
11	Khanty-Mansiisk	−1.4	18.3	−22.4	40.7	3.2	551.0	212.0	63.0	244.0	64.0	77.1	3.8	28.4
12	Beryozovo	−3.6	16.5	−24.6	41.2	2.8	532.0	185.0	61.0	232.0	68.0	77.3	3.4	28.1
13	Verkhneviluisk	−9.3	17.4	−38.2	55.5	3.1	277.0	116.0	32.0	159.0	18.0	70.1	2.8	27.3
14	Chebyda	−9.0	18.3	−38.6	56.9	3.1	266.0	124.0	35.0	129.0	22.0	68.0	2.7	27.3
15	Viluisk	−9.0	18.3	−38.6	56.9	3.1	266.0	124.0	35.0	129.0	22.0	68.0	2.7	27.3
16	Hydropost	−9.0	18.3	−38.6	56.9	3.1	266.0	124.0	35.0	129.0	22.0	68.0	2.7	27.3
17	Tangnary	−9.0	18.3	−38.6	56.9	3.1	266.0	124.0	35.0	129.0	22.0	68.0	2.7	27.3
18	Khatyryk-Khomo	−10.8	17.7	−41.3	59.0	3.1	252.0	110.0	31.0	121.0	24.0	70.2	2.8	27.2
19	Namtsyr	−9.7	18.9	−41.5	60.4	3.2	235.0	114.0	31.0	121.0	19.0	67.9	2.8	27.3
20	Biol Base	−9.7	18.9	−41.5	60.4	3.2	235.0	114.0	31.0	121.0	19.0	67.9	2.8	27.3

Note. Climate variables marked with an asterisk (MART = mean annual range of temperature, MAP = mean annual precipitation) were not included in the CLAMP analyses. MAT = mean annual temperature, WMMT = warm month mean temperature, CMMT = cold month mean temperature, GSP = growing season precipitation, MMGSP = mean monthly growing season precipitation, 3-WET = precipitation during the three wettest months, 3-DRY = precipitation during the three driest months, RH = relative humidity, SH = specific humidity.

land displays the most extreme anomalous behavior so far documented, presumably because it has been more or less genetically isolated since it broke away from greater Antarctica in the early Late Cretaceous. Since then, New Zealand plants have been exposed to varying environmental constraints as a function of both global climate change and tracking to ever-lower latitudes. Foliar physiognomic adaptation to such environmental change has taken place within the context of a restricted gene pool. It is little surprise then that the correlation between foliar physiognomy and climate is somewhat different to that of the rest of the world's vegetation, and in particular to that in the northern hemisphere where such isolation has never occurred to the same extent.

Clearly, biogeographic history can have an effect on the CLAMP calibration, but to what extent this also applies to climatic regimes that are outside those encompassed by the existing calibration data sets is questionable. Applying CLAMP to climatic regimes not encompassed in the reference data sets invites problems, and this is particularly marked in tropical regimes. Under warm climates, leaf margins tend to be smooth and lack teeth (Bailey and Sinnott 1915, 1916), and with the loss of margin-related character states, CLAMP loses precision. In effect, this imposes a limit to how useful CLAMP is likely to be in tropical regimes (Kowalski 2002). At the cold end of the climatic spectrum the situation is, however, more critical. A particular

strength of CLAMP is that it not only yields mean annual temperature (MAT) but also provides information on warm month mean temperature (WMMT) and cold month mean temperatures (CMMT), together with a range of precipitation variables, humidity, and enthalpy (table 1). Enthalpy is a function of both temperature and moisture and can be used in paleoaltitude determinations (Forest et al. 1995; Wolfe et al. 1998; Spicer et al. 2003), and because temperature declines with increasing altitude, improving CLAMP performance at low temperatures is particularly important.

Foliar Physiognomy and Climate: Why Is There a Relationship?

The overall appearance of vegetation (i.e., its physiognomy), but not necessarily its taxonomic composition, tends to be characteristic of the particular climatic regime in which that vegetation grows. Vegetation can therefore be classified in terms of its physiognomy, and climatic signals can be related to it independent of taxonomic considerations (e.g., Holdridge 1947). This is because many plant morphologies represent particular adaptations to particular environmental constraints. Plants are spatially fixed and, therefore, have to be well adapted to local conditions in order to survive. Plants lack the homeostatic mechanisms of many animals that effectively isolate those organisms from the external conditions. Furthermore, plants
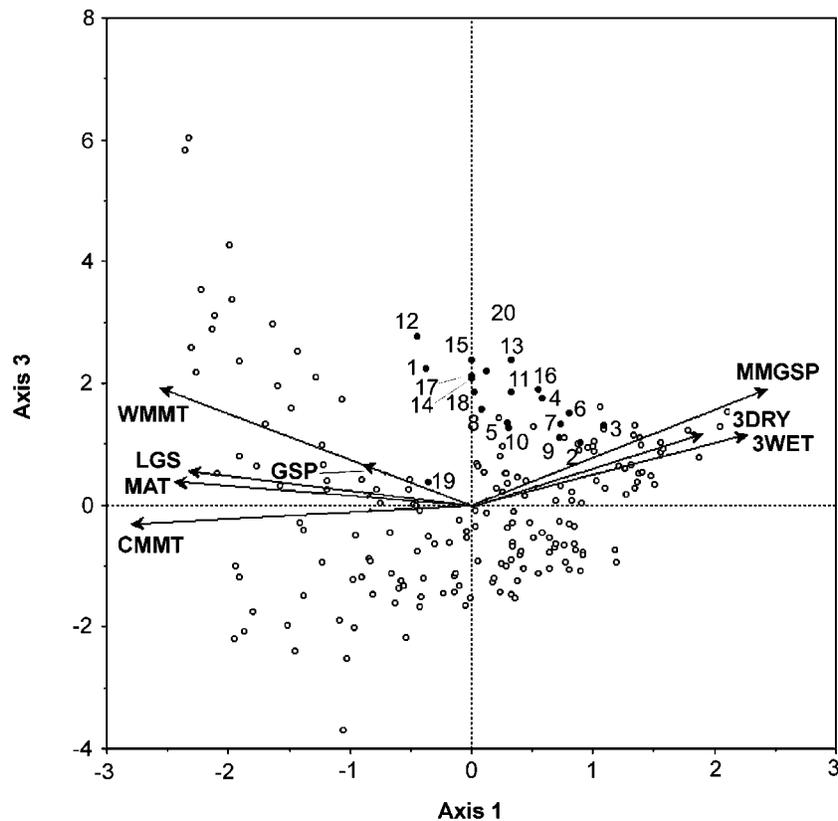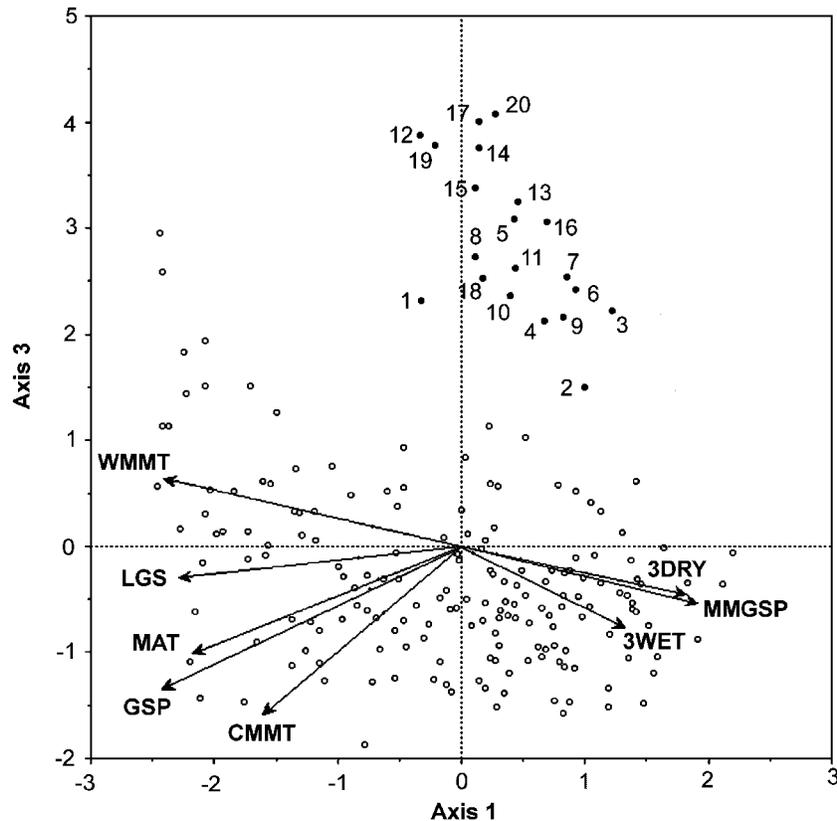
Figure 4. Plot of CANOCO 4.0 Canonical Correspondence Analysis axes 1 against 3 when the cold transect sites (CTS) are entered as passive elements using the PHYSG3AR Climate Leaf Analysis Multivariate Program data set. The CTS (*filled circles*) are numbered as in the previous text.

