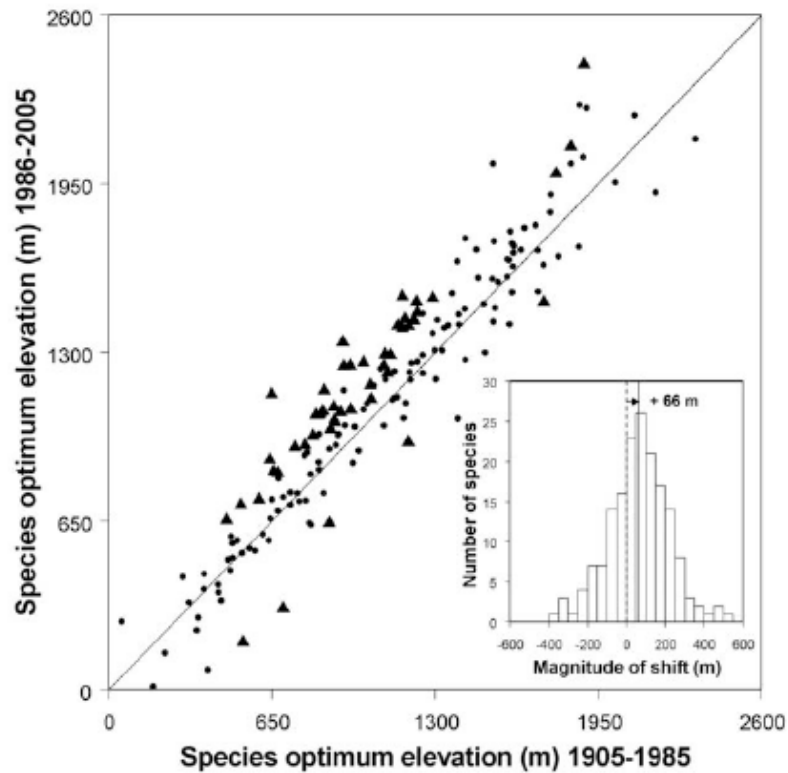


Do C3 and C4 plants respond the similarly to climate change?  
Comparative studies with the C4 grass *Muhlenbergia richardsonis* at high elevations in California's White Mountains

John B Skillman<sup>1</sup>, Rowan F Sage<sup>2</sup>, Archie Meyer<sup>1</sup>

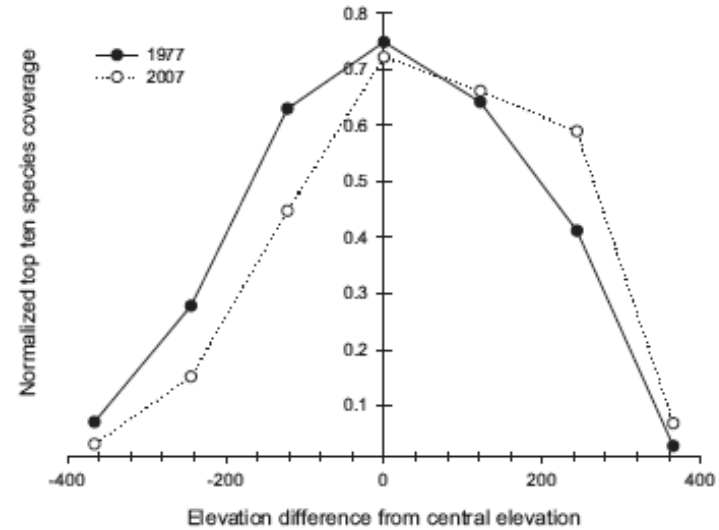
(1) Department of Biology, California State University, San Bernardino, Ca 92407, USA.

