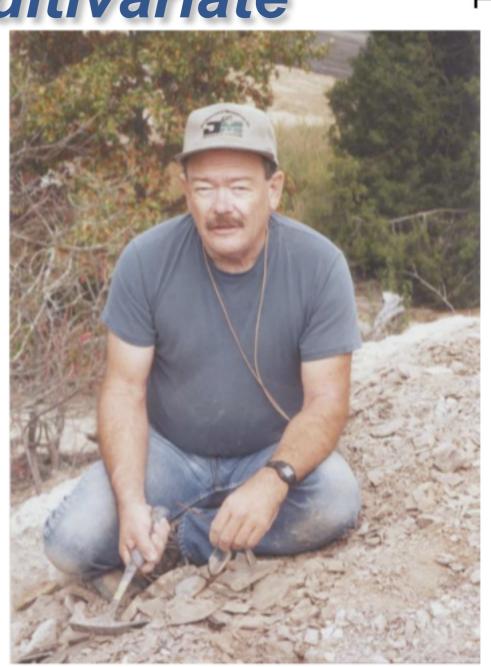


Climate Leaf Analysis Multivariate

Program

Bob Spicer (r.a.spicer@open.ac.uk)

A palaeoclimate proxy based on leaf physiognomy initially developed by the late Jack A Wolfe.



Jack a Wolfe

Friday, 24 April 2009

**CLAMP** 

Climate Leaf Analysis Multivariate Program

A palaeoclimate proxy based on leaf physiognomy initially developed by the late Jack A Wolfe.

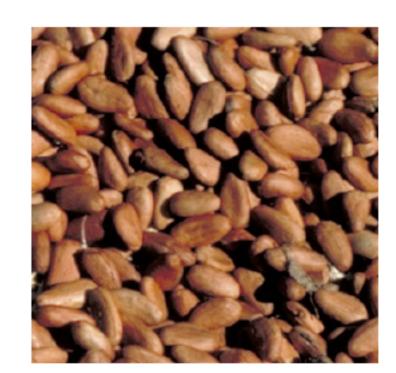
### Plant Palaeoclimate Proxies



Palaeoclimate proxies may be divided into two types:

- 1) those based on the environmental tolerances of assumed living relatives (nearest living relative approaches) and
- 2) those that are based on aspects of plant architecture constrained by environmental conditions (physiognomic approaches).





Nearest living relative techniques (NLR) can be applied to all plant organs assignable to modern taxa but are most useful for those plant organs lacking known morphological adaptations to the physical environment (e.g. seeds and pollen). However they are restricted to timescales where evolutionary change at the species level is unlikely. In most cases <1-5Ma, although techniques that involve protocols for examining populations (e.g. Co-existance Analysis and Overlapping Distribution Analysis) can be extended further back in time.





2

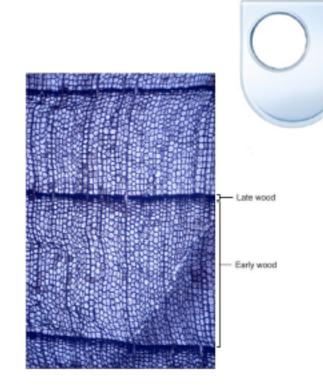
Friday, 24 April 2009

Plant palaeoclimate proxies may be divided into two types: 1) those based on environmental tolerances of assumed nearest living relatives, and 2) those based on aspects of plant architecture constrained by environmental conditions. The first type has the advantage is being applicable to all identifiable plant organs but it is subject to evolutionary change. It can only be reliably used, therefore, where evolutionary affects can be regarded as being minimal (e.g. < 1Ma).

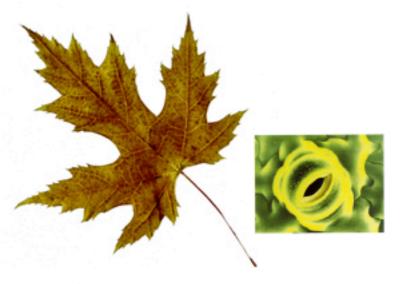
## Plant Palaeoclimate Proxies

**Physiognomic** - Climatic signals encoded in plant architecture as a developmental and growth response to the environment, honed by selection to maximise functional efficiency. Examples - wood anatomy, leaf architecture and stomatal analysis.

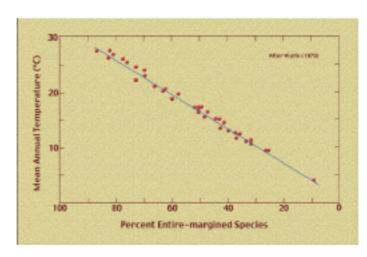
These techniques have the advantage of being useful over long timescales that encompass previous greenhouse climates, but are restricted to comparatively rare leaf and wood assemblages.



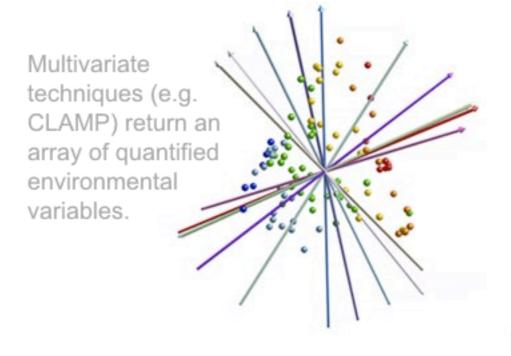
Wood records almost daily variations in growth conditions but is difficult to quantify unambiguously in terms of climate variables.



Stomatal analysis can yield estimates of ppCO<sub>2</sub> and, in ideal circumstances, estimates of elevation.



Univariate Techniques - Leaf Margin Analysis - return a single variable e.g. mean annual temperature.



Friday, 24 April 2009

The second type is referred to as a physiognomic approach. The advantage of the physiognomic approach is that it can be applied in deep time (> 1Ma) because it is based on time-stable laws of physics such as gas diffusion, radiation and fluid flow.



In desert regions where water is in short supply leaves are either small or have been dispensed with altogether in favour of photosynthetic stems. Additional adaptations include stem enlargement for water storage.



These adaptations are universal and are governed by the physics of evaporation. A small surface area to volume ratio is advantageous in limiting evaporation.

Because this represents a general "engineering solution" to the problem of water loss similar morphologies have evolved in similar environments independent of taxonomic affiliations.



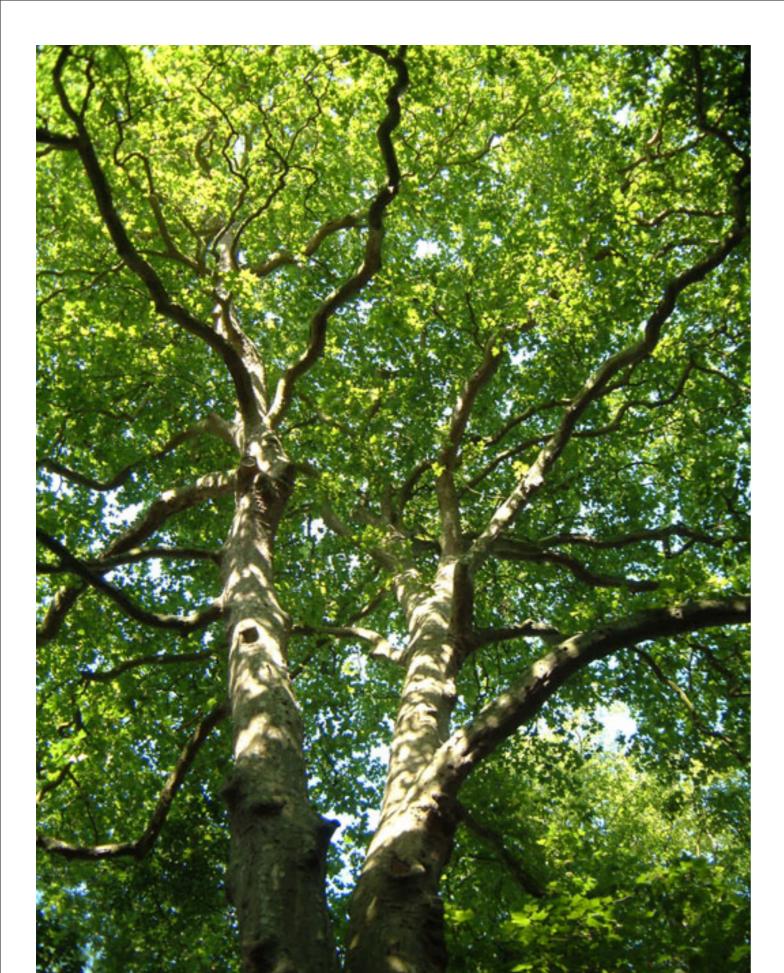
Friday, 24 April 2009

In desert regions where water is in short supply leaves are either small or have been dispensed with altogether in favour of photosynthetic stems. Additional adaptations include stem enlargement for water storage.

