



The functional significance and phylogenetic distribution of leaf teeth

Brad Boyle

University of Arizona

PIRE Course in Peru, June-July 2011

Mesophytic-cold-temperature

	Entire, Per Cent.	Non-entire, Per Cent.
Trees	10	90
Shrubs	14	86
Woody	13	87

Temperate

Moist-lowland-tropical

	Entire, Per Cent.	Non-entire, Per Cent.
Trees	90	10
Shrubs	87	13
Woody	88	12

Tropical

Dicotyledonous plants in a few Cretaceous and Tertiary floras are recorded in the next table.

Tertiary

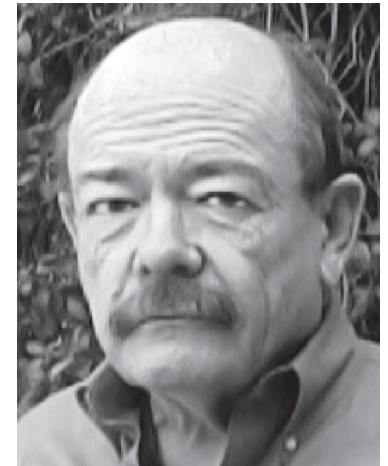
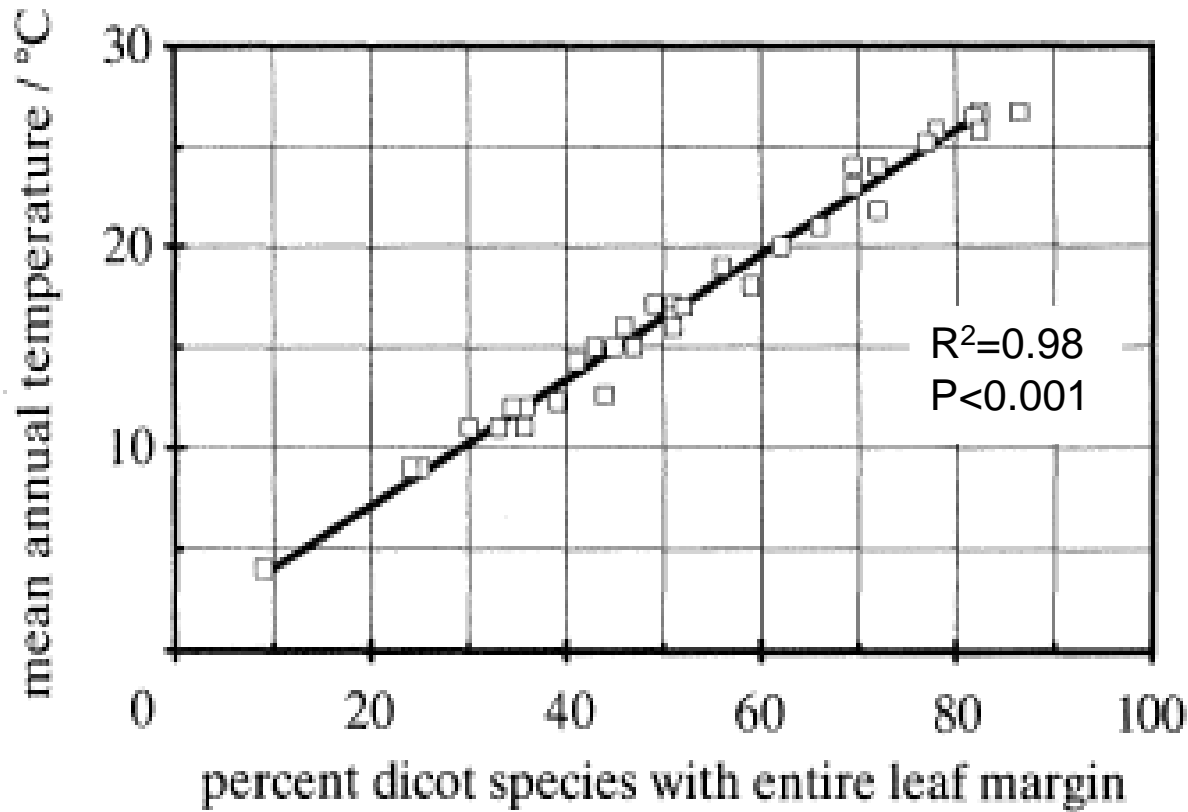
	Entire, Per Cent.
Eocene-Green River-Lesq	29
Eocene-Arctic-Heer	29
Eocene-Spitzbergen-Heer	46
Eocene-Bad Lands-Lesq	29

Cretaceous

	Entire, Per Cent.
Montana-Knowlton	62
Pateet-Arctic-Heer	51
Atana-Arctic-Heer	81
Amboy-Newberry	67
Dakota-Lesq	54
Haritan-Berry	71

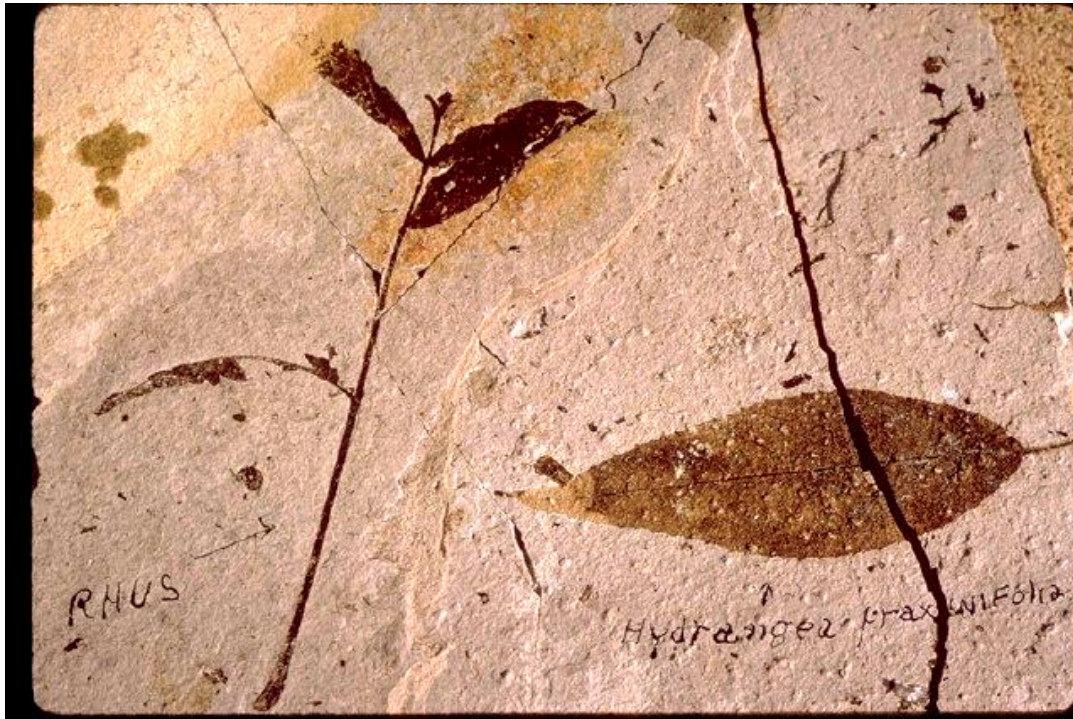
From this table it is clear that leaves with non-entire margins are of very infrequent occurrence in lowland tropical floras, and those with entire margins in mesophytic cold-temperate ones. In fact the correlation between leaf structure and climate is so intimate in

Percent toothed leaves predicts mean annual temperature



Jack Wolfe

Fossil leaves as “paleothermometers”?