process the atmosphere for their existence because the exchange of oxygen and carbon dioxide is essential for photosynthesis. Plants are therefore intimately linked to the atmosphere and must be adapted to the climate in which they find themselves growing. Only those plants with a genome that affords certain appropriate phenotypic expressions are able to survive in particular environmental regimes. Inappropriate phenotypes fail to survive, either by the physical environment taking its toll directly or as a result of competition from better-suited plants.

Although all parts of a plant throughout all stages of the life cycle contribute to the overall success or failure of the individual, it is the leaf that plays the most critical role in environmental adaptation. The photosynthetic function of a leaf demands that it is efficient at intercepting light and exchanging gases with the atmosphere while affording the minimum water loss concomitant with the maintenance of water flow within the plant and evaporative cooling of the leaf surface. All this must be

achieved with the minimum of structural tissue investment because building leaf tissue costs energy and ultimately food resources. Thus, there are only a limited range of "engineering solutions" that can satisfy, approximately, the often conflicting constraints that exist in a given set of environmental conditions. Inevitably many environmental variables, as well as foliar adaptations to them, are cocorrelated. Because the unchanging laws of gas diffusion, fluid flow, and mechanics impose these constraints, these solutions are time stable and independent of taxonomic affinity (Spicer 2000).

Foliar physiognomic "tuning" to the environment can be seen to operate not only across different plant lineages, and between individual plants within lineages (ecophenotypes), but also within the individual plant itself. Moreover, this tuning is not only spatial but also temporal. For example, leaves at the top of a tree crown exposed to high light levels and wind energies tend to be small, thick, and robust, whereas those in the darker, more sheltered, humid subcanopy space tend to be

Figure 5. Plot of CANOCO 4.0 Canonical Correspondence Analysis axes 1 against 3 when the cold transect sites (CTS) are entered as active elements (i.e., accompanying meteorological data are also supplied and used to constrain physiognomic space) with the PHYSG3AR CLAMP data set. The CTS are numbered as in the previous text.

larger and thinner. If the environment around a tree changes with time, for example, through removal of surrounding trees, subsequent cohorts of leaves will display different appropriate morphologies. The genome of such trees must therefore be capable of generating a variable phenotype in response to the environmental conditions immediately surrounding each leaf on a season-by-season basis.

Plants must produce leaves that are adaptive to the entire growing season and not just to the conditions that exist at the leaf development or expansion stage. This ability to seemingly "predict" future likely conditions must be genetically predetermined through ancestral selection. For example, plants in the Mediterranean region, California, and Chile receive abundant rainfall during the spring when the new leaf crop is produced, but this is followed by extreme summer drought. If the plants responded only to the spring rains and produced large leaves, these leaves would be nonadaptive during the dry summertime. Clearly, selection favors genotypes that are tuned to the overall cli-

matic conditions and not just those experienced by the plant at the time of leaf production. Vegetation in recently glaciated and nonglaciated parts of the Northern Hemisphere also demonstrates a good correlation with climate as is represented by the PHYSG3AR/3BR data sets. This shows that genetic and phenotypic tuning of foliar physiognomy takes place over geologically short time scales ($\ll 1$ m.yr.) as a result of taxonomic elimination and migration, as well as by selection for novel genotypes that arise as the result of chance mutation or hybridization.

It could be argued that a plant might be largely insensitive to climatic conditions while dormant. Deciduous trees that have no leaf load during the winter would experience few, if any, selection pressures that would influence foliar architectures indicative of winter conditions. However, this cannot be the case because the existing PHYSG3AR data set, which includes the so-called alpine nest, clearly codes for CMMTs below zero, even though many of the taxa sampled are deciduous. To some extent it could be that CMMT is determined by a
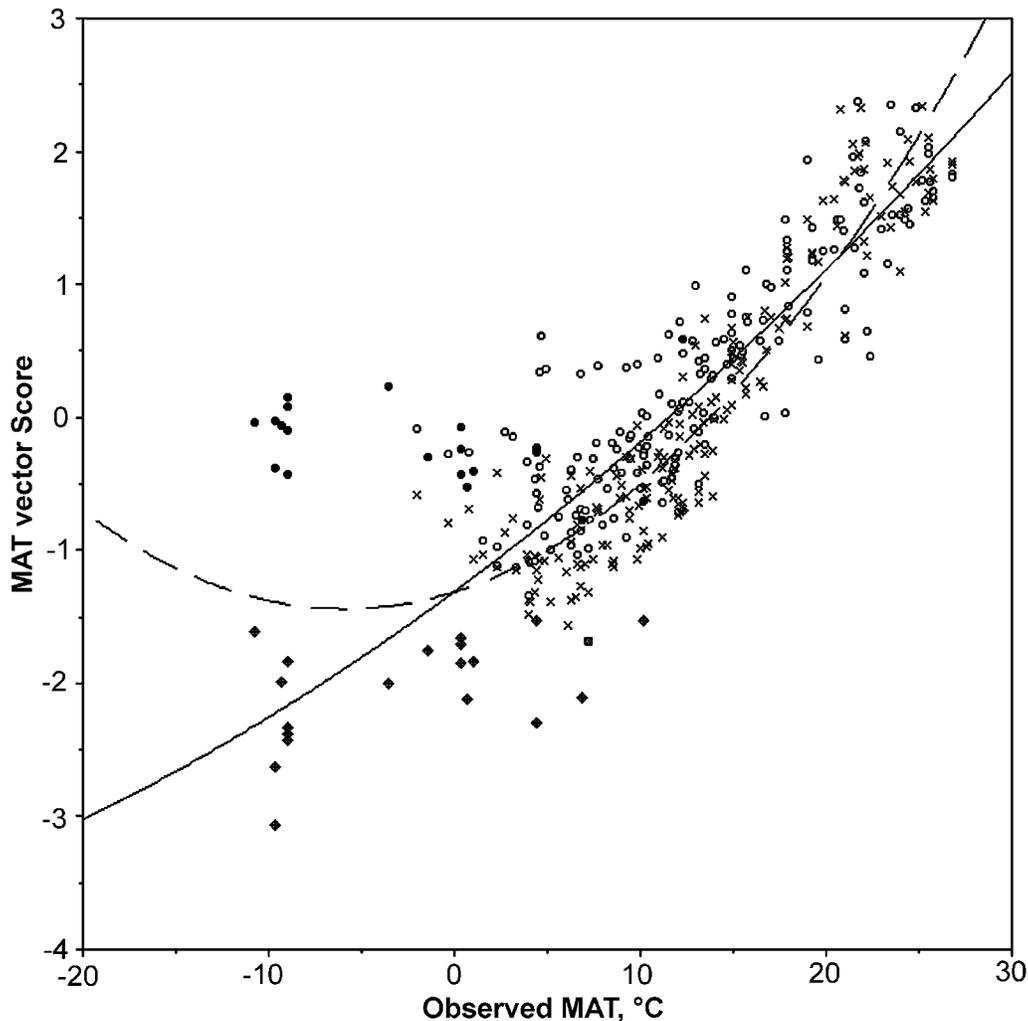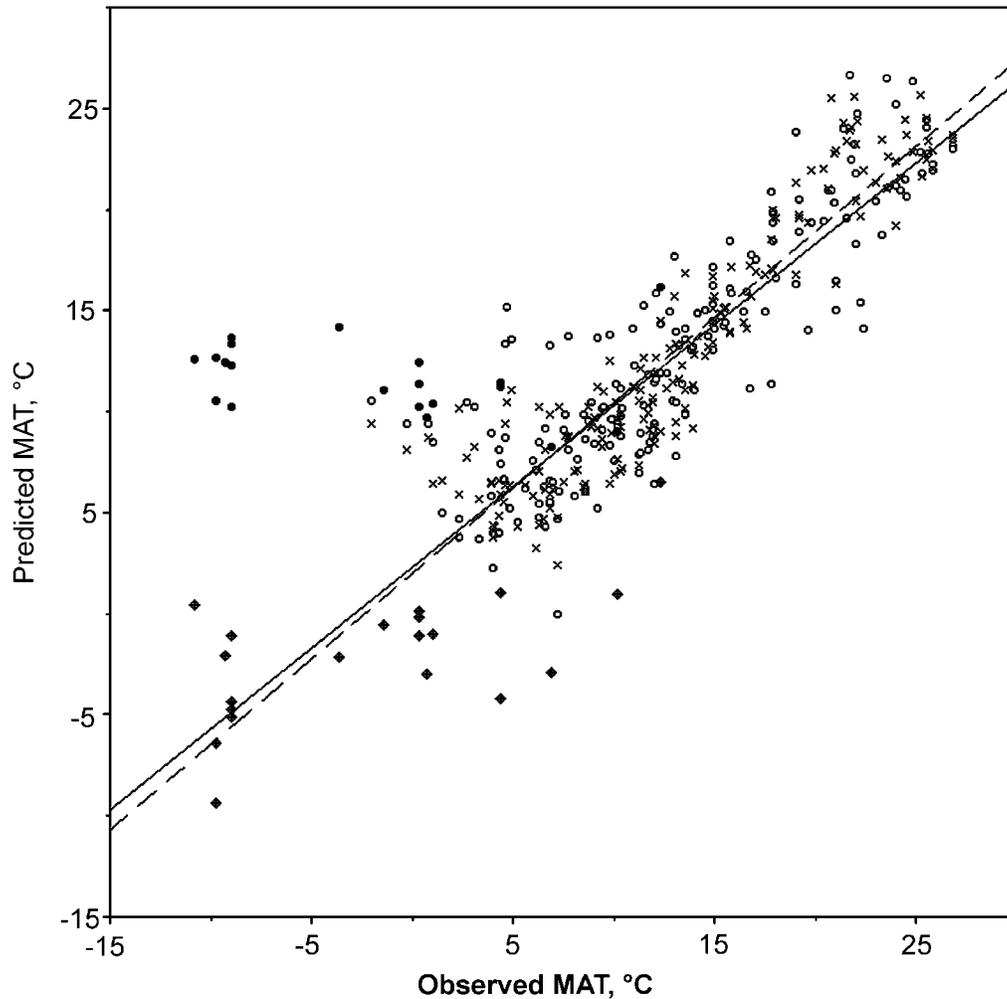
Figure 6. Observed mean annual temperature plotted against the mean annual temperature vector score. Crosses represent the positions of sites comprising the PHYSG3AR data set when the cold transect site (CTS) data are passive; open circles are the positions of PHYSG3AR sites when the CTS data are active; filled circles are the positions of the CTS when passive; the filled diamonds are the positions of the CTS when active. The dashed regression curve is when the CTS are passive ($r^2 = 0.875$), and the solid line is when the CTS are active ($r^2 = 0.806$).