These adaptations are universal and are governed by the physics of evaporation. A small surface area to volume ratio is advantageous in limiting evaporation.

Because this represents a general "engineering solution" to the problem of water loss similar morphologies have evolved in similar environments independent of taxonomic affiliations.

The lower right image demonstrates that in extreme cases plants with no close taxonomic affinities can have highly convergent morphologies as in the case of the Old World member of the Euphorbiaceae (left) and the New World Cactaceae (right).





In environments where water supply is not limiting a much larger leaf surface area can be supported without desiccation. Leaf area indices (total leaf area/unit area of ground surface) > 12 can be observed in rain forests. Individual leaf size range can be large.

However leaves also reflect the local microclimate: leaves at the top of the tree crown are exposed to high insolation and wind speeds so are smaller and thicker than leaves in the darker, more humid, understory.

5

Friday, 24 April 2009

In environments where water supply is not limiting a much larger leaf surface area can be supported without desiccation. Leaf area indices (total leaf area/unit area of ground surface) > 12 can be observed in rain forests. Individual leaf size range can be large where water is not limiting.

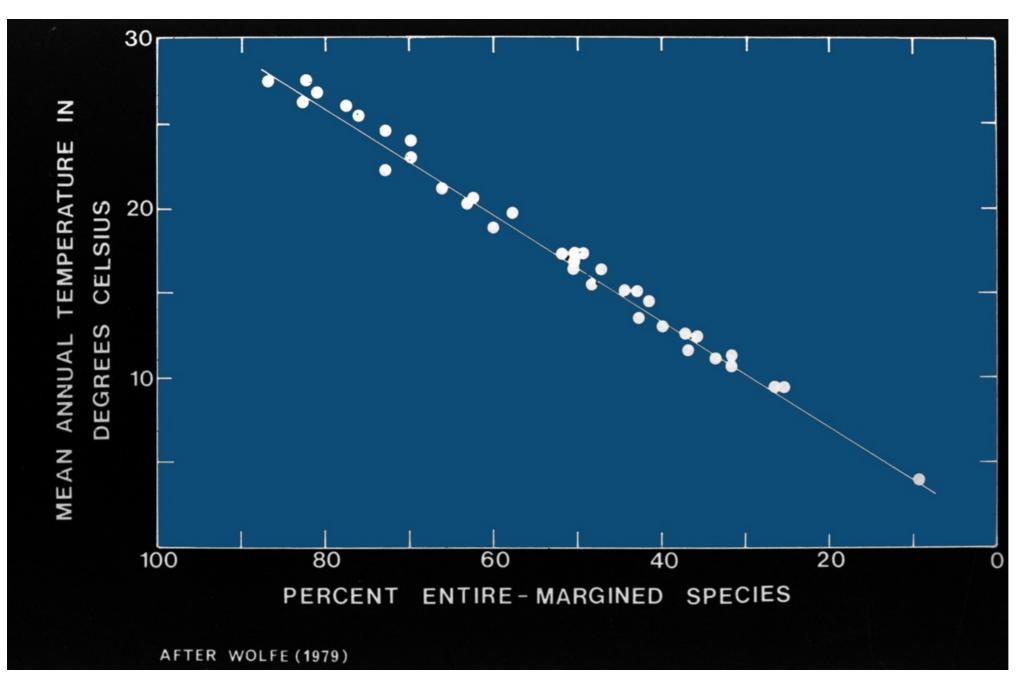
However leaves also reflect the local microclimate: leaves at the top of the tree crown are exposed to high insolation and wind speeds so are smaller and thicker than leaves in the darker, more humid, understory. I using leaves as a palaeoclimate indicator this leaf polymorphism must be taken into account.





Other aspects of leaf architecture vary with environment. As long ago as 1915 Bailey and Sinnott noted in Science that for woody dicots in North America the proportion of taxa bearing toothed versus entire margined leaves varies with mean annual temperature.





In 1979 Wolfe retested this relationship using leaves from S.E. Asia.

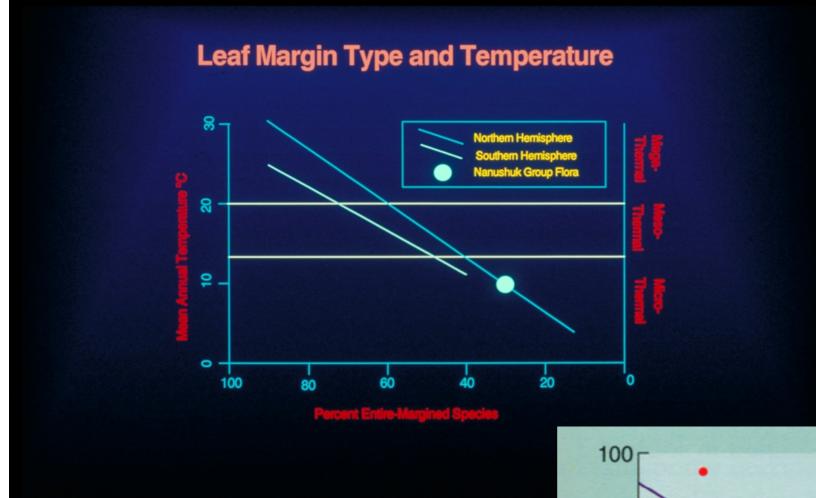
The relationship only works where water is not limiting, i.e. in humid to mesic forests.

Friday, 24 April 2009

Other aspects of leaf architecture vary with environment. As long ago as 1915 Bailey and Sinnott noted in Science that for woody dicots in North America the proportion of taxa bearing toothed versus entire margined leaves varies with mean annual temperature.

In 1979 Wolfe retested this relationship using leaves from S.E. Asia. This graph is taken from that work.

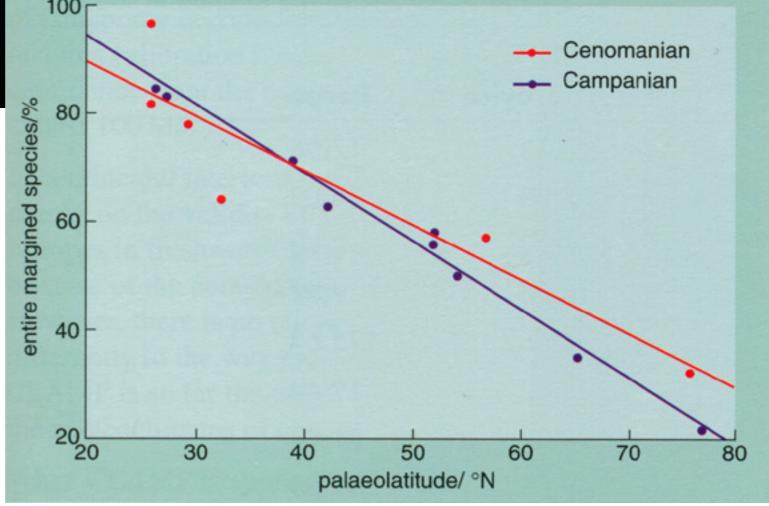
The relationship only works where water is not limiting, i.e. in humid to mesic forests.



Wolfe also noted that the relationship, as evidenced by the slope of the regression line, differs between Northern and Southern Hemispheres.

When tested using fossil floras Wolfe also noted that the percentage of entire margined taxa when plotted against palaeolatitude tracks changes in equator-to-pole temperature gradients (and global mean surface temperature).

There appears to be no change in slope associated with the polar light regime (>66°).