Earth and Planetary Science Letters 245 (2006) 95–114

Using leaf margin analysis to estimate the mid-Cretaceous (Albian) paleolatitude of the Baja BC block

Ian M. Miller^{*}, Mark T. Brandon, Leo J. Hickey

PALAIOS

Emphasizing the impact of life on
Earth's history

PALAIOS, 2010, v. 25, p. 234–238
Research Article
DOI: 10.2110/pal.2009.p09-129r



Annu. Rev. Earth Planet. Sci. 1995. 23:119–42
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LEAF MARGIN ANALYSIS: A NEW EQUATION FROM HUMID TO MESIC FORESTS IN CHINA

TAO SU,^{1,2,3} YAO-WU XING,^{1,2,3} YU-SHENG (CHRISTOPHER) LIU,^{4*} FRÉDÉRIC M.B. JACQUES,¹ WEN-YUN CHEN,^{1,2}
YONG-JIANG HUANG,^{1,2} and ZHE-KUN ZHOU^{1*}

PALEOCLIMATIC ESTIMATES FROM TERTIARY LEAF ASSEMBLAGES

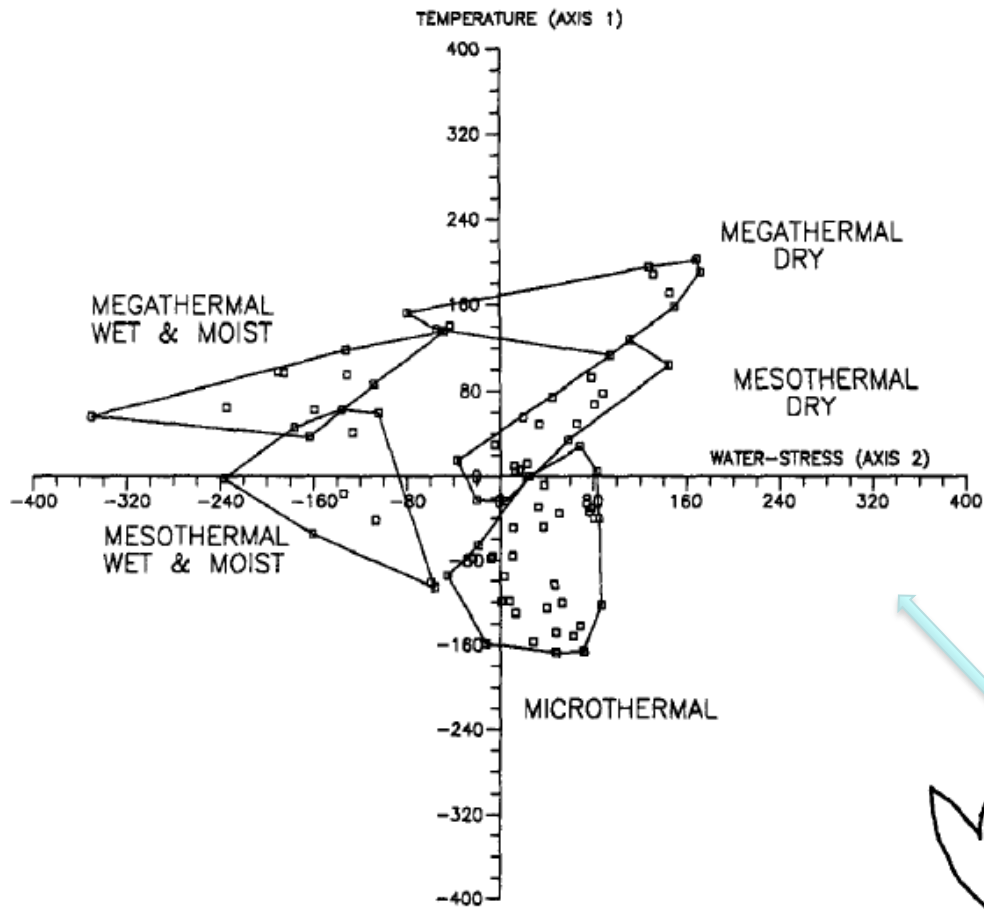
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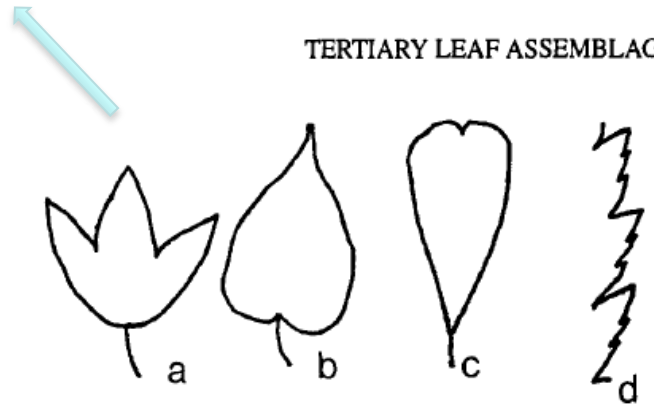
American Journal of Botany 85(12): 1796–1802. 1998.