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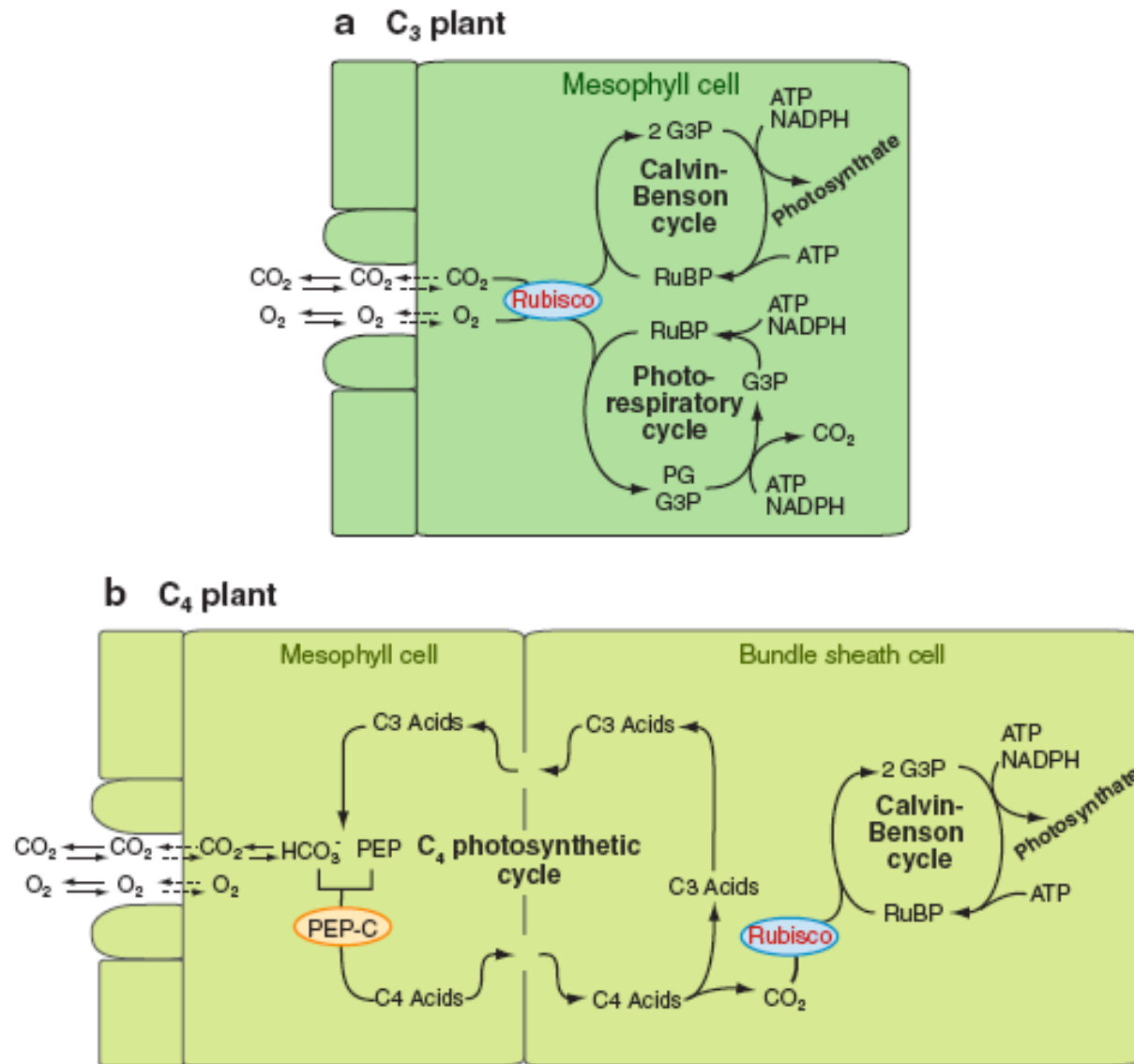
**Fig. 2.** Scatter diagram of forest plant species ( $n = 171$ ) optimum elevation (i.e., altitude value at maximum probability of presence) for the periods 1905–1985 and 1986–2005. Each point represents one species: Species showing nonoverlapping 95% CIs around the optimum elevation between periods are displayed as solid triangles ( $\blacktriangle$ ) ( $n = 46$ ), whereas species with overlapping 95% CIs are displayed as solid circles ( $\bullet$ ) ( $n = 125$ ) (see tables S1 and S2 for details) (23). **(Inset)** The distribution of the species differences in optimum elevation between periods. The vertical dotted line marks zero shift, and the vertical solid line marks the median shift. The arrow describes the direction of the shift.

Western European  
mountain ranges



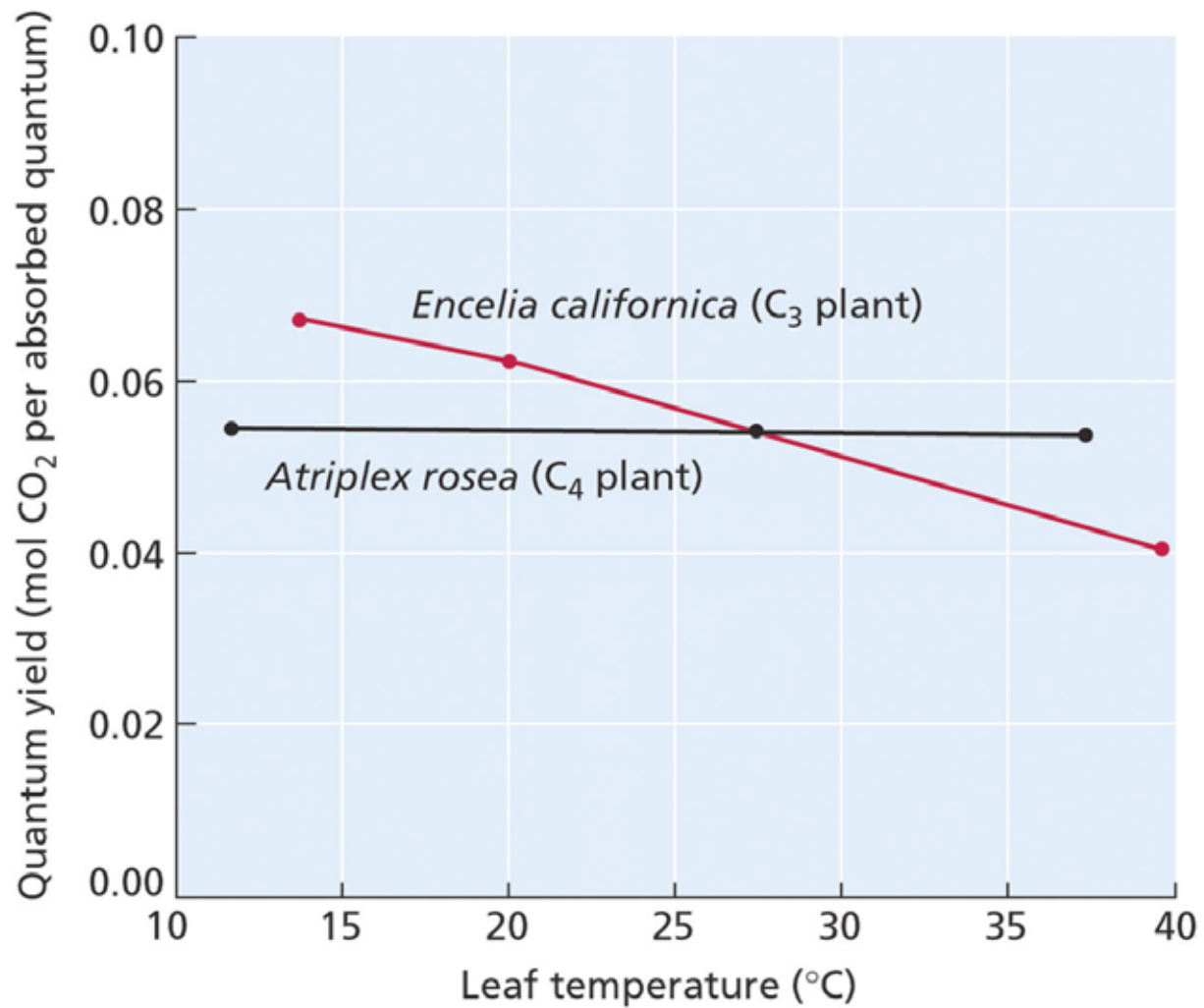
**Fig. 3.** Changing vegetation distribution from 1977 to 2006–2007. Elevation distribution of the mean normalized vegetation coverage of the ten most widely distributed species in 1977 and 2006–2007.