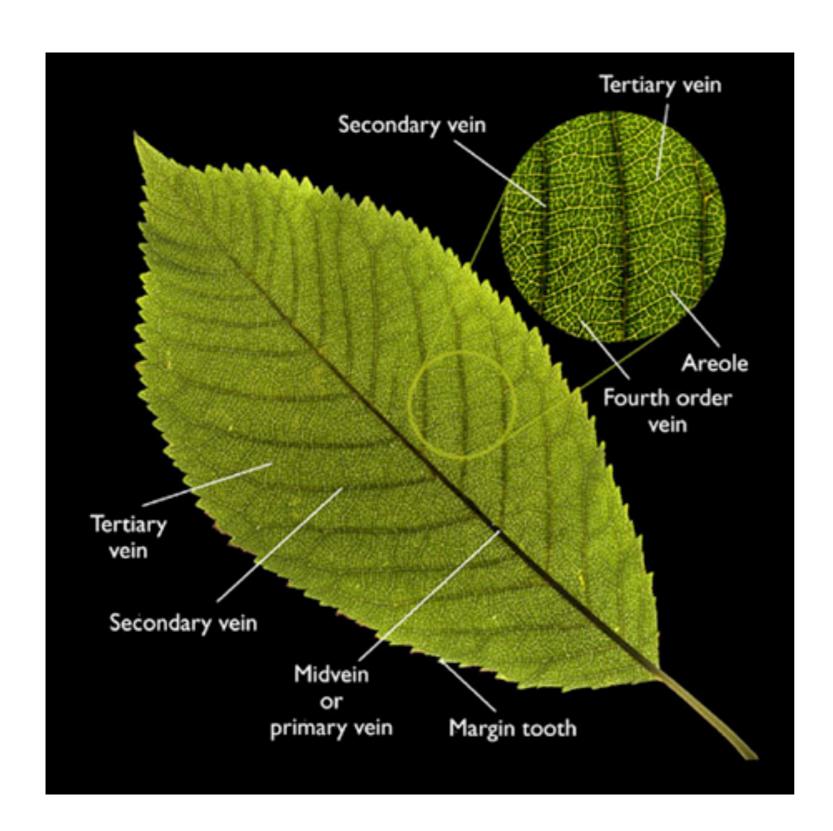
Friday, 24 April 2009

Wolfe also noted that the relationship, as evidenced by the slope of the regression line, differs between Northern and Southern Hemispheres. This relationship have been revisited and refined by others (e.g. Wilf, P. 1997. When are leaves good thermometers? A new case for Leaf Margin Analysis, Paleobiology 23: 373-390). The underlying cause is unclear, but it likely to involve several factors including maintaining leaf temperature and fluid flow within the plant. As with all leaf architectural features there is no simple relationship between any given feature and any given climate parameter.

When tested using fossil floras Wolfe also noted that the percentage of entire margined taxa when plotted against palaeolatitude tracks changes in equator-to-pole temperature gradients (and global mean surface temperature) even in the late Cretaceous when thermal equator to pole gradients are thought to have been shallower than today.

There appears to be no change in slope associated with the polar light regime (>66°).





Wolfe surmised that if leaf size was primarily related to water loss and margin characteristics were primarily related to mean annual temperature, then it was likely that many other leaf architectural characteristics might carry environmental signals.

However it is unlikely that each architectural (physiognomic) feature relates to a separate environmental parameter (variable).

8

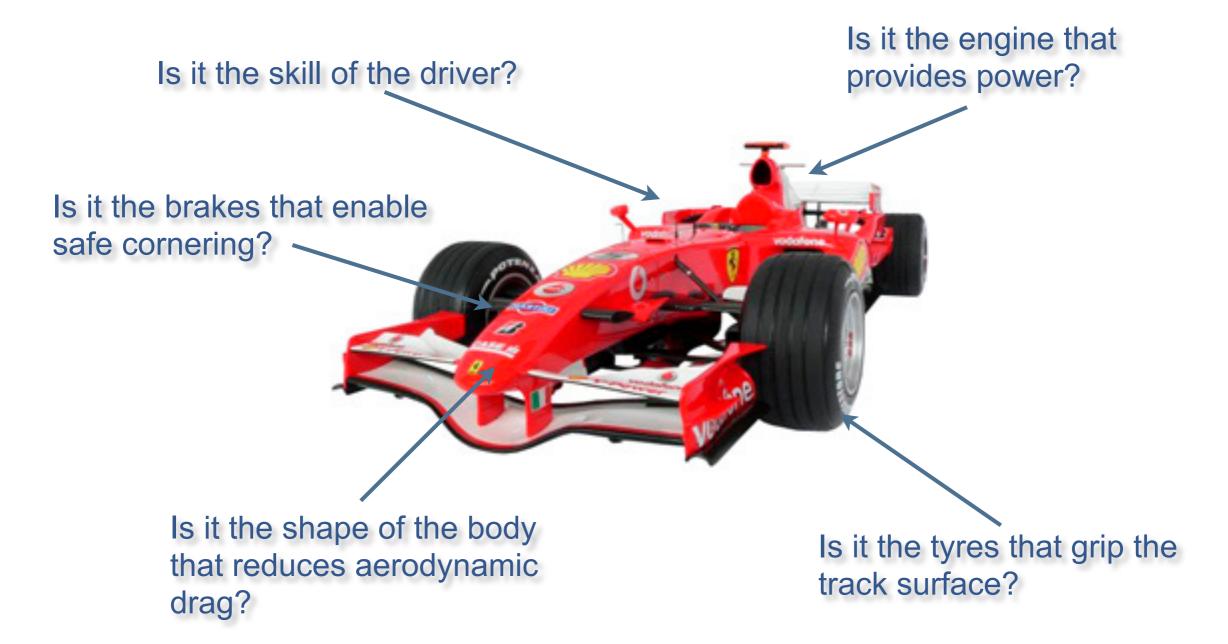
Friday, 24 April 2009

Wolfe surmised that if leaf size was primarily related to water loss and margin characteristics were primarily related to mean annual temperature, then it was likely that many other leaf architectural characteristics might carry environmental signals.

However it is unlikely that each architectural (physiognomic) feature relates to a separate environmental parameter (variable). What is required is a multivariate approach.

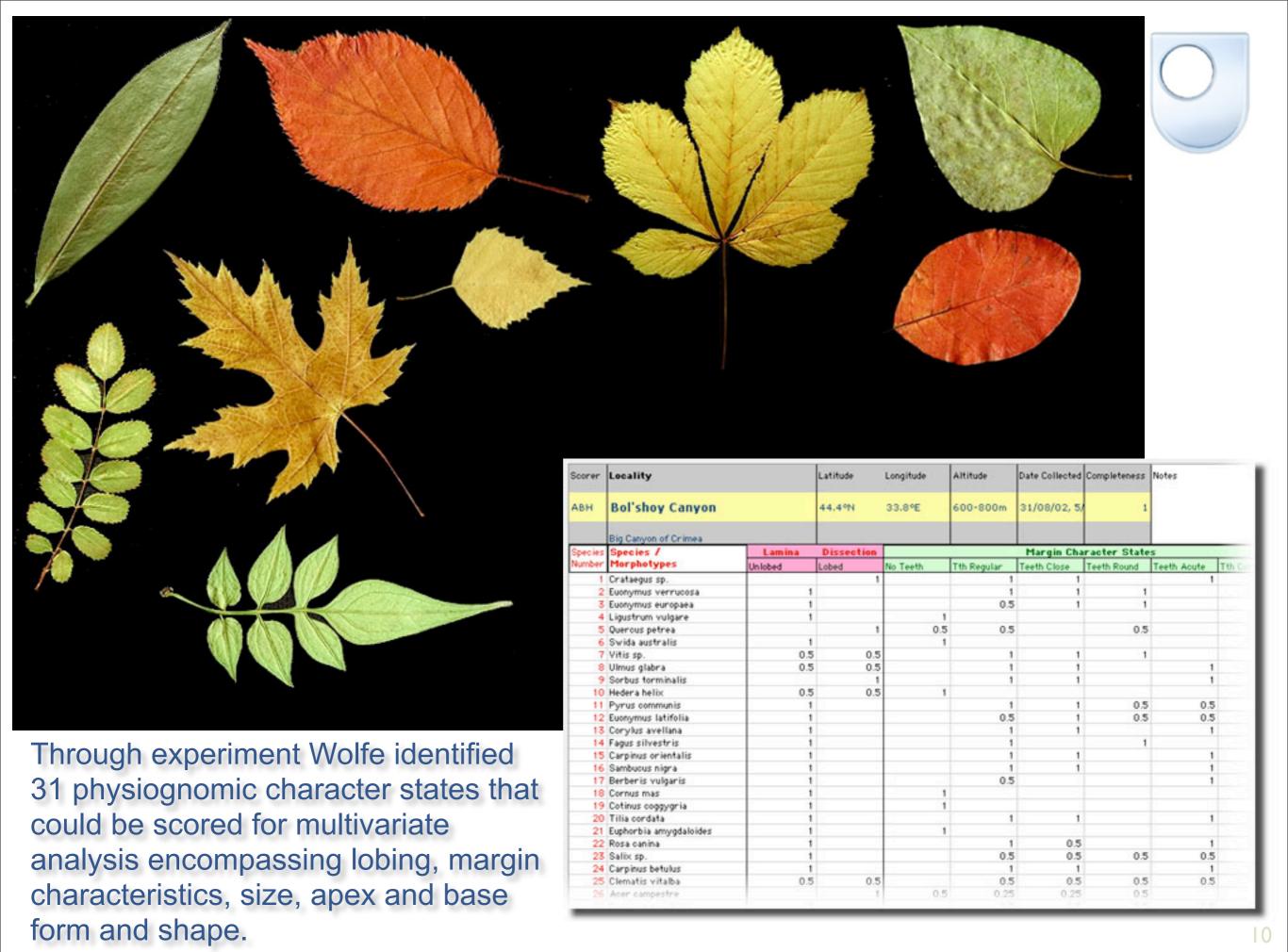
# What feature of an F1 racing car make it capable of outcompeting other F1 cars in a race?