ESTIMATION OF TEMPERATURE AND PRECIPITATION FROM MORPHOLOGICAL CHARACTERS OF DICOTYLEDONOUS LEAVES¹

MICHAEL C. WIEMANN,² STEVEN R. MANCHESTER,^{2,5} DAVID L. DILCHER,²
LUIS FELIPE HINOJOSA,³ AND ELISABETH A. WHEELER⁴



TERTIARY LEAF ASSEMBLAGES 123

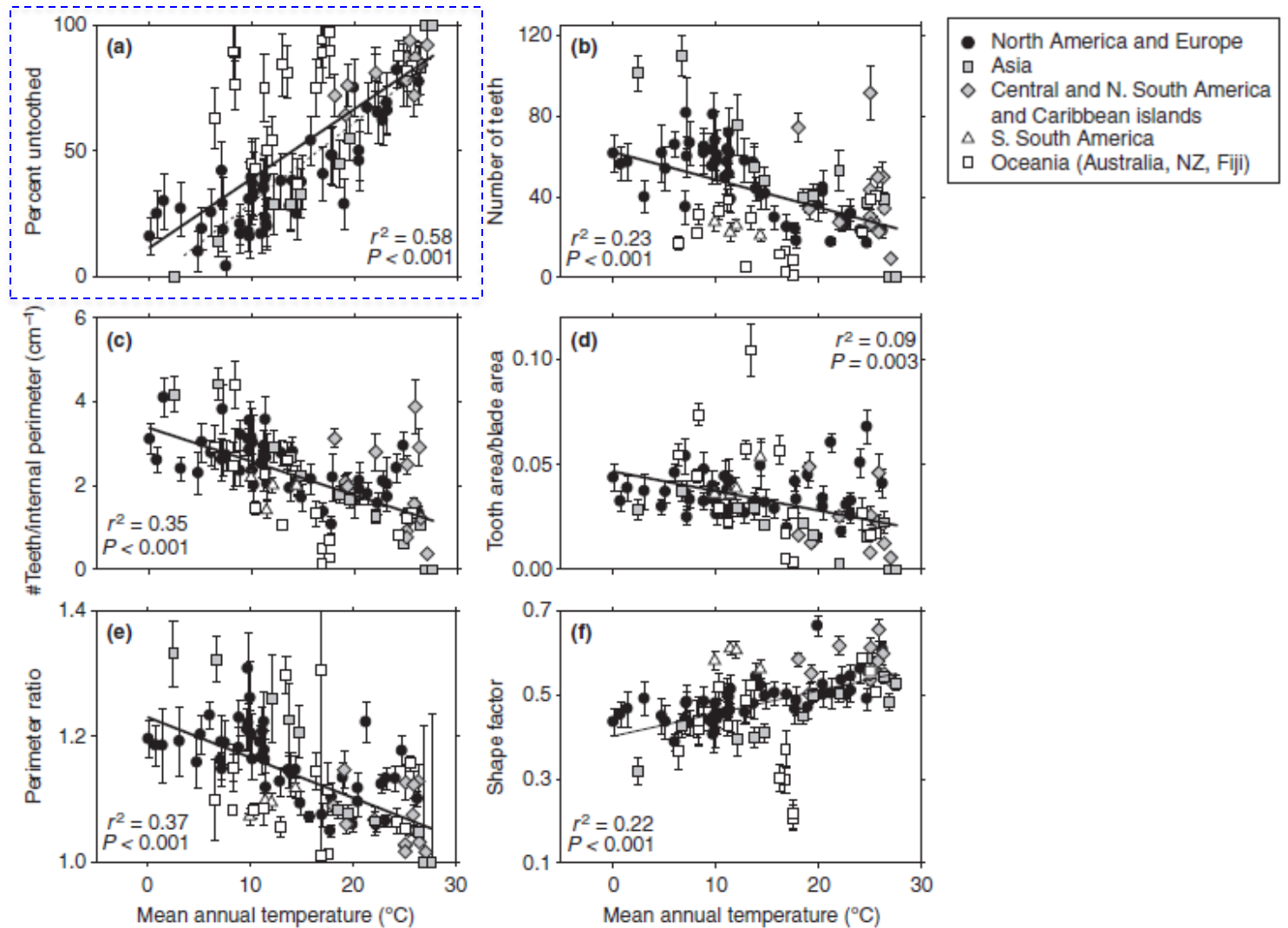


Wolfe 1995. Paleoclimatic Estimates from Tertiary Leaf Assemblages

Problems

- Regional variation
 - Global equations noisy
 - E.g., Percent toothed - temperature: $R^2 < 0.50$
- Local (habitat) variation
 - More toothed taxa in areas with saturated soils
- Taphonomic artifacts
 - Most fossil deposits near lakes, streams
 - “Cool bias”
- Variation with phylogeny, growth form
- Mechanistic basis poorly understood

Regional variation



Local variation

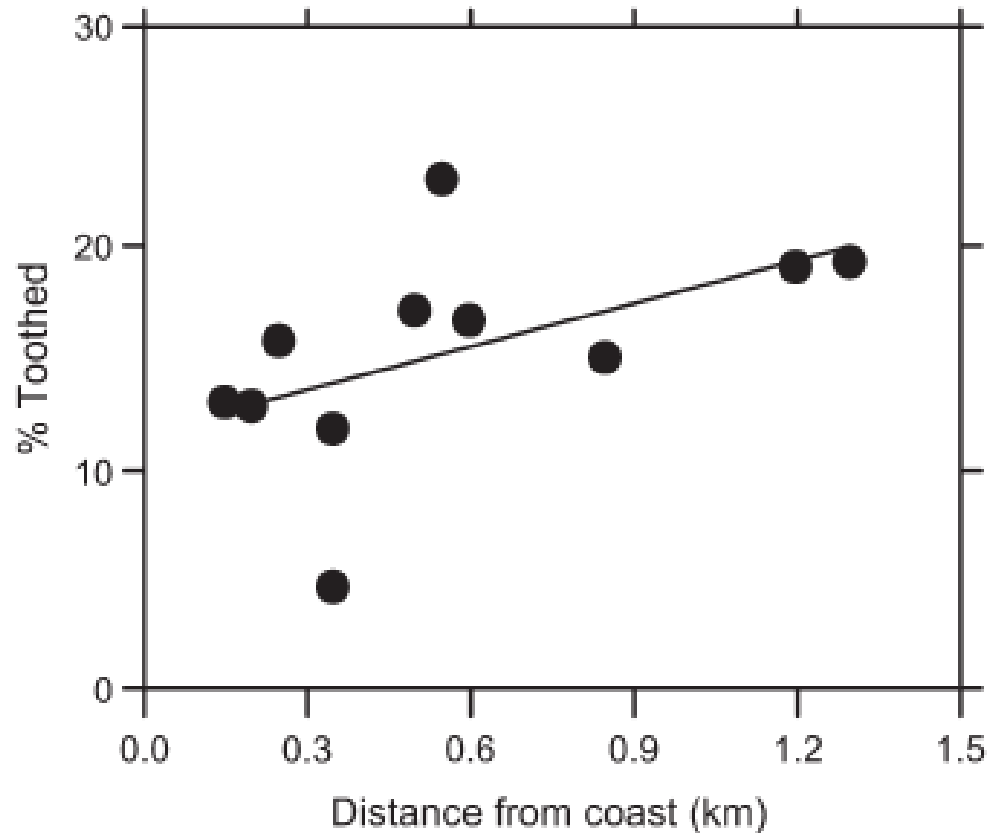
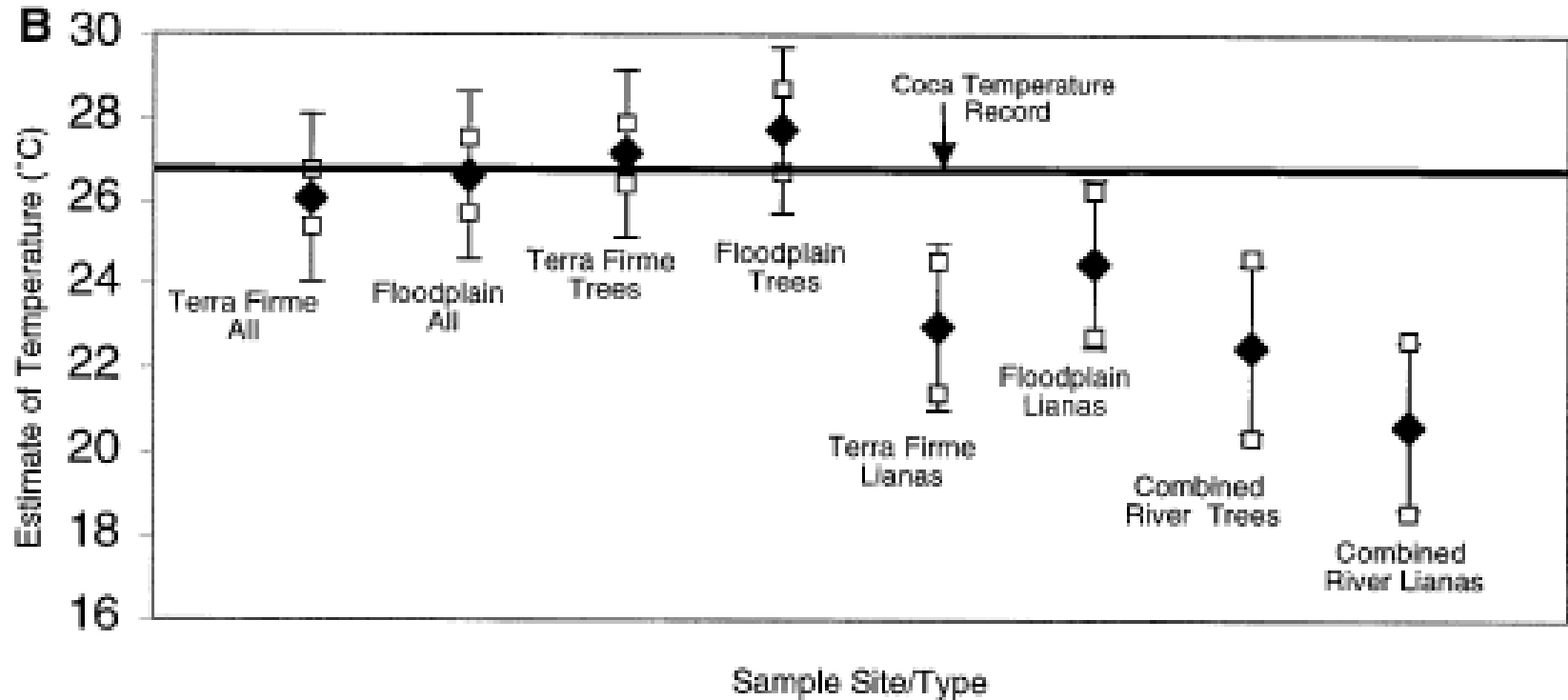