Santa Rosa Mountains,  
Southern California



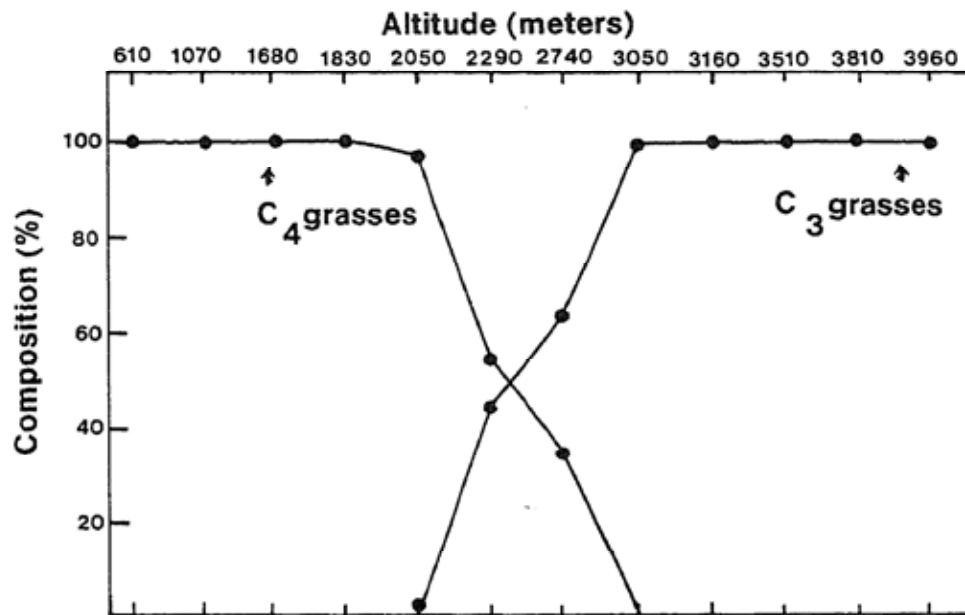
**Figure 1**

Schematic of the (a) C<sub>3</sub> and (b) C<sub>4</sub> plant physiology and biochemical pathways. Both C<sub>3</sub> and C<sub>4</sub> plants possess the Calvin-Benson cycle; however, the unique physiology of the C<sub>4</sub> plants provides a spatial separation between carbon assimilation and CO<sub>2</sub> fixation.



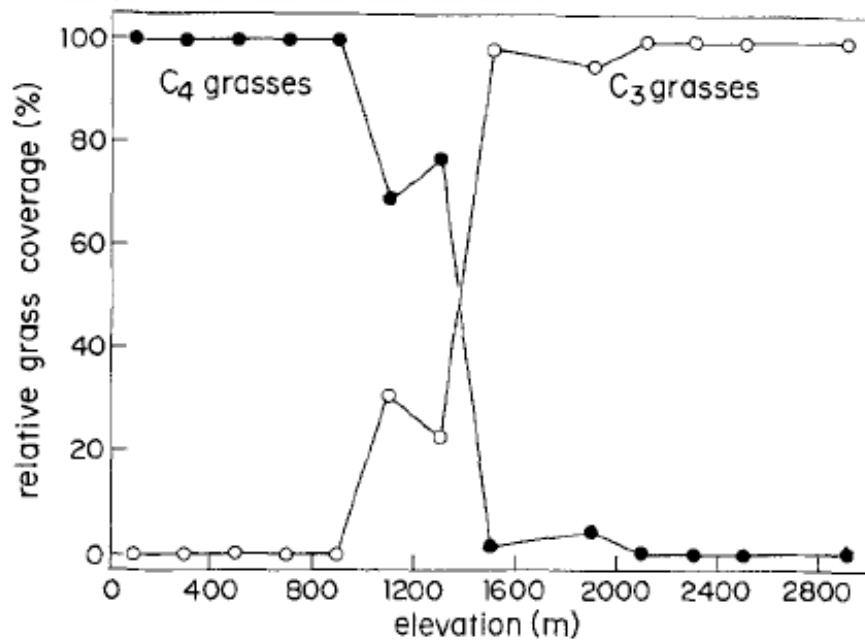
PLANT PHYSIOLOGY, Third Edition, Figure 9.23 © 2002 Sinauer Associates, Inc.