Friday, 24 April 2009

This concept can best be illustrated by considering what makes a racing car outcompete others in a race. Success is not down to any single factor but many, some seemingly working against one another. So it is with leaves. They need to be large to intercept that maximum amount of light but size carries structural costs and leads to significant water loss. In any given situation leaf size ends up as a compromise engineering solution to maximize light interception while minimizing resource investment. So it is with other leaf features and environmental constraints.



Friday, 24 April 2009

Through experiment Wolfe identified 31 physiognomic character states that could be scored for multivariate analysis encompassing lobing, margin characteristics, size, apex and base form and shape.

# A typical CLAMP scoresheet



11

0	00	Bereyozovo correct.xls [Read-Only]												
>	Α	В	С	D	E	F	G	Н		J	K	L	M	
1 2	Scorer	Locality	Latitude	Longitude	Altitude	Date Collected	Completeness	Notes						
3	ABH	Beryozovo	63° 54.469N	64° 56.707E	63'	1/8/02	1							
1														
5	Species	Species /	Lamina	Dissection			Margin Charac	ter States						
6	Number	Morphotypes	Unlobed	Lobed	No Teeth	Tth Regular	Teeth Close	Teeth Round	Teeth Acute	Tth Compound	Nanophyll	Leptophy II I	Leptophy II II	
7	1	"Bilberry" sp.1	1			0.5		0.5	0.5		0.33	0.33		
3	2	Sorbus	1			1	0.5		1	0.5			0	
9	3	Populus tremula	1				0.5	0.5	0.5	0.5			0.2	
0	4	Rosa sp.	1			1	1	0.5	0.5	0.5	0.2	0.2	0.	
11	5	Vaccinium vitis-idaea	1		1						0.25	0.25	0.2	
12	6	Alnus sp.	1			1	1		1	1				
13	7	Salix sp. 4	1		1							0.2	0.	
4	8	Salix sp. 2	1		1							0.33	0.3	
15	9	Vaccinium uliginosum	1		1						0.25	0.25	0.2	
16	10	Unknown sp. 1	1		0.5		0.5		1		0.2	0.2		
17		Unknown sp. 2	1		1							0.33		
18		Empetrum sibiricum	1		1						1			
19		Betula sp. 1*	1			1	1		1	1				
20		Betula verrucosa *	1			1	1		1	1				
21	15	Betula nana	1			1	1	1		0.5	0.25	0.25	0.2	
22	16	Salix sp. 1	1			1		1			0.25	0.25	0.2	
23	17	Salix sp. 3	1		0.5			1				0.25	0.2	
24		Salix sp. 5	1		0.5			1				0.25		
25		Ledum palustre	1		1						0.33	0.33		
26	20	Cranberry	1		1							1		
27														
28														
10		No. Character States Present		20	20	20	20	20	20	20	20	20	2	
11														
12		Percentage Score		0	48	38	38	28	33	25	15	22	. 2	
13 14														
14														

Friday, 24 April 2009

These character states are coded according to strict protocols and entered into a scoresheet like this one that also identified the location of the site (latitude, longitude and altitude), the person who scored it, the date it was collected and how complete it is. In the case of a living sie this will usually be 1, but a fossil assemblage may be missing some features for some morphotypes. In this case the completeness is less than one. Any site where the completeness score falls below 0.66 should be discarded because the climate estimates will have a large error associated with them. Also a minimum of 20 taxa (morphotypes) of woody dicot leaves are required to get an reliable CLAMP climate estimate. Almost all the calibration files meet this criteria. The overall score for any given site is summarized by the Percentage Score shown highlighted in pink on the scoresheet.

# A typical CLAMP scoresheet



11

						xls [Read-Only]												
	X	Y	Z	AA	AB	AC	AD	AE	AF	AG	AH	Al	AJ					
						ALCO DE		9 -	Denta I									
			6					0										
								No.		- 1								
								The same of the sa	10000									
						A 10	25		The same of	TE BO								
	Dana Cha	t State-		Lee	and an Milable Ch	States States		200	Chana Ch	Chatas Chatas								
ten.	Base Cordate	Pase Pound	Base Acute	L:W<1:1	gth to Width Ch L:W 1-2:1		L:W 3-4:1	L:W>4:1	Obovate	aracter States Elliptic	Ovate							
cen.	base cordate	0.5	0.5		0.5			LWM	Obovate	Elliptic	1							
		0.5	0.5		0.5	0.33	0.33	0.33			1							
	0.33	0.33	0.33		0.5				0.5	0.	5							
		0.5	0.5		0.5						1							
		0.5	0.5		0.5	0.5			0.5	0.	5							
		0.5	0.5		1						1							
			1					1			1							
		0.5	0.5			0.33					1							
			1		0.33		0.33		0.5	0.	5							
			1		0.33		0.33				1							
		0.5	1			0.5	0.5		0.5	0.	5							
		0.5	0.5		0.5		0.5	0.5		0.	5 0.5							
		0.5	0.5							0.								
		1	0.5	0.5	0.5				0.5									
		'	1	0.5	0.25		0.25	0.25		0.	1							
			1		0.25	0.33	0.33				1							
			1			0.5	0.5				1							
		0.5	0.5					1			1							
		1				0.5	0.5				1							
20	20	20	20	20	20	20	20	20	20	) 2	0 20	l						
20	20	20	20	20	20	20	20	20	20		20	Copy th	nis line into the f					
0	2	37	62	10	27	25	20	19	13	8	3 5		of the reference					
													spreadsheet.					

Friday, 24 April 2009

These character states are coded according to strict protocols and entered into a scoresheet like this one that also identified the location of the site (latitude, longitude and altitude), the person who scored it, the date it was collected and how complete it is. In the case of a living sie this will usually be 1, but a fossil assemblage may be missing some features for some morphotypes. In this case the completeness is less than one. Any site where the completeness score falls below 0.66 should be discarded because the climate estimates will have a large error associated with them. Also a minimum of 20 taxa (morphotypes) of woody dicot leaves are required to get an reliable CLAMP climate estimate. Almost all the calibration files meet this criteria. The overall score for any given site is summarized by the Percentage Score shown highlighted in pink on the scoresheet.

A CLAMP calibration matrix consists of a number of modern vegetation sites each with a numerical description of the leaves found on at least 20 woody dicot species in each site.