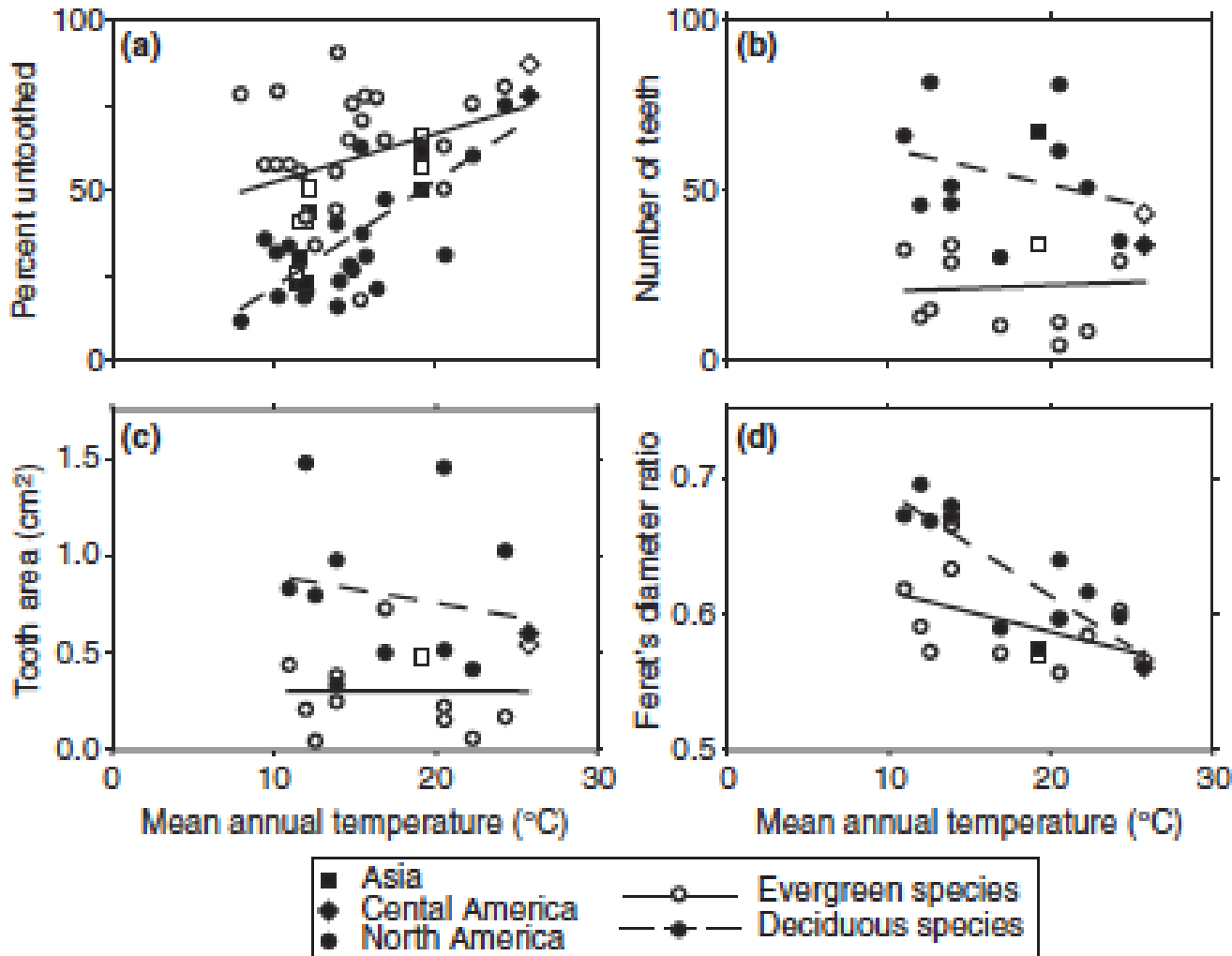
Fig. 3. Relationship between the percentage of toothed species and distance from coast for the CNVF coastal sample. Dots represent individual sites. Least-squares linear regression statistics: $r^2 = 0.27$, $P = 0.10$.

Habitat variation



Wet areas, lianas → more teeth → cooler temperature estimates

Plant growth form variation



Deciduous species have more, larger leaf teeth

Hypothesized functions of leaf teeth

1. Herbivore defense

- Deterrence (chemical, mechanical)
 - *Populus* tooth resins (Curtis & Lersten 1974)
 - Spiny teeth (Ehrlich & Raven 1967, Givnish 1979)
- Attraction of protective mutualists
 - Nectary production (Curtis & Lersten 1974, Belin-Depoux 1989)

2. Reduced necrosis between teeth in dry environments

- Givnish 1979

Hypothesized functions of leaf teeth

3. Hydathode hypothesis

- Haberlandt 1914; Rea 1929; Feild et al. 2005

4. Gas exchange hypothesis

- Gottschlich & Smith 1982, Baker-Brosch & Peet 1997, Wilf & Royer 2006

Hydathode hypothesis

Plant, Cell and Environment (2005) 28, 1179–1190

Hydathodal leaf teeth of *Chloranthus japonicus* (Chloranthaceae) prevent guttation-induced flooding of the mesophyll