combination of the MAT and WMMT, but the question then must be asked how leaf physiognomy codes for MAT if the plants are insensitive to winter conditions.

To explore the relationship between foliar physiognomy and climate when winter dormancy is a significant event in the annual cycle of growth, we sampled vegetation across an environmental gradient that included the most extreme present-day continental climate regime. We sampled an east-west transect across European Russia, the Crimean Peninsula, and Siberia. We will refer to these as the cold transect sites (CTS).

The Interior Continental Climate of Central Eastern Siberia

Figure 2 summarizes the annual cycle of temperature and precipitation for Viluisk, Yakutia, central-Eastern Siberia. Starting in January, the CMMT is close to $-40°C$, and precipitation is also low at about 10 mm. Through to mid-April, temperatures remain below freezing, and the local continental interior internal circulation of moisture remains low. However, as soon as the thaw sets in, evaporation increases, leading to a rise in precipitation such that in July the mean monthly precip-

Figure 7. Observed mean annual temperature plotted against the mean annual temperature predicted by both the PHYSG3AR data set (*crosses, dashed regression line* as in fig. 6) and the PHYSG3AR data together with the cold transect site (CTS) data (*circles, solid regression line*). Cold transect site samples are shown as solid circles when behaving passively and as filled diamonds when active. Passive regression $r^2 = 0.847$; active regression $r^2 = 0.800$.

itation is nearly 50 mm. With warm temperatures, evaporation is high and stays high throughout the fall until the winter freeze sets in. The pronounced loop in the annual cycle is also a function of the movement of the polar front, which travels southward in the winter as a high-pressure cell develops over the cold continental interior (the center of this cell being near the village of Oymyakon, close to Viluisk) and northward again as the continental interior heats up in the summer.

Plants growing in this region therefore experience more than half the year with temperatures below freezing, but the spring, when water movement within the plant is most critical for leaf ex-

pansion, is also a time of comparative drought. The maximum period of growth does, however, coincide with the period of greatest water availability. If the plants were only adapting to the conditions experienced during the growing season, then there should be little reflection of the CMMT, or the associated hydrological conditions, in the physiognomy of the Siberian leaves.