Source: Taiz & Zeiger, 2002



Mt Kenya

Source: Tieszen et al., 1979

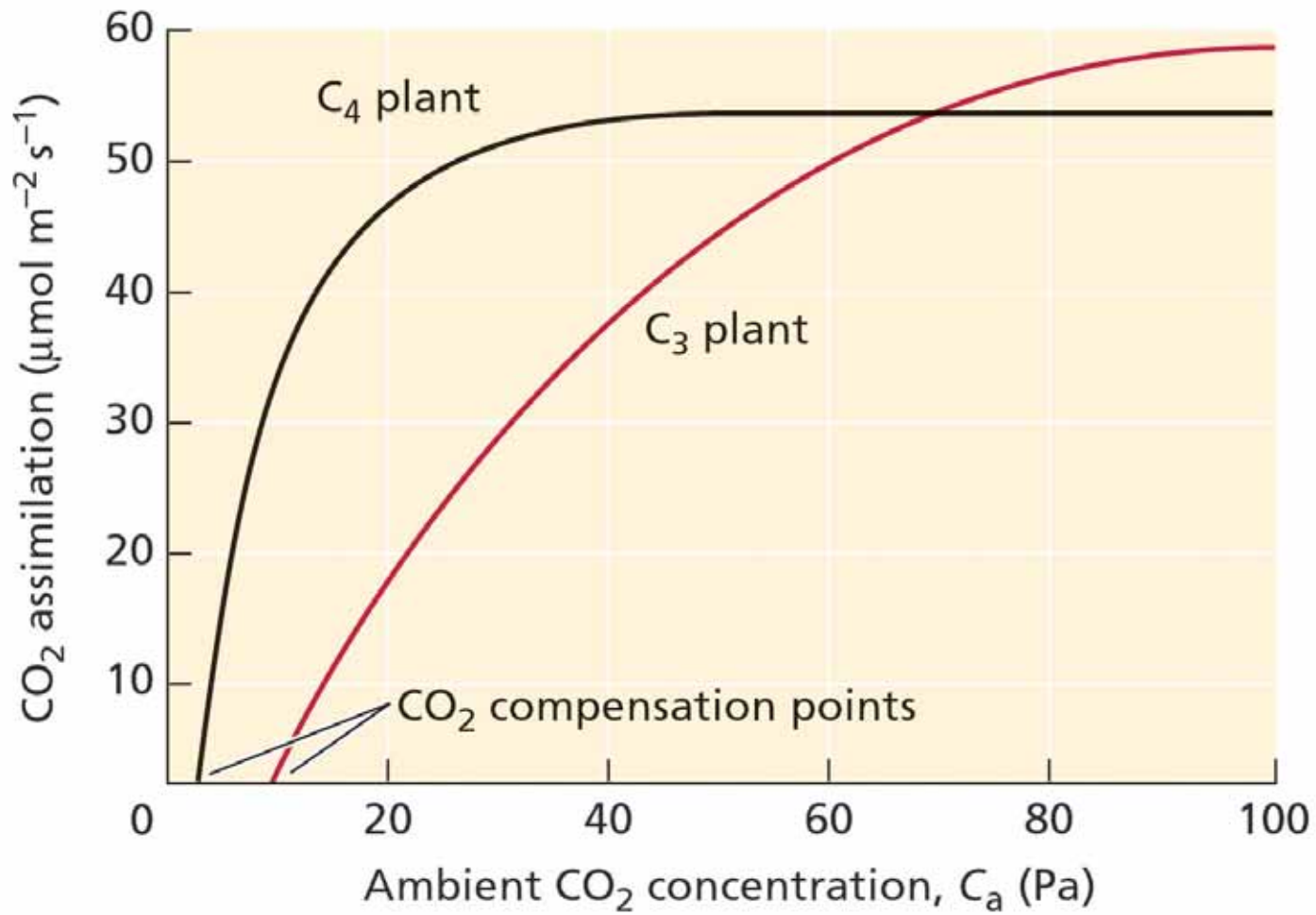


Hawaii

**Fig. 1.** Relative grass species composition and coverage along an elevational gradient in Hawaii Volcanoes National Park. Data adapted from Newell (1968)