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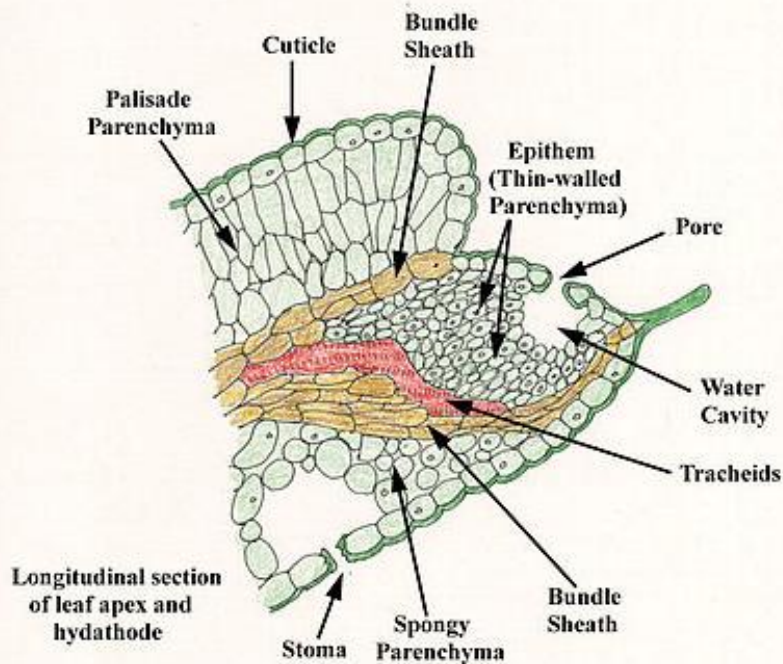


Hydathode



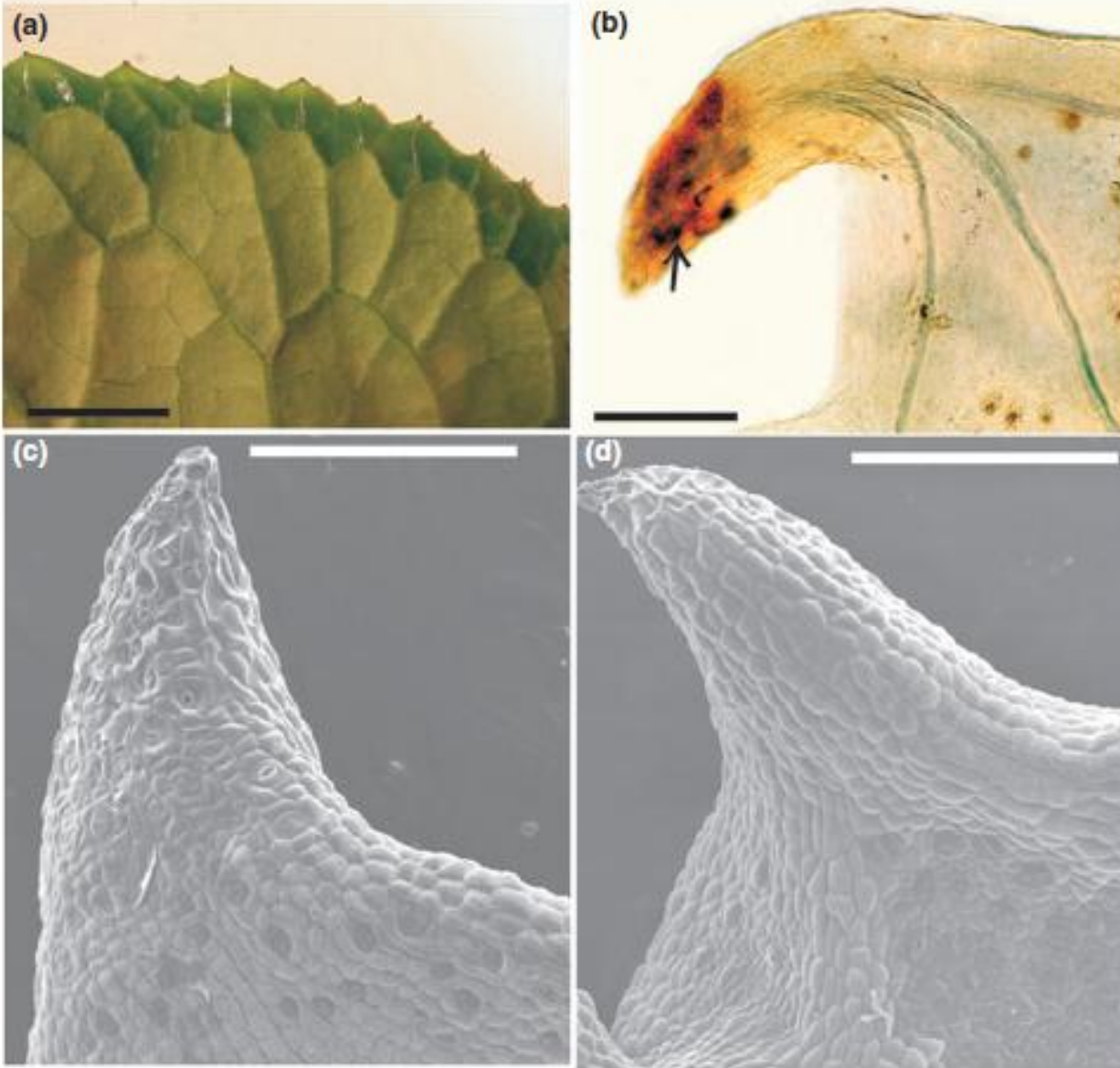
Guttation-exudation of water from hydathodes of leaf margins is caused by root pressure. It is often mistaken for dew in the morning because it occurs at night when water is not processed as quickly within the plant.

Leaf with guttation droplet from hydathode



Hydathode:

- specialized stomata on leaf surface
- exudes excess water, salts



Hydathode hypothesis

- Hydathodes at teeth exude excess water via guttation
- Prevent flooding of mesophyll and consequent depression of photosynthesis

Hydathode hypothesis

- Teeth advantageous in cool, wet areas due to increased photosynthesis
- Disadvantageous in warm, dry climates due to increased water loss

Gas exchange hypothesis

Boundary layer:

- Air movement reduced by surface friction
- Reduced gas exchange

Leaf teeth:

- Increased turbulence, thinner boundary layer
- High density of vein endings, stomata
- Increased gas exchange, photosynthesis