Methods

In total, 20 modern vegetation sites across European Russia, the Crimean Peninsula (Ukraine), Western Siberia, and Yakutia (Eastern Siberia) were
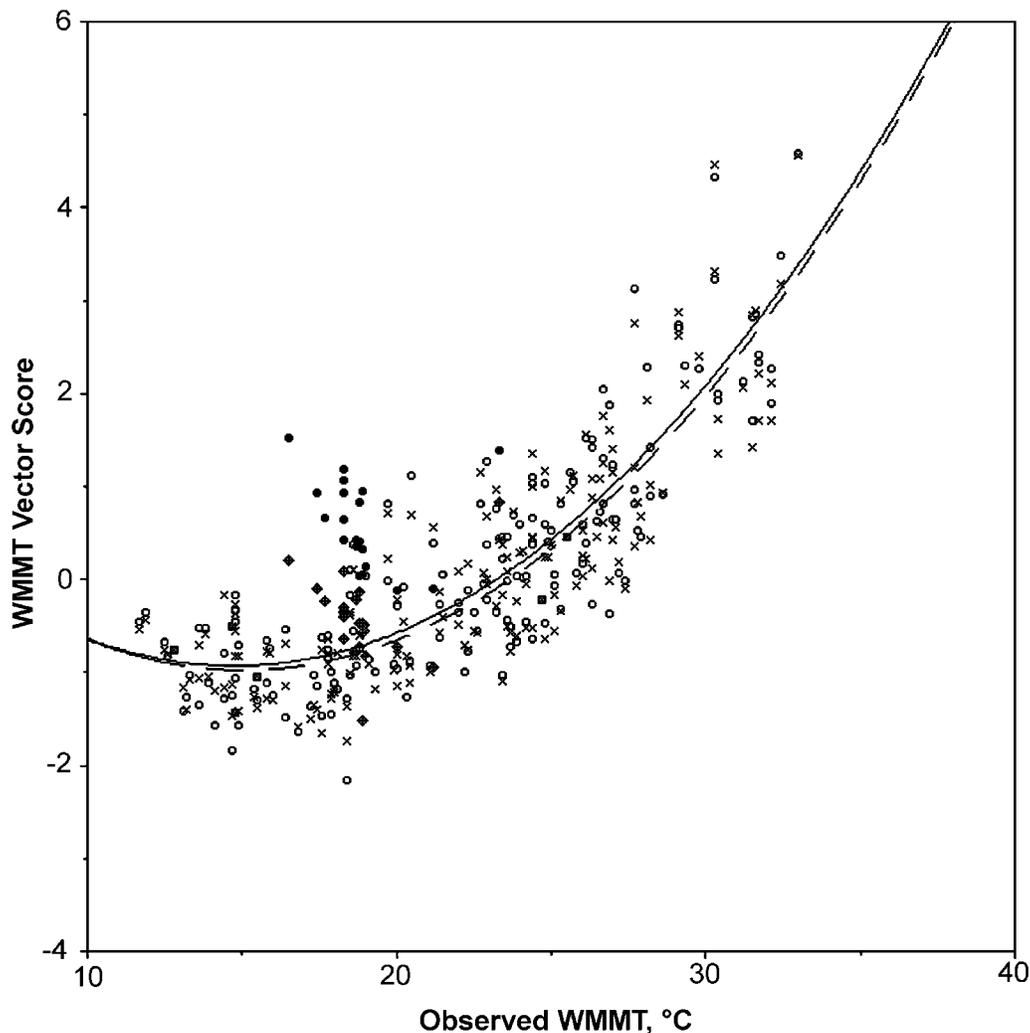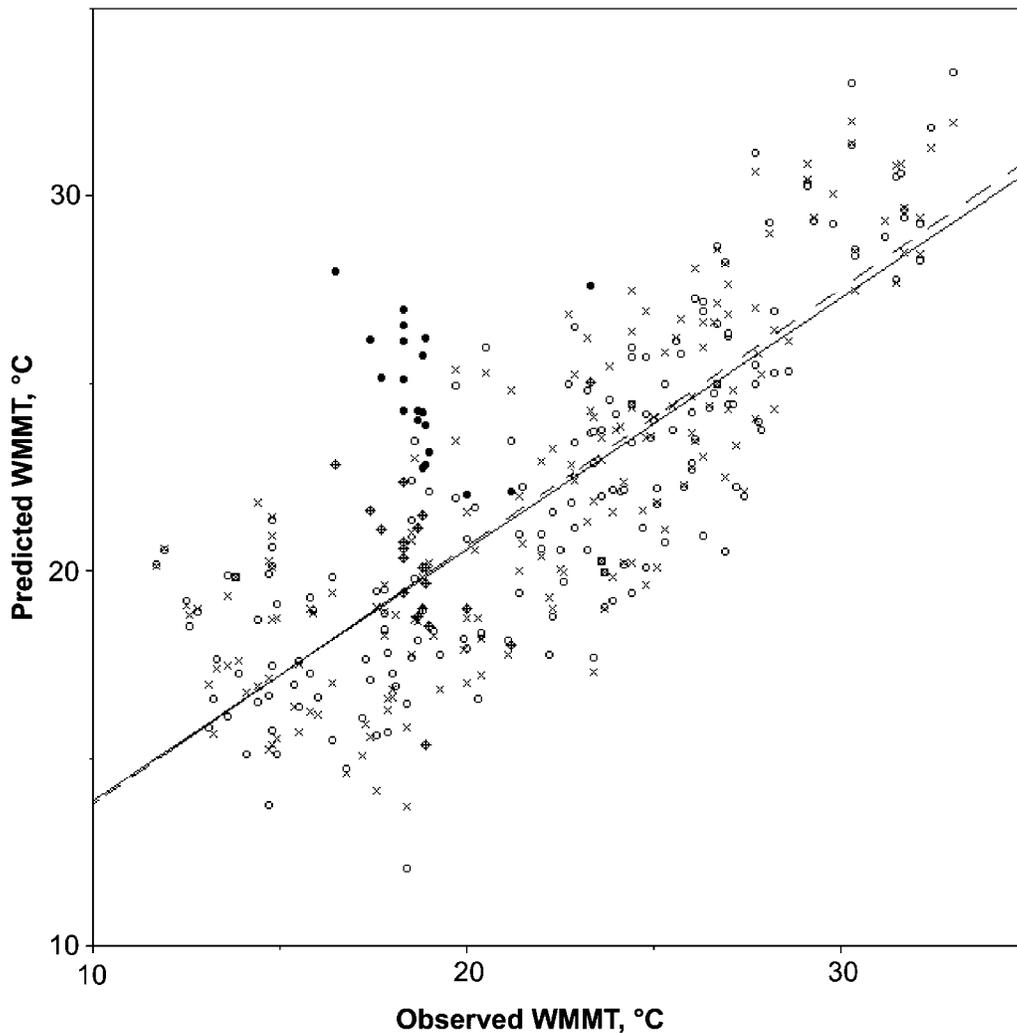
Figure 8. Observed warm month mean temperature plotted against the warm month mean temperature vector score. Legend as in figure 6. Passive regression $r^2 = 0.754$; active regression $r^2 = 0.746$.

sampled during the summers of 2002 and 2003 (fig. 3). The full morphological range of leaf types from a minimum of 20 woody dicot taxa at each site were scored for the 31 different character states as defined in Wolfe (1993; http://tabitha.open.ac.uk/spicer/CLAMP/Clampset1.html). The sites were selected for the necessary woody dicot diversity in stable vegetation near meteorological stations. In some instances, fewer than 20 species were found, and with these samples, the uncertainties arising from the lower diversity will be larger than the norm for CLAMP. Also, in some instances meteorological stations were some distance away from the vegetation sites, but in the flat topography of much of the area under consideration and corresponding uniform local climate, this has lit-

tle consequence. The locations, species diversity, and distance to the meteorological stations for the cold transect sites are given subsequently. Meteorological data (the mean annual summaries of which are shown in table 2) were supplied by the All-Russian Research Institute of Hydrometeorological Information, World Data Center, Obninsk, Russia.

Area A (Fig. 3): Crimean Peninsula (Ukraine). Two sites were sampled at different altitudes: (1) Cape Martyan National park near Yalta/Nikita (weather station within the National Park at 200-m elevation), 44.5°N, 34.3°E; elevation, 50–300 m. Species sampled: 26. (2) Crimean Bol'shoy Canyon (17 km to weather station at the same altitude); 44.4°N, 33.8°E, elevation, 600–800 m. Species sampled: 29.
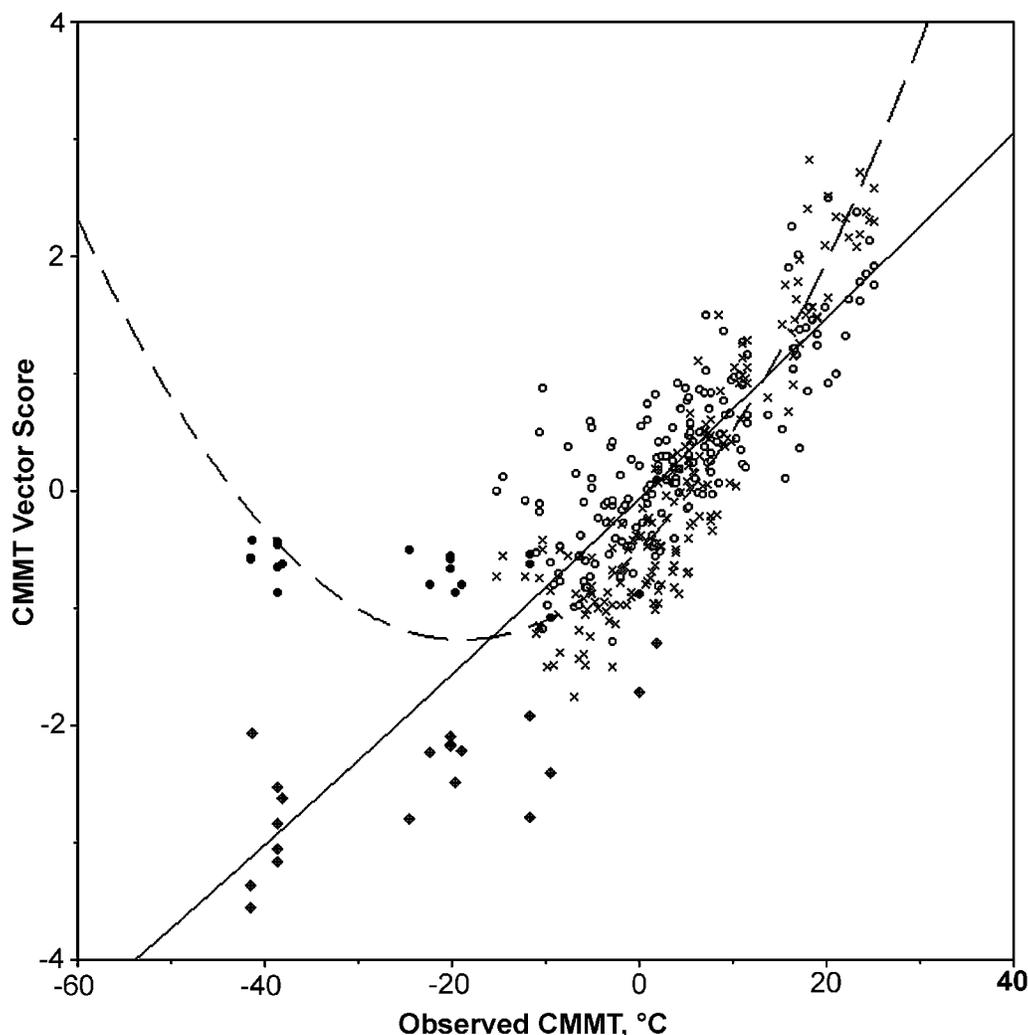
Figure 9. Observed warm month mean temperature plotted against predicted warm month mean temperature. Legend as in figure 7. Passive regression $r^2 = 0.67$; active regression $r^2 = 0.688$.