The numerical description is made up of 31 numbers representing an overall percentage score for each of the 31 characters states.

For the PHYSG3BR calibration set the result is a two dimensional array of 144 x 31 numbers.

A	В	С	D	E	F	G	Н	1	J	K	L	M	N	0	P	(
Sample	Lobed		Regular te	Close teet		Acute teet	Compound	Nanophyll	Leptophyl	Leptophyl				Mesophyll	Mesophyll	Mes
Guanica, Puerto Rico	3	83	6	9	9	8	6	1	6			24		3	1	
Cabo Rojo, Puerto Rico	0	87		7	13			5							1	
Mocuzari A, Sonora	2	74	5	5	26		3	17							3	
Mocuzari-B, Sonora	3	74	_	6	24	2	0	12	13						1	
Natua, Fiji	0	79		9	18		2	0	_		_					
Borinquen, Puerto Rico	0	83		6	15	_	4	1	5						1	
Cambalache, Puerto Rico	0	87	10	4	12		3	3	_							
Tres Hermanos, Sonora	6	75		6	23		2	11	8							
Keka, Fiji	0	88		4	8	_	0	0	_	_						
Guajatica, Puerto Rico	1	72		8	19	_	4	1	2						10	
Susua Alta, Puerto Rico	0	80		4	20	0	4	4	12					5	4	
Cabo San Lucas, Baja California S	6	82	7	8	18	3	5	23	24					1	0	
Quiriego, Sonora	4	71	9	13	23	5	4	17	9	15	17				4	
Seqaqa, Fiji	0	61	16	11	38	2	7	0	0	0	8			17	26	
Nuri, Sonora	5	62	9	12	33	5	6	16	8	12	20	24	16	5	0	1
Santiago, Baja California Sur	7	81	9	7	14	4	1	15	15	23	21	15	6	4	1	
Alamos, Sonora	5	66	8	9	28	5	4	9	8	13	18	21	19	8	3	
Empalme, Sonora	0	77	10	14	17	6	6	24	24	26	16	9	2	0	0	
Baie d'Magenta, New Caledonia	6	69	6	3	27	4	0	0	0	6	26	35	18	8	3	
Avon Park, Florida	5	73	16	13	13	15	2	2	5	9	26	32	16	8	2	
Orlando, Florida	7	68	16	17	28	4	3	2	5	14	17	33	22	6	1	
Todos Santos, Baja California Sur	4	81	5	7	16	2	1	25	27	28	10	8			1	
Buena Vista, Puerto Rico	0	81	10	6	18	1	3	0	6	14	25	30	15	7	1	
San Bartolo, Baja California Sur	3	69	15	19	26	5	3	20	16	20	16	16	10	3	0	
Canyon Lake, Arizona	2	78	7	10	18	3	0	41	29	16	9	6	0	0	0	
Los Divisaderos, Baja California Su	0	78	4	2	16	4	2	12	18	18	22	14	9	5	2	!
Maricao, Puerto Rico	1	81	9	4	19	0	0	0	0	5	17	29	26	13	5	
Riv. Bleue, New Caledonia	0	57	10	9	35	9	4	0	0	0	8	12	14	24	22	
Bartlett Resyr., Arizona	0	80	10	13	10	10	5	30	20	24	18			0		
Mt. Koghis, New Caledonia	0	69	19	12	26	5	4	0	0	2	7	15	19	23	18	
Lake George, Florida	13			13			4	0	2							
Castle Cr., Arizona	2	73		14	24	3	2	26								
Silver Bell, Arizona	7	80	13	13		9	6	43				6	0	0	0	
Saguaro Lake, Arizona	4	75		15	22	3	2	21	28					0	0	
Superior, Arizona	2			16		5	5	35					_	0	0	
Roosevelt Lk. Arizona	0						2	24			42				0	
6 Akagawa Spa, hima		0.0	10	56			52	2		8	24					
6 Akagawa Spa, i hima	11	-10	64				39	0			40				7	
7 Republic, Washington	30			64				0								
8 Wanakena, New York	15			65				0		1-					3	
9 Hanawa-Obono, Honshu	13			56				0								
0 Teshio, Hokkaido	12			58				0								
1 Kogawa, Hokkaido	14			61				0								
Z Tadenoumi, Honshu	18			73				0							7	
3 Lake Placid, New York	23			68				0							_	
4 Suganuma, Honshu	12			91				0								
5 Nukabira, Hokkaido	21	9	78	69	26	66	48	0	1	2	2	18	40	25	8	

Friday, 24 April 2009

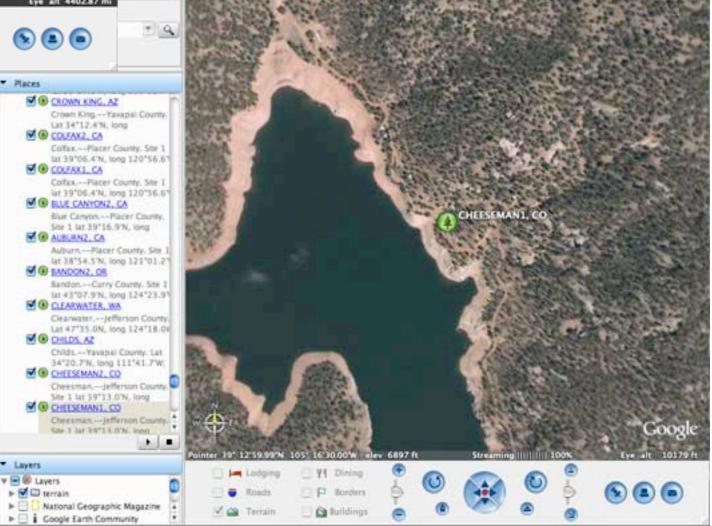
This percentage score is then added to a data array of modern calibration sites similarly scored. This is an example of the Physg3br calibration dataset. An unknown site for which a climate prediction is required is added to the end of such an array.





The geographical locations of the existing CLAMP calibration sites can be seen using Google Earth after downloading a .kmz file from the CLAMP website.

Most of the existing sites represent temperate vegetation in N.America, Europe and Japan.



Friday, 24 April 2009

▶ □ National Geographic Magazine
▶ □ i Google Earth Community

The positions and associated data for the physiognomic calibration data can be found on Google Earth. The Google Earth .kmz file with these data can be downloaded from the CLAMP website.

13

CLAMP uses a multivariate statistical engine called Correspondence Analysis (CA).

Unlike other multivariate methods such as multiple regression CA does not assume that the variables are independent.

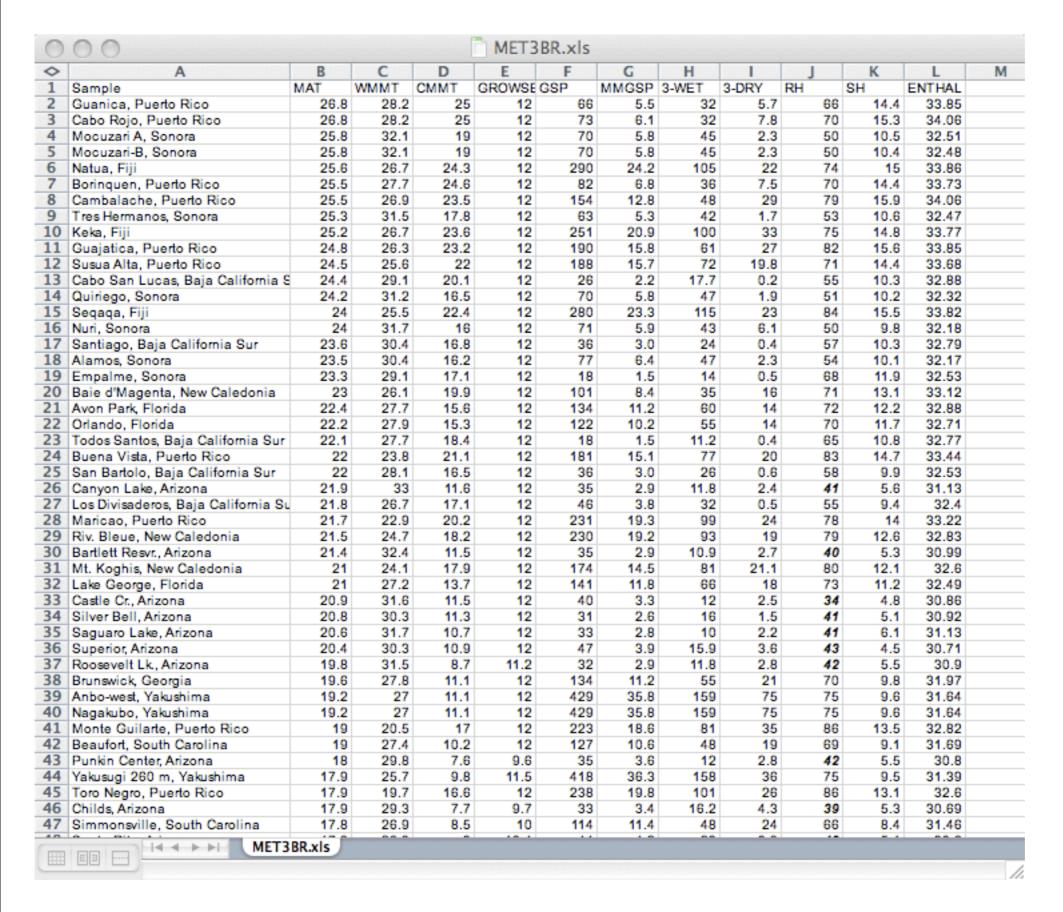
CA is also robust to missing data and is less sensitive to some variables having rare values.