Gas exchange hypothesis

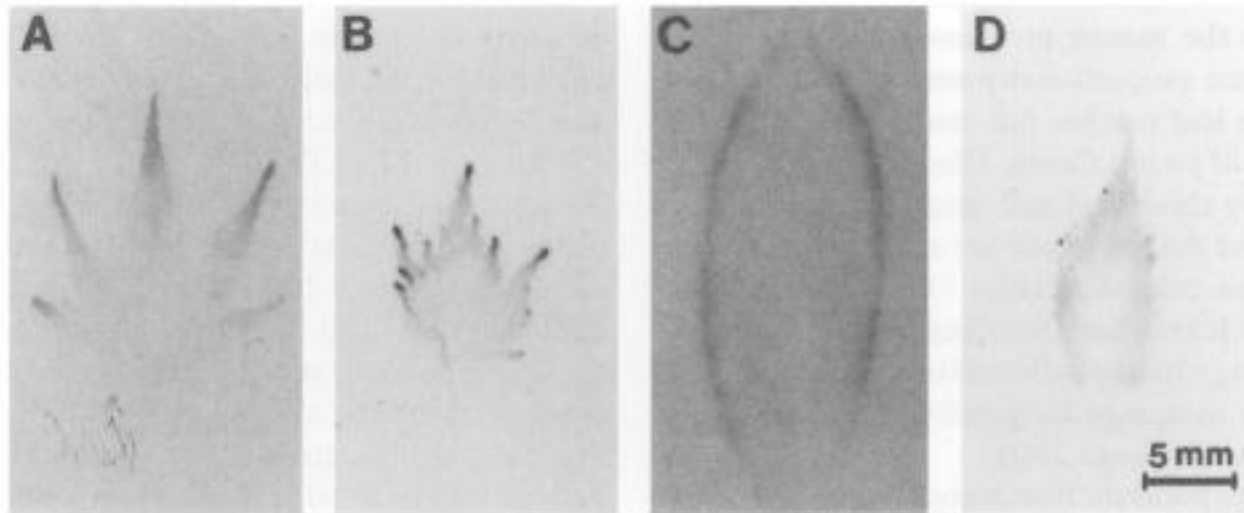


FIG. 2. Autoradiography of immature leaves. The dark regions indicate ^{14}C assimilation due to heightened photosynthetic activity in the marginal teeth and lobes. (A) *Liquidambar styraciflua*; (B) *Acer rubrum*; (C) *Carya alba*; (D) *Ulmus alata*.

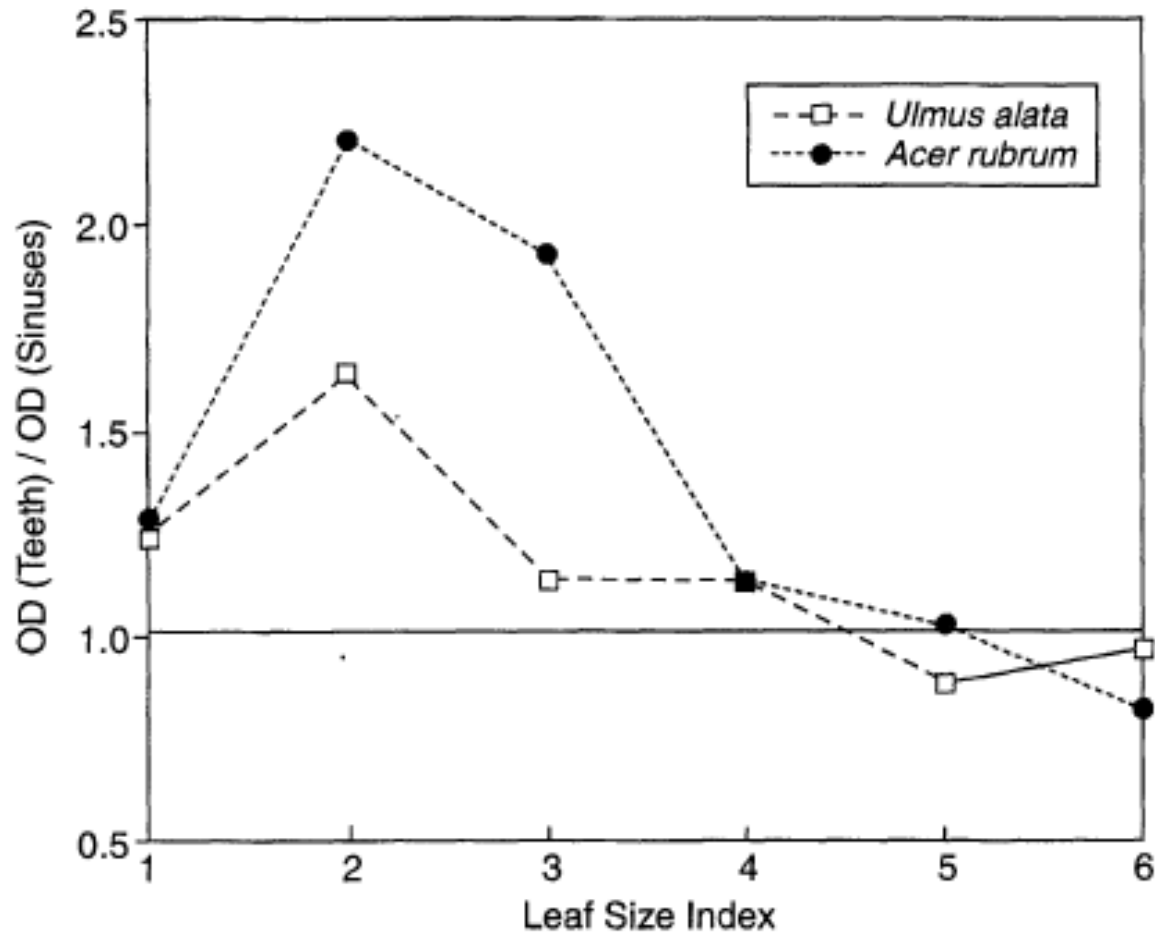
TABLE 1. Presence or absence of photosynthetic activity in the margins of juvenile leaves of 18 temperate forest tree and shrub species.

Species	Type†	Photosynthetic activity‡
Leaves with lobes/teeth		
With photosynthetic margins		
<i>Acer rubrum</i>	c	L, M
<i>Aesculus sylvatica</i>	u	M
<i>Carya alba</i>	c	M
<i>Liquidambar styraciflua</i>	c	L
<i>Quercus alba</i>	c	L
<i>Q. rubra</i>	c	L
<i>Q. stellata</i>	c	L
<i>Ulmus alata</i>	c	M
Without photosynthetic margins		
<i>Liriodendron tulipifera</i>	c	...
<i>Prunus serotina</i>	c	...
<i>Viburnum acerifolium</i>	s	...
<i>V. prunifolium</i>	s	...
<i>V. rafinesquianum</i>	s	...
Leaves with entire margins		
With photosynthetic margins		
None
Without photosynthetic margins		
<i>Cercis canadensis</i>	u	...
<i>Cornus florida</i>	u	...
<i>Fagus grandifolia</i>	c	...
<i>Nyssa sylvatica</i>	c	...