Area B (Fig. 3): Central (European) Russia. Three sites were sampled: (3) Voronezh, 50.9°N, 39.5°E; elevation, 115 m. Species sampled: 30. (4) Pogostische, 55°18′N, 40°15′E; elevation, 114 m. Species sampled: 19. (5) Tyurvischi, 55°21′N, 40°16′E; elevation, 116 m. Species sampled: 17.

Area C (Fig. 3): Western Siberia. Seven sites were sampled spanning a latitudinal range of more than 6° and across the width of the taiga belt from mixed woodland in the south to forested tundra in the north: (6) Near Yarkovo Village (95 km northeast from Tyumen' Town, approximately 3–4 km from a weather station); 57°23.014′N, 67°01.498′E; elevation, 96 m. Species sampled: 24. (7) Vagai River/ Village (55 km southeast from Tobolsk Town, ap-

proximately 5–6 km from a weather station); 57°52.759′N, 69°02.289′E; elevation, 50 m. Species sampled: 26. (8) Suklyom River, near Podrezovo Village (near Tobolsk Town, approximately 25 km from a weather station); 58°04.705′N, 67°56.763′E; elevation, 38 m. Species sampled: 23. (9) Tobolsk Town (Chuvashskii Cape, approximately 5 km from a weather station); 58°10.887′N, 68°17.101′E; elevation, 87 m. Species sampled: 25. (10) Bolshoy Ingair River, near Gornoslinkino Village (northeast from Tobolsk Town, approximately 70 km from a weather station); 58°45.302′N, 68°50.594′E; elevation, 27 m. Species sampled: 21. (11) Near Khanty-Mansiisk Town (approximately 8 km from a
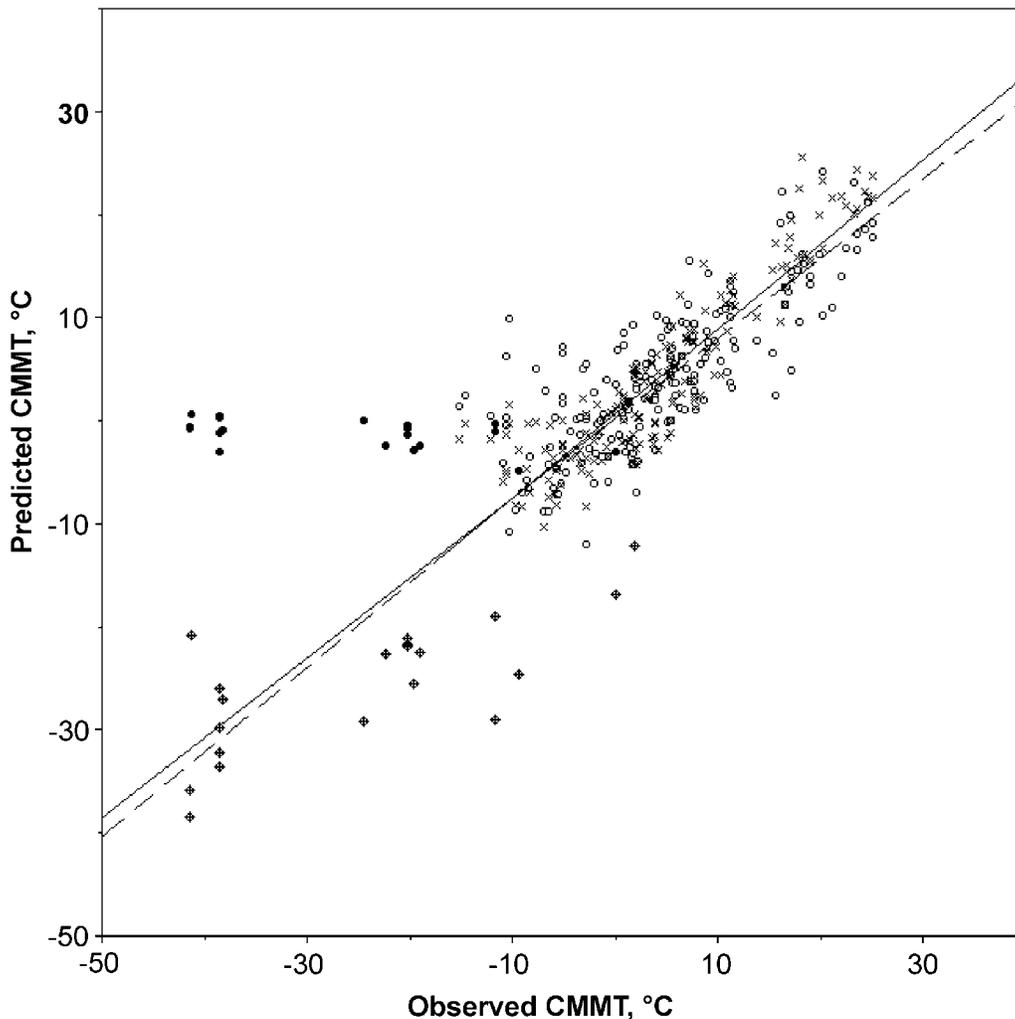
Figure 10. Observed cold month mean temperature plotted against cold month mean temperature vector score. Legend as in figure 6. Passive regression $r^2 = 0.864$; active regression $r^2 = 0.774$.

weather station); 61°03.232′N, 69°15.510′E; elevation, 33 m. Species sampled: 25. (12) Near Beryozovo Village (the northernmost site in this area, approximately 7 km from a weather station); 63°54.469′N, 67°64.707′E; elevation, 19 m. Species sampled: 20.

Area D: Yakutia (Eastern Siberia). Eight sites were sampled: (13) Verkhneviluisk, 63°26.599′N, 120°22.505′E; elevation, 105 m. Species sampled: 21. (14) Chebyyda, 63°35.247′N, 121°09.643′E; elevation, 103 m. Species sampled: 23. (15) Viluisk, 63°46.201′N, 121°39.679′E; elevation, 86 m. Species sampled: 27. (16) Borogon Village Hydropost (Tangnary River near Borogon Village), 63°49.197′N, 123°34.248′E; elevation, 100 m. Species sampled: 23. (17) Tangnary River, 63°50.819′N,

123°40.056′E, elevation, 100 m. Species sampled: 22. (18) Khatyryk-Khomo, 63°56.681′N, 124°50.530′E; elevation, 72 m. Species sampled: 18. (19) Namtsyr, near Yakutsk (closest meteorological station is in Yakustk), 62°08.793′N, 129°39.770′E; elevation, 145 m. Species sampled: 23. (20) Biological Base, near Yakutsk, 62°14.817′N, 129°37.266′E; elevation, 100–210 m. Species sampled: 21.

The CLAMP scoresheets for all 20 sites are available at the CLAMP Web site. The CLAMP scores were added to the PHYSG3AR data set and analyzed using Canonical Correspondence Analysis (ter Braak 1986) within CANOCO 4.0 (see the CLAMP Web site, http://tabitha.open.ac.uk/spicer/CLAMP/clampset.html, for further details) both as

Figure 11.   Observed cold month mean temperature plotted against predicted cold month mean temperature. Legend as in figure 7. Passive regression $r^2 = 0.820$; active regression $r^2 = 0.776$.