In a variant called Canonical Correspondence Analysis a second data array consisting of environmental data is used to position environmental vectors in the ordination.

This is what is done in the current version of CLAMP.

Friday, 24 April 2009

The statistical engine underpinning CLAMP is Canonical Correspondence Analysis (ter Braak, 1986). Widely used in plant ecology this method has a number of advantages over other statistical technique for dealing with incomplete data that do not necessarily conform to 'normality' in the statistical sense. In CLAMP the Physiognomic data array is analyzed along with an environmental (climate) data array that calibrates the leaf physiognomy of modern forests in terms of observed climate.



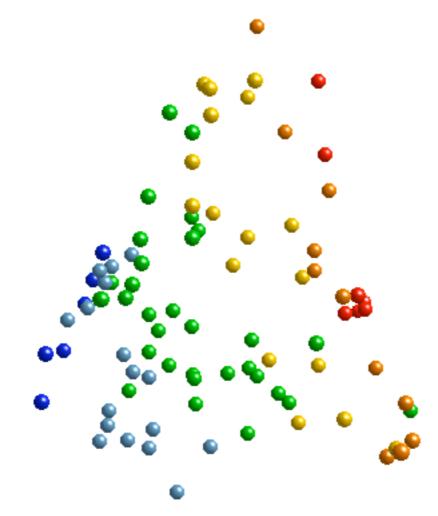


Part of the MET3BR modern observed meteorological data array.

Friday, 24 April 2009

This is an example of a typical climate calibration file. In this case the Met3br array that accompanies the Physig3br physiognomic array. Note that the sites are common to both.

- △ > 25°C
- 20 24.9°C
- 15 19.9°C
- 10 14.9°C
- 5 9.9°C
- < 5°C





Here is a CANOCO plot of the Physg3br modern calibration sites, colour coded for the Mean Annual Temperature (MAT) under which they were growing. The relative positions of the sites in physiognomic space are determined by leaf architecture.

Friday, 24 April 2009

16

16

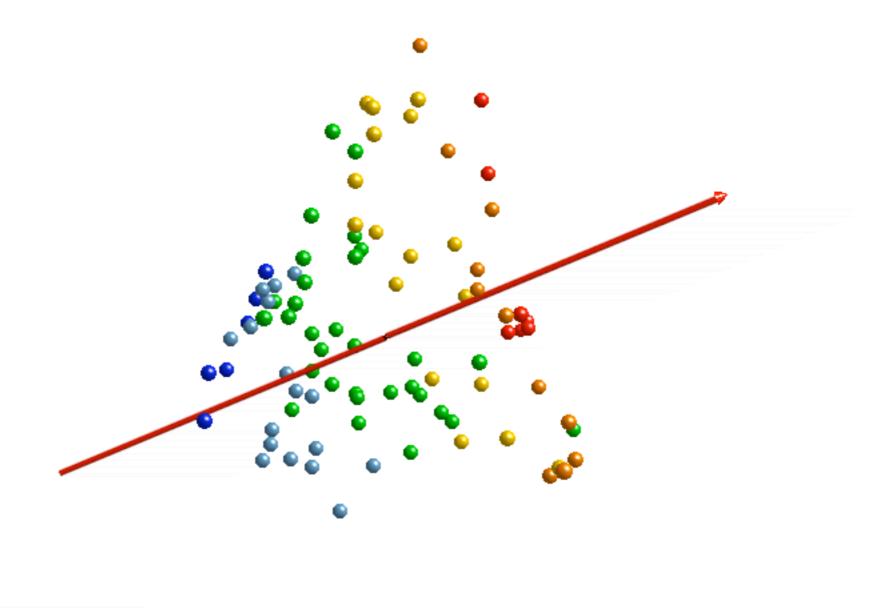
Here is a CANOCO plot of the Physg3br modern calibration sites, colour coded for the Mean Annual Temperature (MAT) under which they were growing (using the observations in the Met3br file). The relative positions of the sites in physiognomic space is determined by leaf architecture alone. The Met3br file only calibrates the structure of physiognomic space in terms of climate. Note that although this plot is two dimensional if static or three dimensional is you are viewing this as a movie in reality the technique analyses the site data in 31 dimensional space defined by the leaf character state scores. Almost 70% of all the structure in 31 dimensional space resides in the first three dimensions so this way of looking at physiognomic space is a reasonable representation of reality.