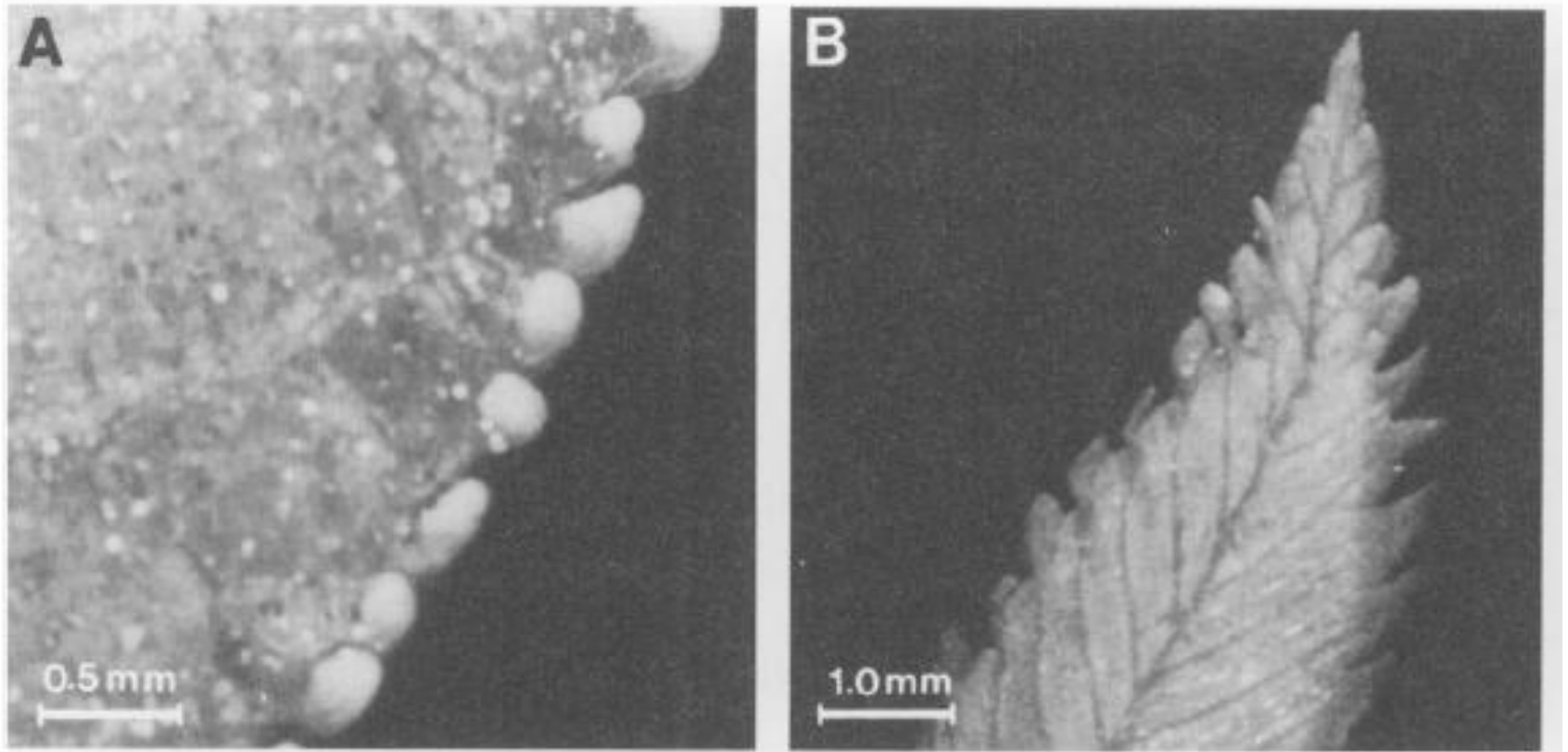
† c = canopy tree species, u = obligate understory tree, s = shrub.

‡ L = photosynthetic activity in lobe tip; M = photosynthetic activity in marginal teeth.

Tooth photosynthetic activity declines during leaf expansion



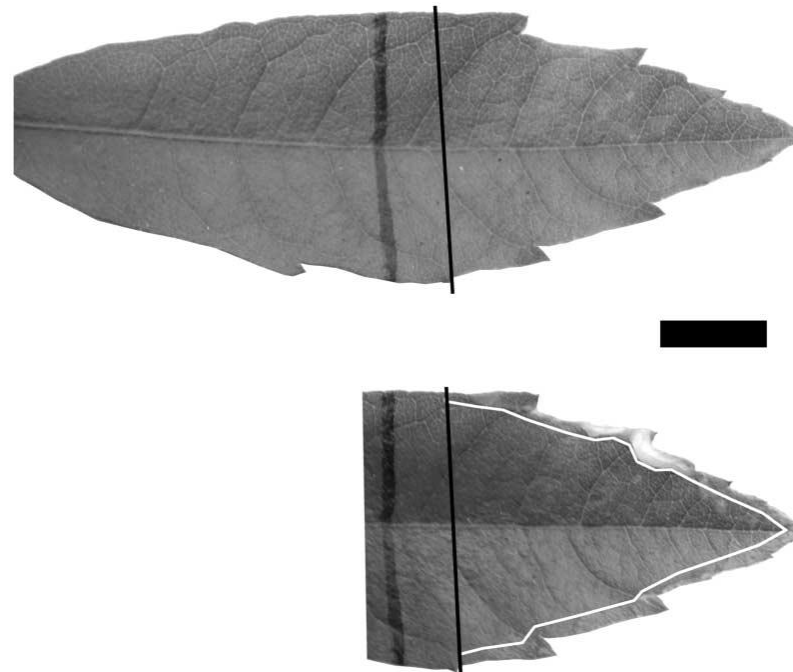
Teeth proportionally large,
photosynthetically active in young leaves



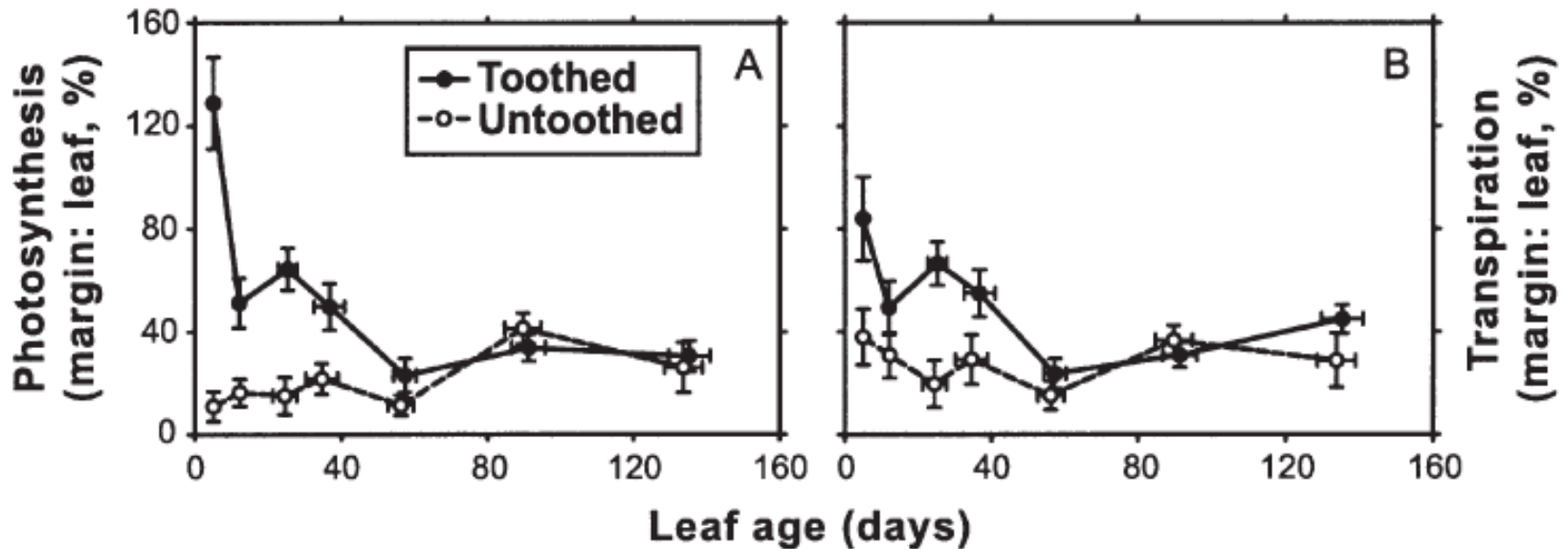
WHY DO TOOTHED LEAVES CORRELATE WITH COLD CLIMATES? GAS EXCHANGE AT LEAF MARGINS PROVIDES NEW INSIGHTS INTO A CLASSIC PALEOTEMPERATURE PROXY