(1) passive samples (i.e., without accompanying meteorological data) so that the PHYSG3AR data were used to predict the climates of the sites as if they had been fossil assemblages and (2) active samples with their observed meteorological data so as to reposition and recalibrate the climate vectors. Results are shown in figures 4–16.

Results and Discussion

When the cold transect sites were treated as passive samples, they plotted within the main cluster of PHYSG3AR in axis 1–2 space, but in a distinct cluster on axis 3 (the axis of the third greatest variation in the data set; fig. 4). This immediately suggests that the physiognomy of the leaves from these sites is distinctive compared with that present in the

main body of the PHYSG3AR reference set, even though that set contains the "alpine nest" sites. The cold transect cluster appears aligned to some extent with the WMMT vector as one might expect, but when the data in table 2 are examined, it is clear that there is no obvious ordering in terms of WMMT.

Figure 5 shows axis one-third space when the cold transect sites are treated as active, and the plot is partially constrained by their associated data. The distinctiveness of the sites is even more apparent, and the direction of the climate vectors has moved, as one would expect, because of the influence of the new data. Within the cold transect cluster there is some substructure with the warm, dry, Crimean sites (Martian and B. Canyon) plotting to the lower part of the cluster while the coldest sites
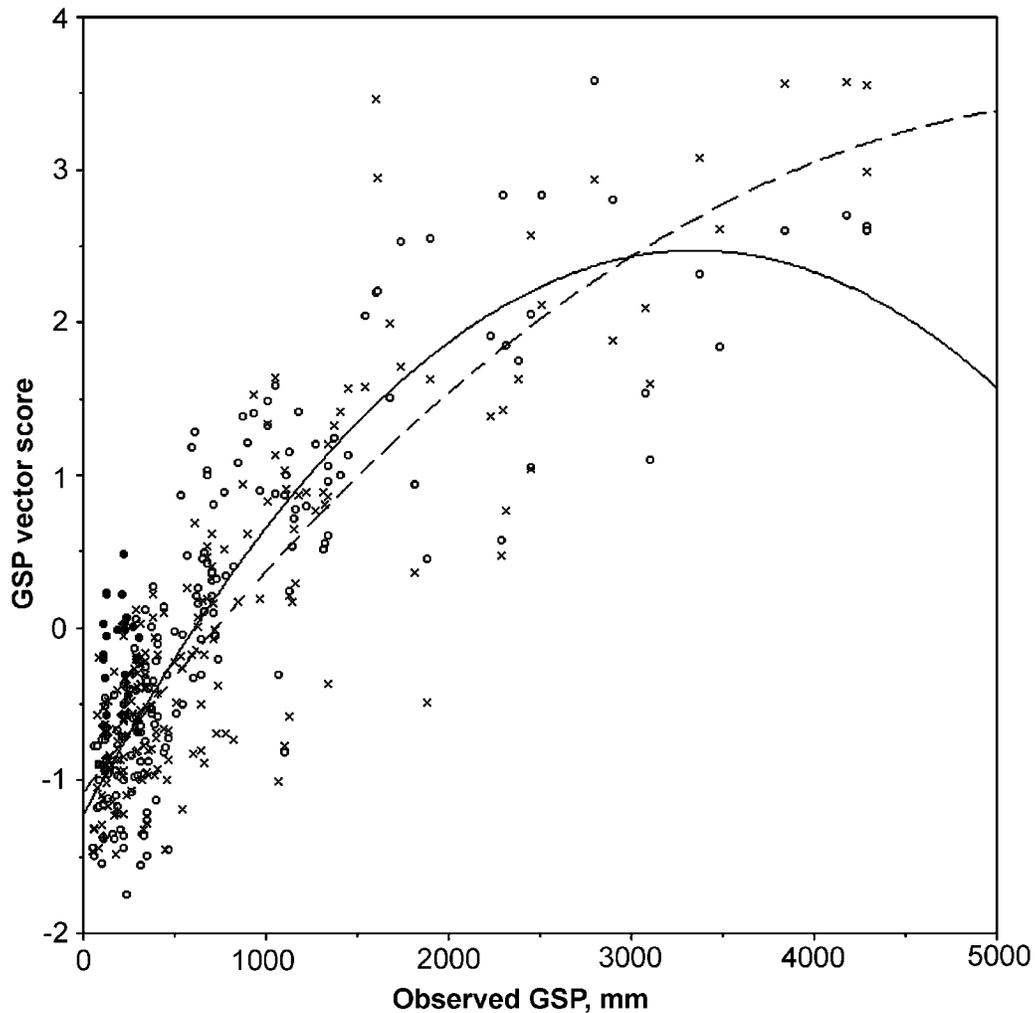
Figure 12.   Observed growing season precipitation plotted against the growing season vector score. Legend as in figure 6. Passive regression $r^2 = 0.755$; active regression $r^2 = 0.789$.

tend to plot higher. However, the long axis of the cluster is not aligned with the MAT or the WMMT vector. In fact, it shows no obvious ordering in terms of the climate vectors currently used in CLAMP, and further research is required to identify which environmental constraints select for such a distinctive physiognomy on the cold transect leaves, particularly those from Western Siberia and Yakutia. Nevertheless, with the modified position of the climate vectors following the addition of the cold transect sites to the PHYSG3AR, it is possible to explore to what extent the physiognomy of the CTS leaves reflect the CMMT.

Figure 6 shows the observed MAT (actual meteorological measurements taken at the sites where vegetation used in the plots is growing) plotted against the MAT vector score for the PHYSG3AR