- 20 24.9°C
- 15 19.9°C
- 10 14.9°C
- 5 9.9°C
- < 5°C

#### Climate Vectors

MAT





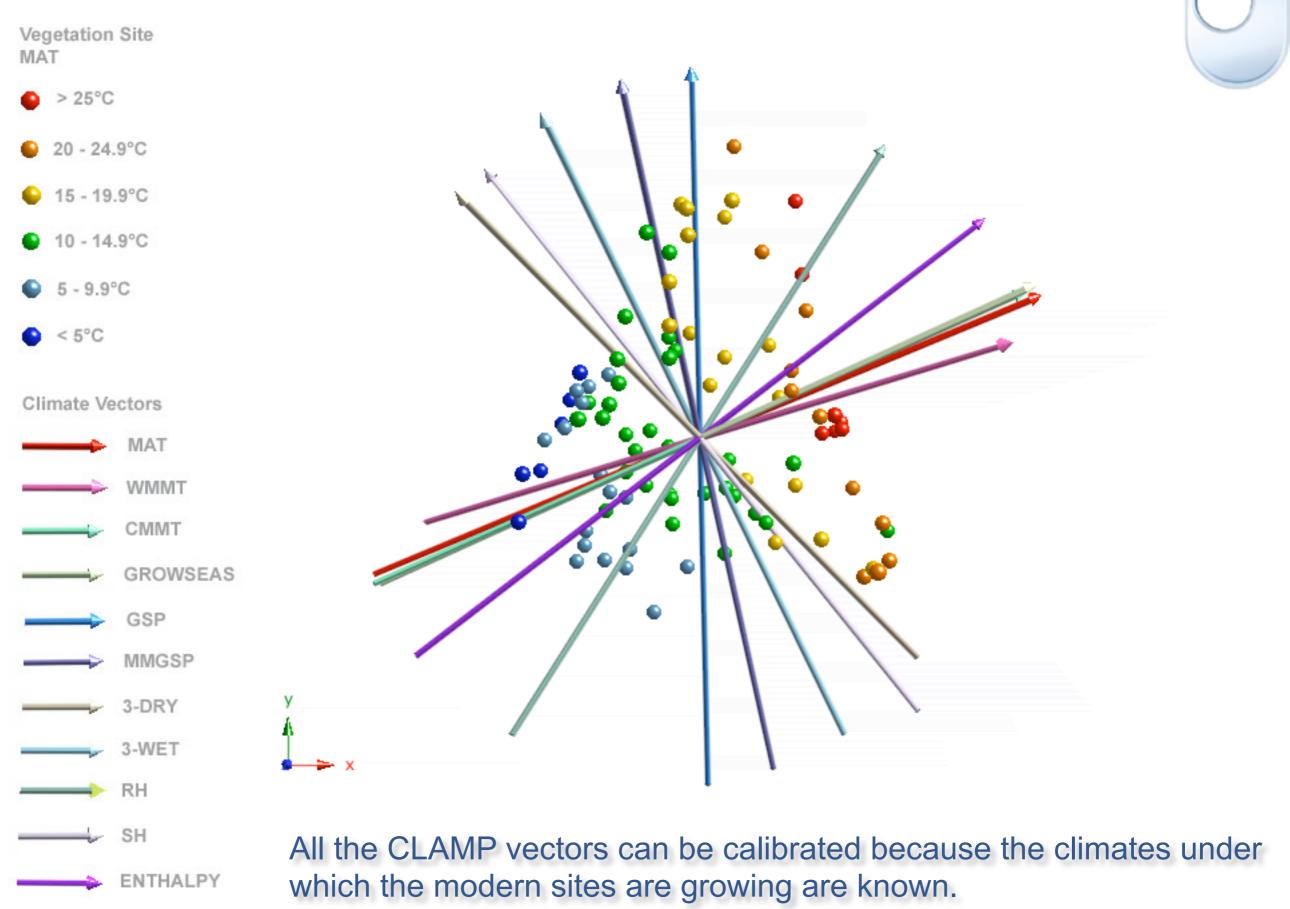
17

Other vectors for warm month mean temperature (WMMT), cold month mean temperature (CMMT), length of the growing season (GROWSEAS) and growing season precipitation (GSP) can also be added.

Friday, 24 April 2009

Other vectors for warm month many temperature (WMMT), cold month many temperature (CMMT), length of the growing account (CDOWSEAS) and growing

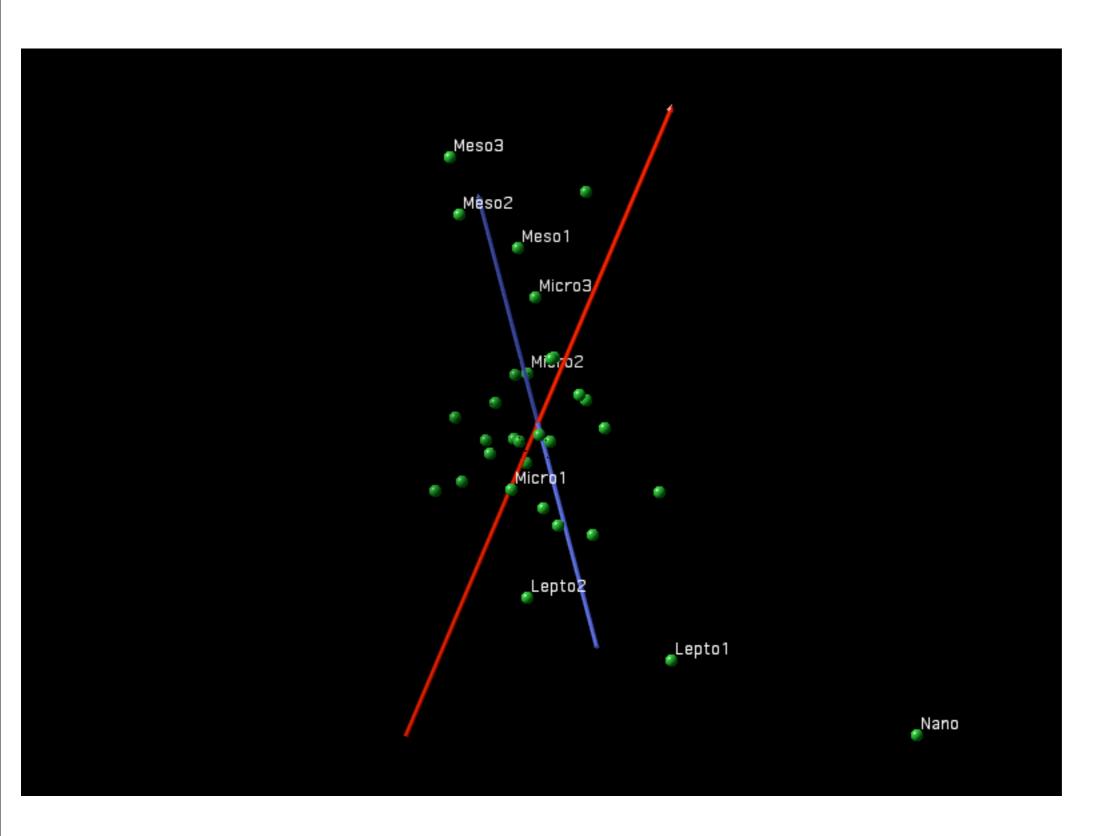
Other vectors for warm month mean temperature (WMMT), cold month mean temperature (CMMT), length of the growing season (GROWSEAS) and growing season precipitation (GSP) can also be added.



Friday, 24 April 2009

All the CLAMP vectors can be calibrated because the climates under which the modern sites are growing are known.





As well as the vegetation sites being plotted it is also possible to plot the positions of the leaf characters in physiognomic space.
This shows the relationships between the characters and the MAT and GSP vectors.

20

20

Friday, 24 April 2009

As well as the vegetation sites being plotted it is also possible to plot the positions of the leaf characters in physiognomic space.

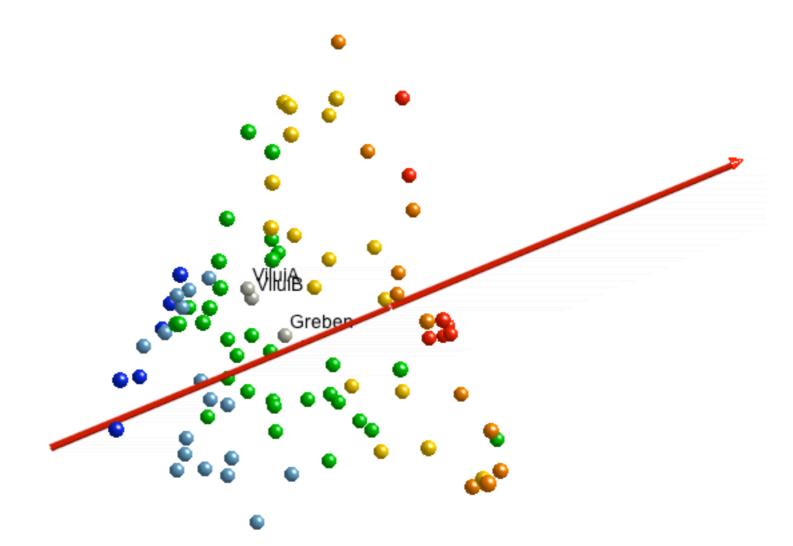
This shows the relationships between the characters and the MAT and GSP vectors. One of the characteristics of the CANOCO statistical technique is that this plot is directly comparable to the site plot but here 31 character states are plotted in a 3-D representation of 144 dimensional space (the number of sites in the Physg3br data array. For clarity only the size categories have been labelled and in this case increasing size describes a helical shape in 3-D, the long axis of which is aligned roughly with the blue precipitation vector. Note that alignment is weak suggesting factors other than water availability are related to leaf size.