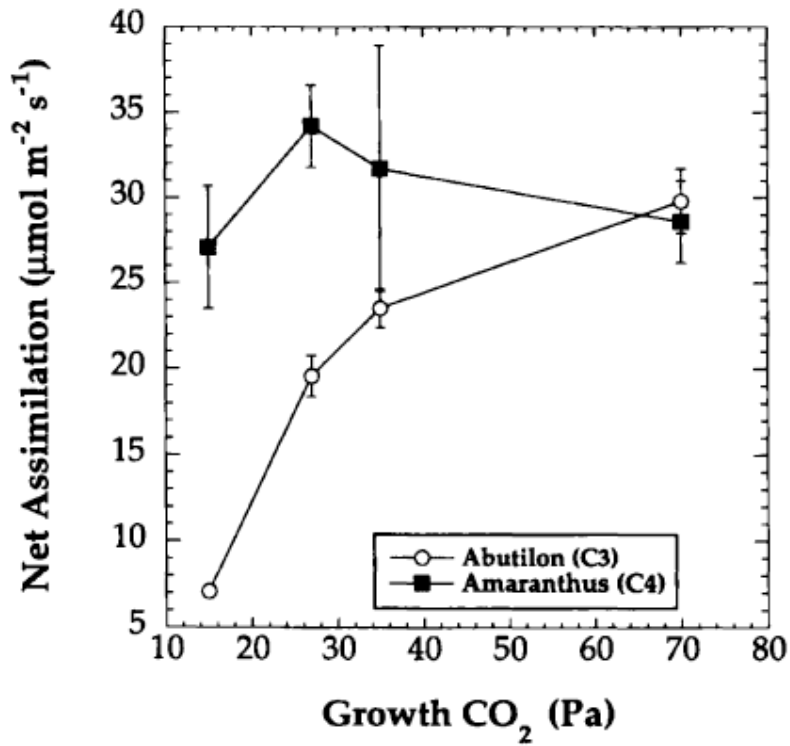
Source: Rundel, 1980

(A)

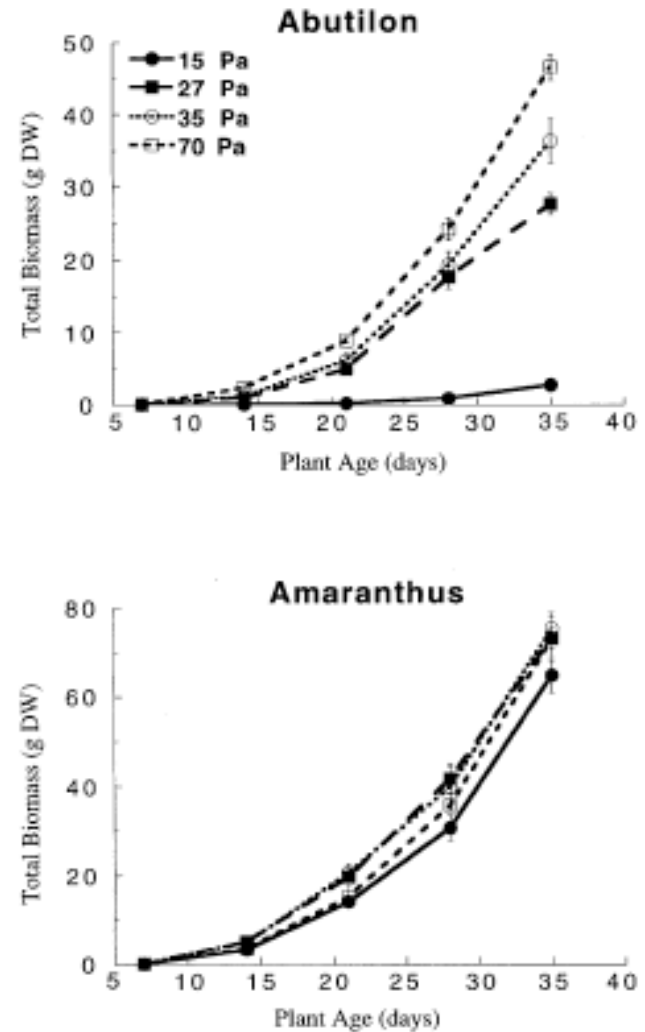


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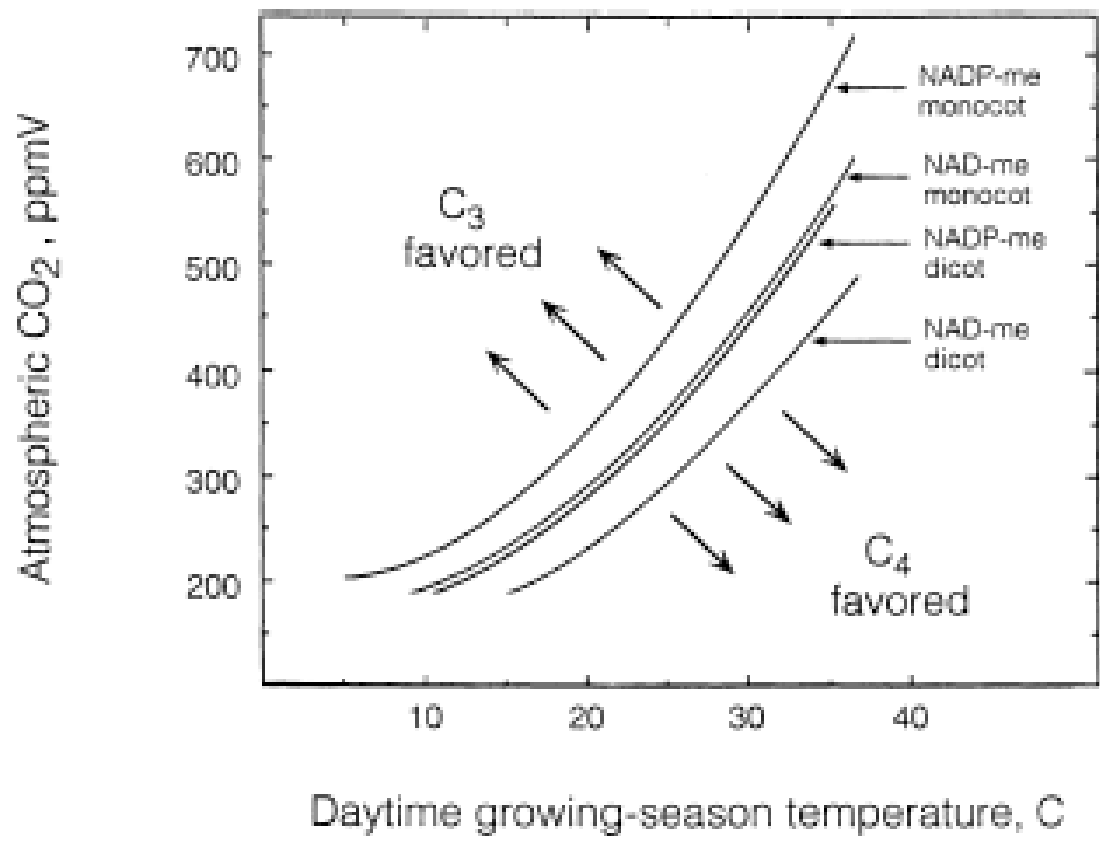
Source: Taiz & Zeiger, 2002