data set (the trend shown in the ordering of the vegetation sites based on leaf physiognomy) with the CTS data as both passive and active elements. When passive, the regression line curves upward at low temperatures, indicating no predictive capability, but when the cold transect data are used to constrain the regression (i.e., they are active), the regression line is almost straight. Figure 7 illustrates the improvement in the predictive capabilities of including the cold transect data as active elements. Ideally, the regression line should be at 45° if the correlation were perfect between the observed and the predicted MAT. However, although the cold transect sites clearly display foliar physiognomic traits that reflect MAT, CLAMP underestimates MAT by as much as 5°C for cold climates where the MAT is −10°C or lower.
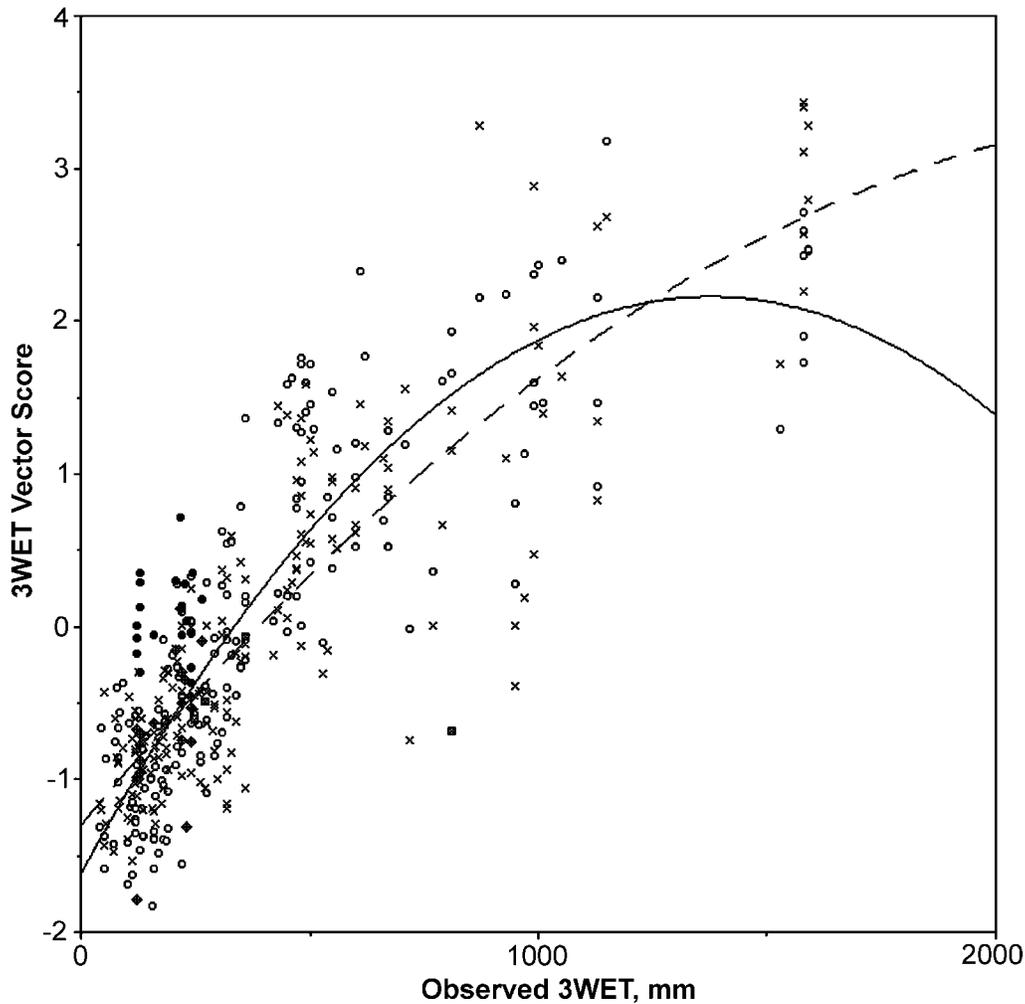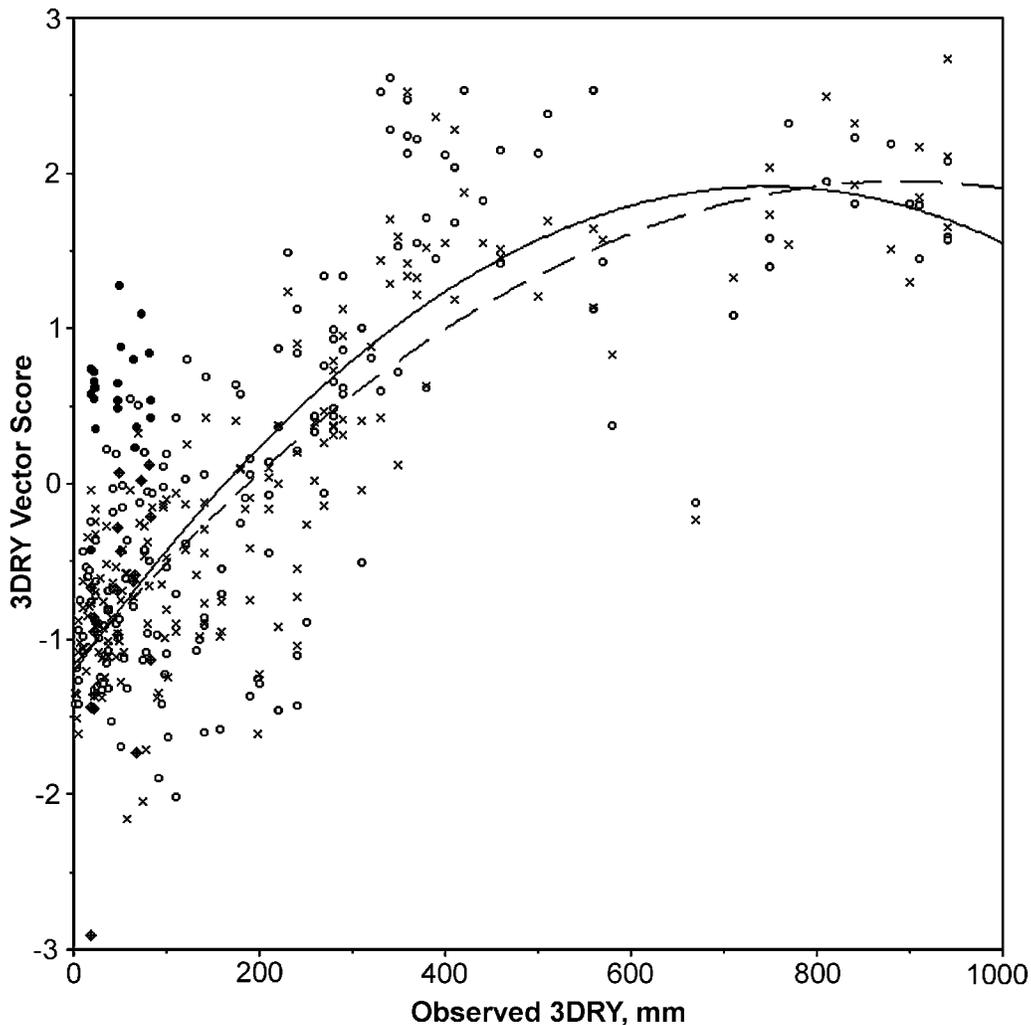
Figure 13. Observed precipitation during the three wettest months plotted against precipitation during the three wettest months vector score. Legend as in figure 6. Passive regression $r^2 = 0.745$; active regression $r^2 = 0.758$.

Adding the cold transect sites as active elements has a far less dramatic effect on CLAMP's ability to accurately predict WMMTs. Figure 8 shows little change in the observed versus vector score regression over the full range of WMMTs. Despite this, there is some improvement in the reliability of WMMT predictions as indicated by the downward translation of the positions of the cold transect sites when treated as active elements. Here again, overall, there is a tendency for CLAMP to overestimate the WMMT by as much as 4°–5°C in cool climates with or without the CTS data (fig. 9). Although a simple regression has been applied here, the distribution of the data points in the upper right quadrant suggests that at warmer temperatures, the predictive capabilities are better.

If the WMMT regression is little affected and the

MAT regression shows a significant improvement when the new sites are added, then it might be expected that the CMMT regression would show the greatest change. This proves to be so and is illustrated in figure 10. Clearly, the cold transect leaf physiognomy is coding for the CMMT because their addition as active elements dramatically affects the regression, effectively straightening it out. In predictive terms, at a CMMT of around freezing, the new data provide for a highly effective tool, but at low temperatures, CLAMP gives an estimate that is too warm by up to 9°C. In the plot of the observed CMMT against the predicted CMMT (fig. 11), the addition of the CTS data affects the regression only slightly, suggesting that the CTS samples are reflecting the CMMT in essentially the

Figure 14. Observed precipitation during the three driest months plotted against precipitation during the three driest months vector score. Legend as in figure 6. Passive regression $r^2 = 0.737$; active regression $r^2 = 0.645$.

same way as those of the PHYSG3AR data set despite the low temperatures experienced.

With respect to precipitation, the GSP regression of observed against the vector score (fig. 12) shows little change at the dry end of the scale where the new data fall. There is a small predictive improvement of up to 60 mm, but overall, CLAMP's ability to predict precipitation during the growing season in dry regimes is good. What is apparent though is that over much of the area covered by the cold transect sites, summer flooding and seasonal thaw of subsurface permafrost maintain a high soil moisture content that appears not to be reflected in leaf physiognomy.

The plots for the precipitation during the three wettest months and the three driest months (figs. 13, 14, respectively) both show a similar pattern to

that of the GSP, in that the effect of adding the cold transect sites has little effect on the PHYSG3AR regressions. There is useful improvement in the predictive potential, but overall, leaves from the cold transect sites react to precipitation in a similar manner to leaves from the PHYSG3AR data set.