Dana L. Royer¹ and Peter Wilf

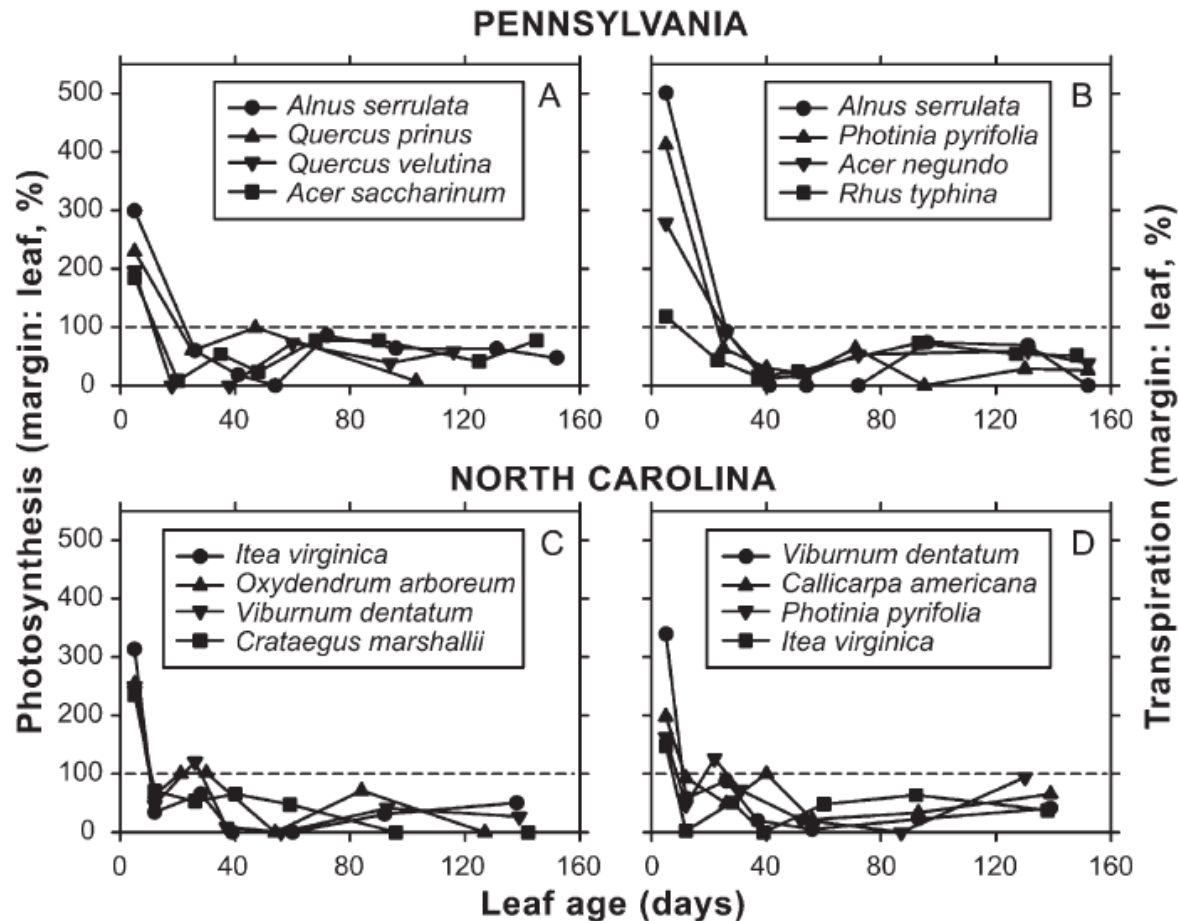
Department of Geosciences, Pennsylvania State University, University Park, Pennsylvania 16802, U.S.A.



Early-season photosynthetic activity higher for toothed margins



Plants native to colder regions have most active leaf margins



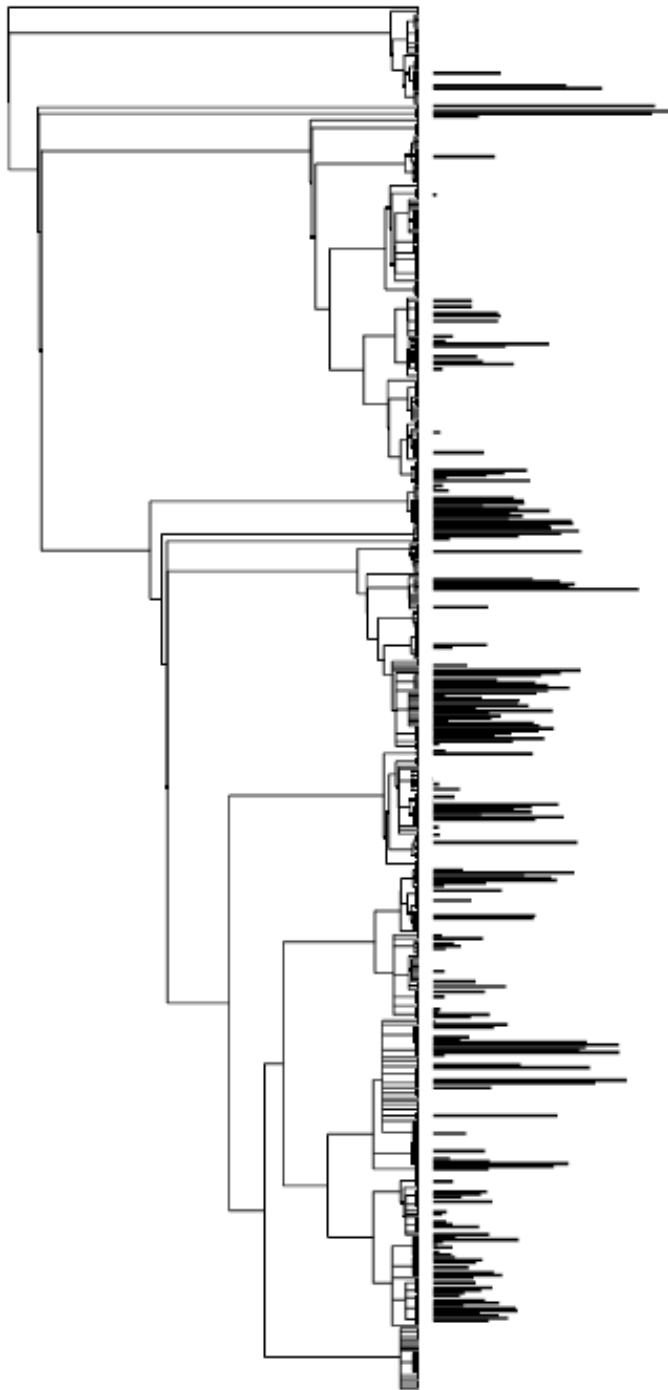
Gas exchange hypothesis

Cool wet climates:

- Rapid early season growth provides net carbon gain

Warmer / drier climates:

- Higher carbon production at leaf teeth is outweighed by increased water loss



Phylogenetic distribution of toothed leaves