**Fig. 2** Net assimilation rate measured under ambient growth conditions for *Abutilon theophrasti* (C<sub>3</sub>) (open circles) and *Amaranthus retroflexus* (C<sub>4</sub>) (closed squares) after 22–26 days at 15, 27, 35 or 70 Pa CO<sub>2</sub>. Values are means ± SEs (n=3)

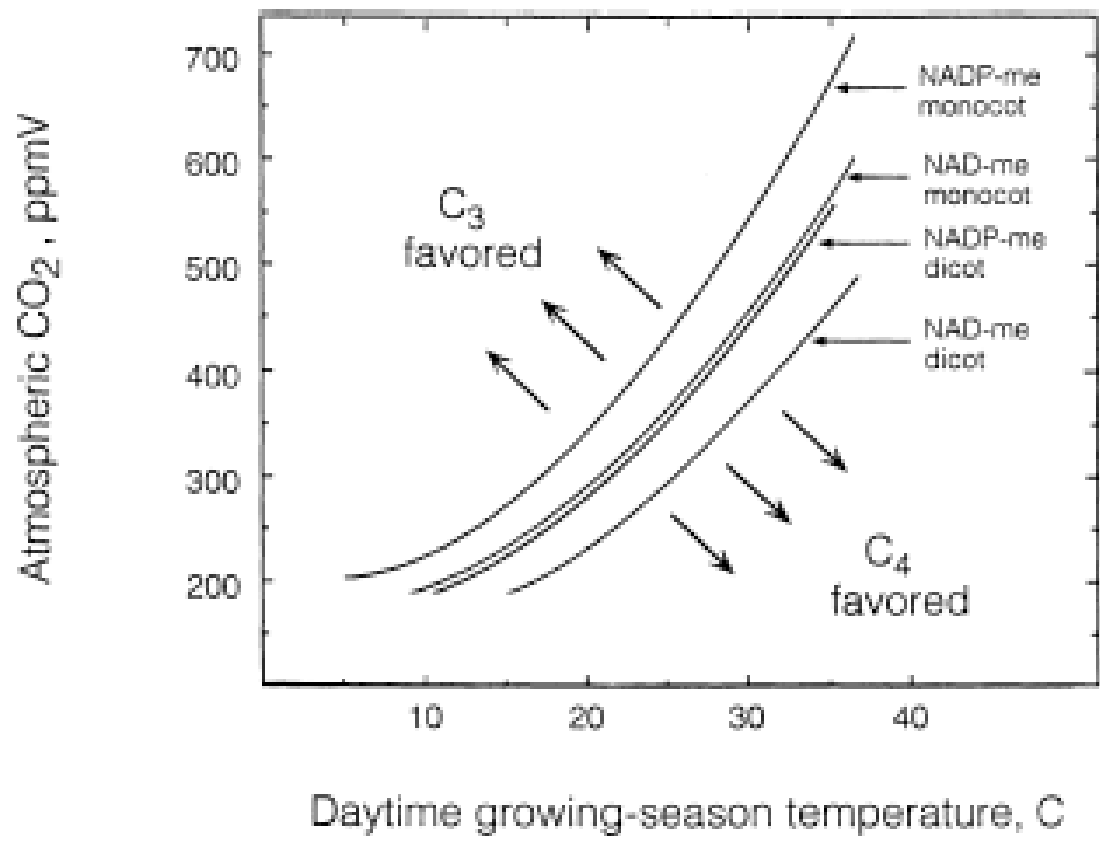


**Fig. 1** Total biomass as a function of plant age and CO<sub>2</sub> partial pressure for *Abutilon theophrasti* and *Amaranthus retroflexus*. Symbols represent means and error bars represent ±1 SE (note difference in scale between graphs)