With enthalpy, which is a function of both temperature and humidity, the effect of adding the cold transect sites is to straighten the regression curve (fig. 15), indicating a uniform relationship between the observed values and the vector score across the entire range of values. This transforms into a predictive improvement of some 20 kJ/kg (fig. 16). At low enthalpy values (less than 270 kJ/kg), there is still a tendency for CLAMP to overestimate enthalpy by 8 kJ/kg, whereas at high values (>340 kJ/kg), CLAMP overestimates enthalpy by a similar
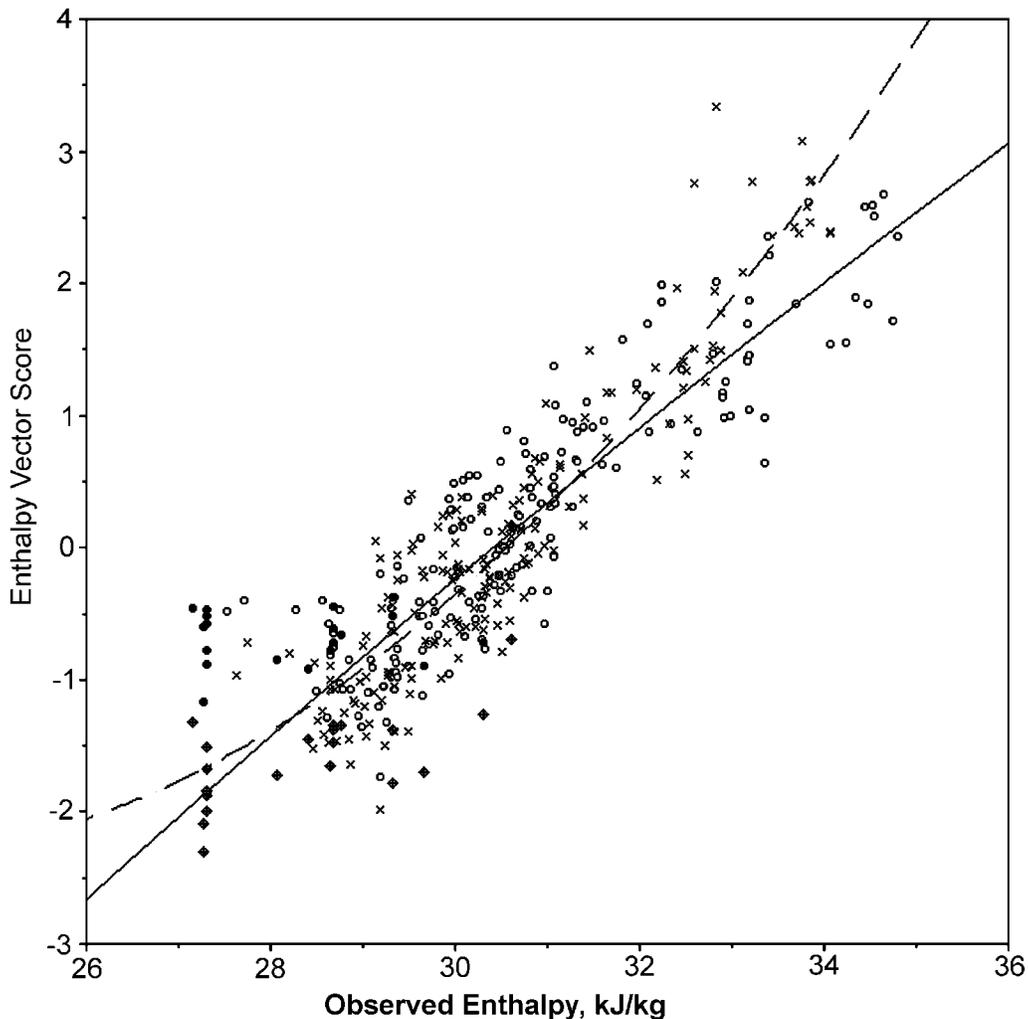
Figure 15. Observed enthalpy plotted against enthalpy vector score. Legend as in figure 6. Passive regression $r^2 =$ 0.852; active regression $r^2 = 0.820$.

amount. In the midrange values (285–335 kJ/kg), this error is less.

Conclusions

Despite winter dormancy, woody dicots from across the continental interior of northern Asia exhibit physiognomies that seem to reflect to a large extent the CMMTs experienced in those regions. Temperatures experienced during the active growing season, the WMMTs, are the most faithfully encoded, and adding the CTS samples had little effect on the WMMT calibration regressions obtained for more equable sites, predominantly from North America and Japan. The addition of the CTS samples did, however, radically improve the predictive capability of CLAMP for the CMMT at low

temperatures. Despite this improvement, CLAMP still tends to underestimate the CMMT, particularly at very low temperatures, but this can be corrected for and ceases to be a problem when CMMTs are near freezing or above. There can be little doubt that foliar physiognomy does code for the CMMT, even in these extreme situations. If it did not, the error in predicting the CMMT would be much greater.

The physiognomic coding in the CTS leaves for precipitation appears to reflect the spring drought conditions more than high moisture availability during the summer. This is perhaps not surprising because nonadaptation to lack of free water during the leaf expansion phase would result in failure of the leaf crop. There is clearly a photosynthetic price for this because the leaves may not be optimally
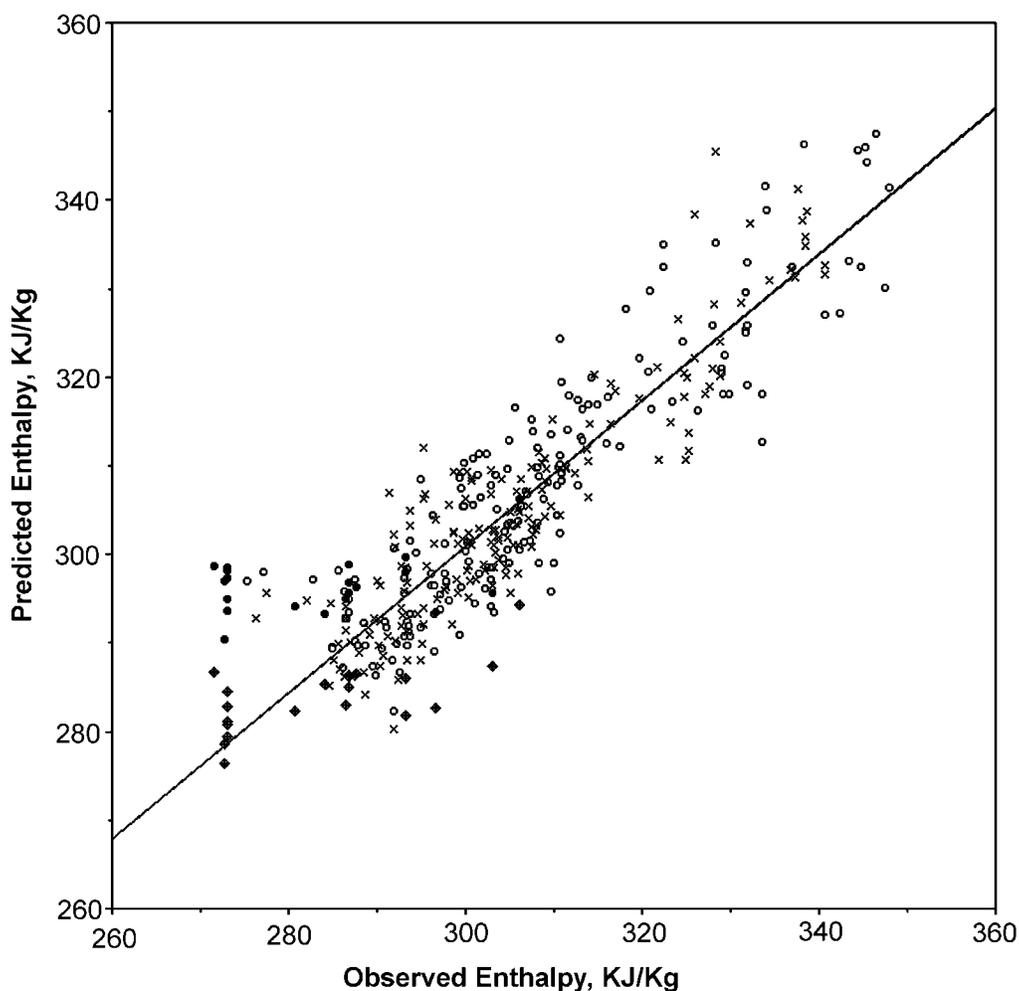
Figure 16. Observed enthalpy plotted against predicted enthalpy. Legend as in figure 7. Passive regression $r^2 = 0.824$; active regression $r^2 = 0.826$. The regression lines are indistinguishable.

adapted for summer conditions. However, if the soil becomes water-saturated in the summer during river flooding (which is common because the mouths of the north-draining rivers are often frozen until mid–late summer), then the roots systems would be stressed, a condition that may be best accommodated by having drought-adapted leaves.

The enthalpy calibration, used for determining palaeoaltitudes was unaffected by adding the CTS samples, suggesting the calibration for enthalpy is uniform across all warm temperate to cold regimes capable of supporting the growth of woody dicots. Thus, enthalpy remains a highly robust approach to determining paleoelevations.

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