#### Vegetation Site MAT

- > 25°C
- 20 24.9°C
- 15 19.9°C
- 10 14.9°C
- 5 9.9°C
- < 5°C

Climate Vectors

MAT



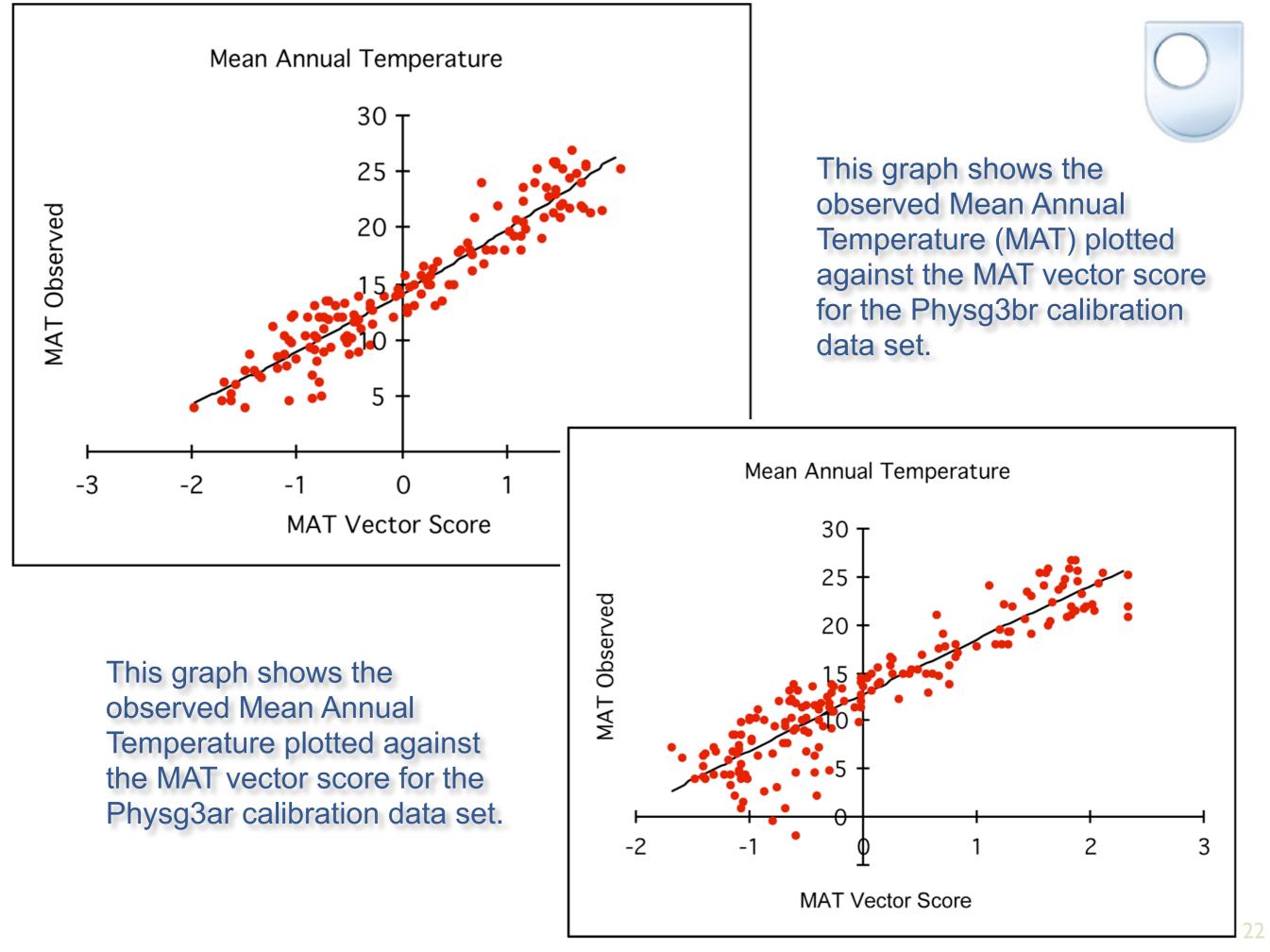
The grey points labelled "Greben", "ViluiA" and "ViluiB" represent fossil samples (in this case from the Cretaceous of Russia). Their positions along the calibrated vectors yield estimates of ancient climate.

21

21

Friday, 24 April 2009

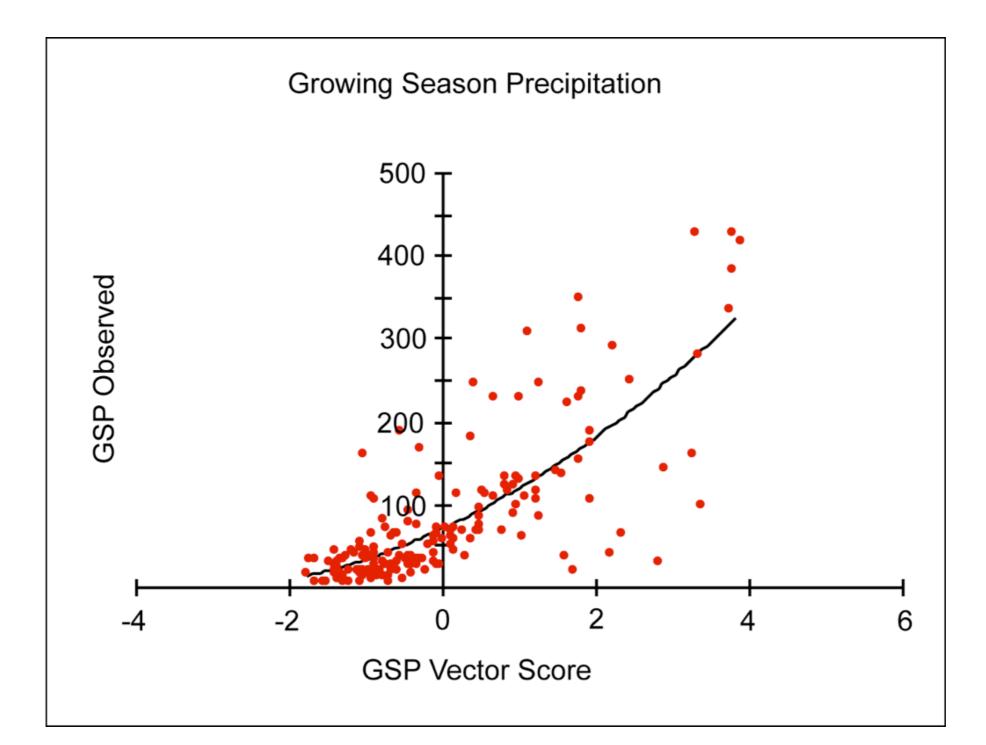
The grey points labelled "Greben", "ViluiA" and "ViluiB" represent fossil samples (in this case from the Cretaceous of Russia). Their positions along the calibrated vectors yield estimates of ancient climate. As with the modern sites a minimum of 20 morphotypes are required in an assemblage for reliable results.



Friday, 24 April 2009

The upper graph shows the observed Mean Annual Temperature (MAT) plotted against the MAT vector score for the Physg3br calibration data set. The spread of the points about the regression line (a 2nd order polynomial) provides a measure of the statistical uncertainty of the technique. These uncertainties, the regression equations and the graphs are given in the spreadsheets (denoted Res3br for the Physg3br and Met3br data sets and downloadable from the CLAMP website) used to calculate the climate predictions.

The lower graph shows the observed Mean Annual Temperature plotted against the MAT vector score for the Physg3ar calibration data set. This data set includes sites where freezing conditions are significant. in general this data set should only be used where cold conditions are suspected because the errors are larger than with the Phys3br data set.

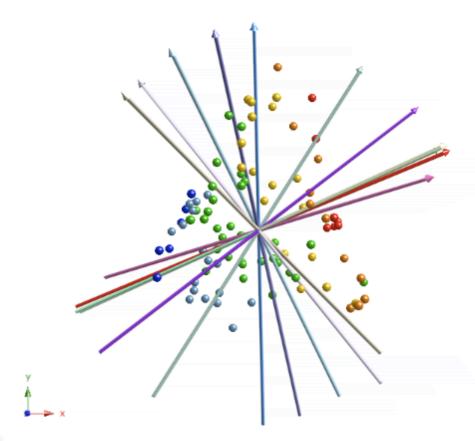




Observed growing season precipitation plotted against the GSP vector score. In dry environments leaf physiognomy maps on to precipitation better than in wet environments.

23

CLAMP offers the most diverse insights into past climates and inevitably is continually being refined and improved. New developments include the use of globally gridded meteorological data and, in due course, the vector based approach will be replaced by the use of nearest neighbours (*sensu* Stranks and England, 1997, The use of a resemblance function in the measurement of climatic parameters from the physiognomy of woody dicotyledons. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 131: 15-28).



For the latest information visit the CLAMP website:

http://tabitha.open.ac.uk/spicer/CLAMP/Clampset1.html