Source: Ehleringer et al., 1997





Source: Ehleringer et al., 1997

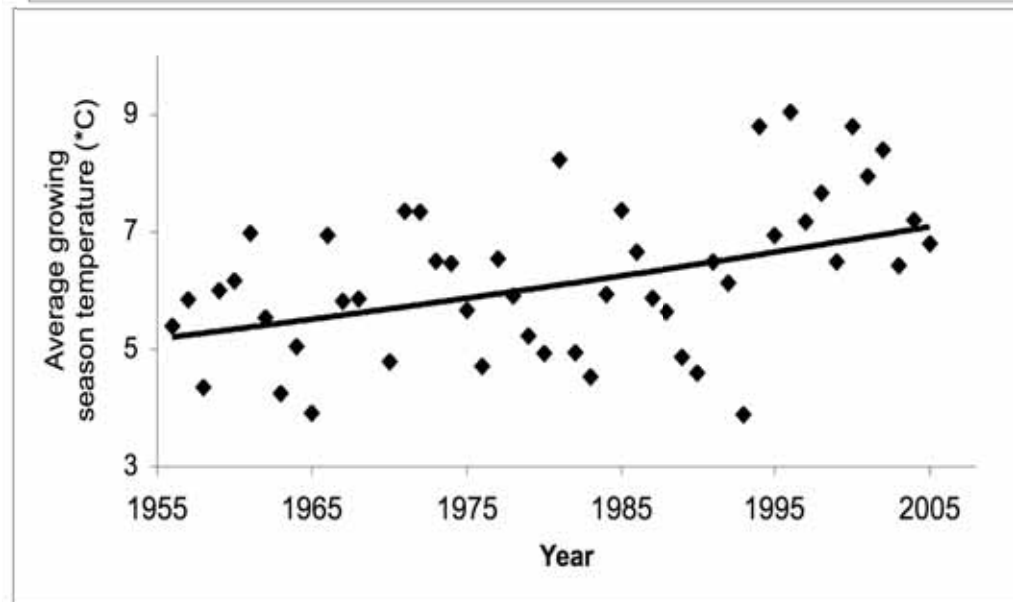
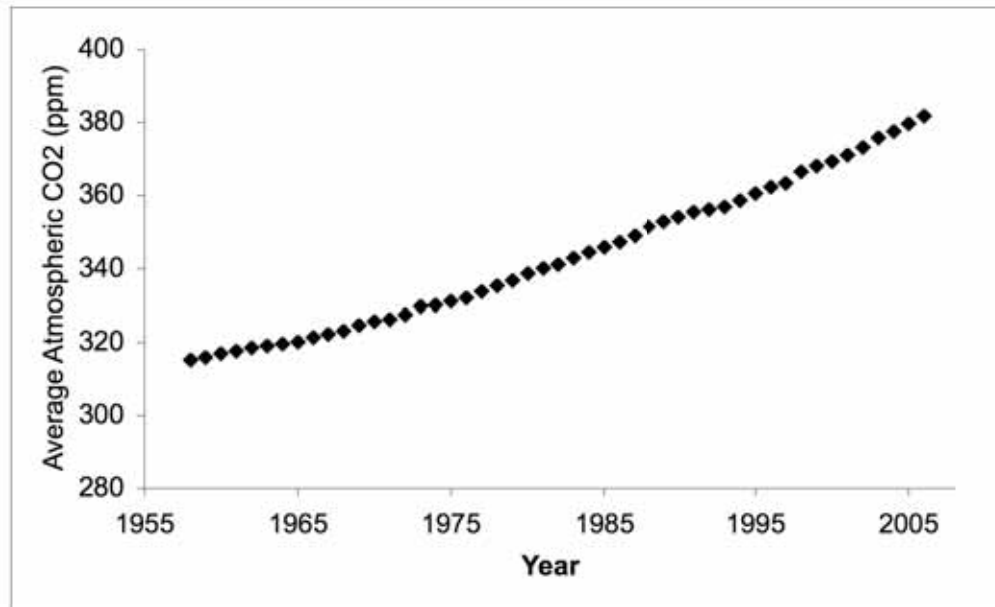


The broad altitudinal range of *Muhlenbergia richardsonis* at high elevations provides an opportunity to better understand how variation in temperature and atmospheric CO<sub>2</sub> affect the photosynthetic ecology of C4 plants and provides a reference for better understanding how these factors affect C3 plants.

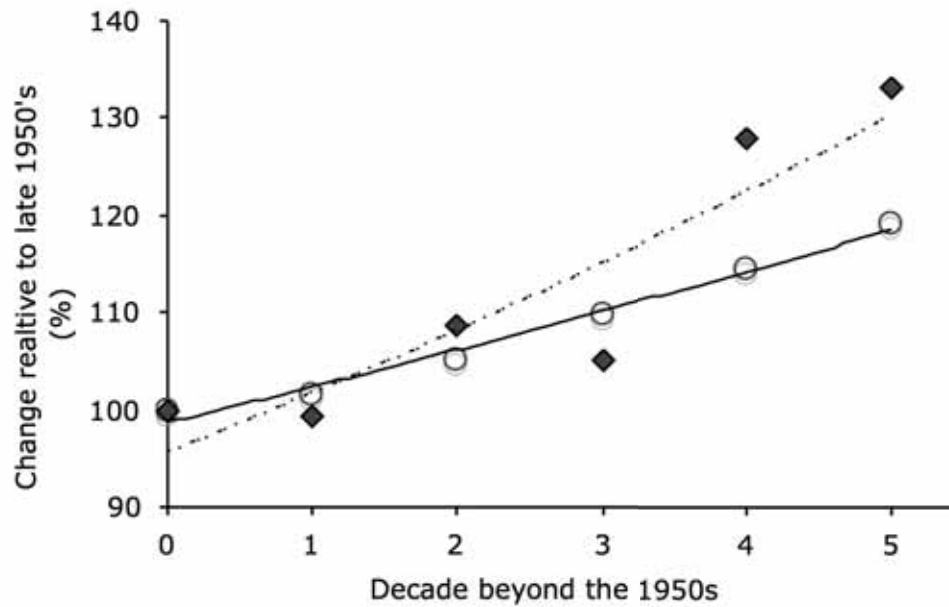
Two sides to the coin...

- How can this C4 plant persist under this cold Alpine climate?
- Is there any advantage to being C4 in these low CO<sub>2</sub> atmospheres at high elevations?

- Is there any advantage to being C4 in these low CO<sub>2</sub> atmospheres at high elevations?
- 1. Which is increasing faster in the mountains, growing season temperature (which might favor Alpine C4 photosynthesis) or pCO<sub>2</sub> (which might favor Alpine C3 photosynthesis)?
- 2. Is there evidence for differential upslope migration of *M. richardsonis* and co-occurring C3 plants in recent years?
- 3. Do C4 leaves respond to changing elevations differently from C3 plants?

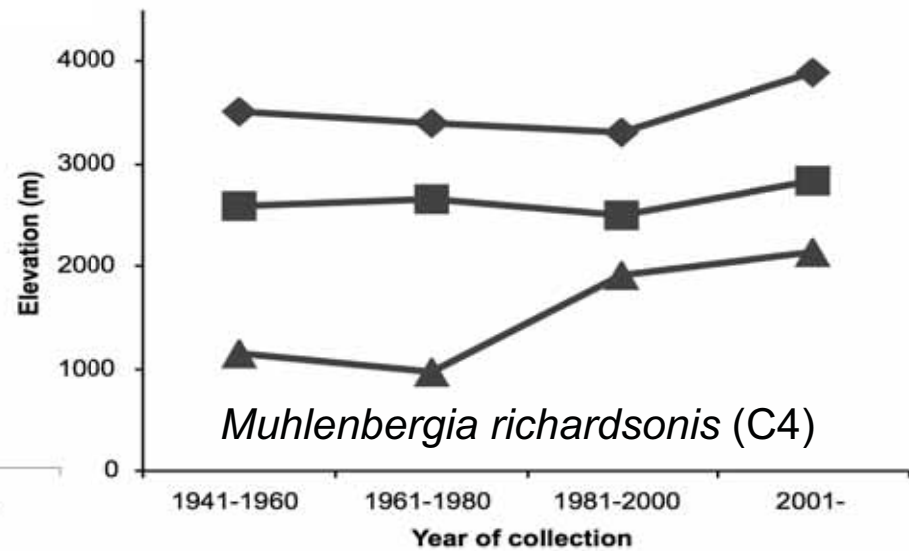
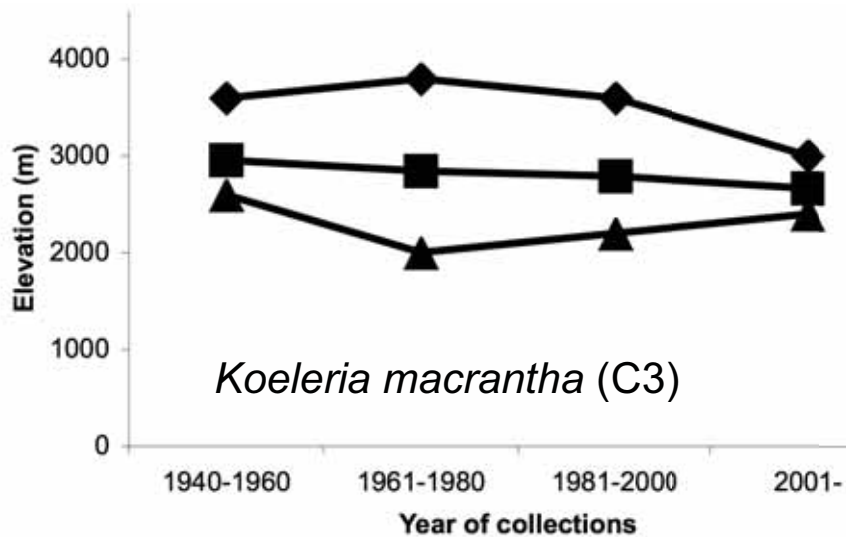
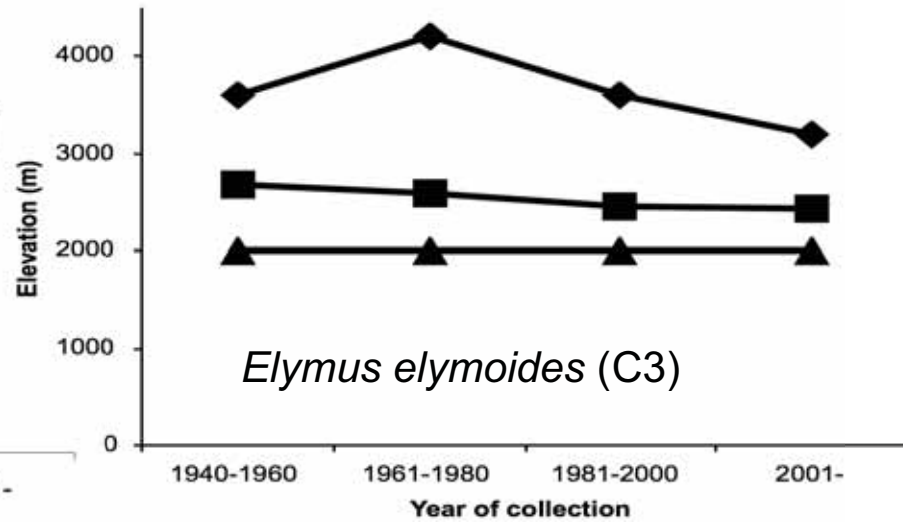
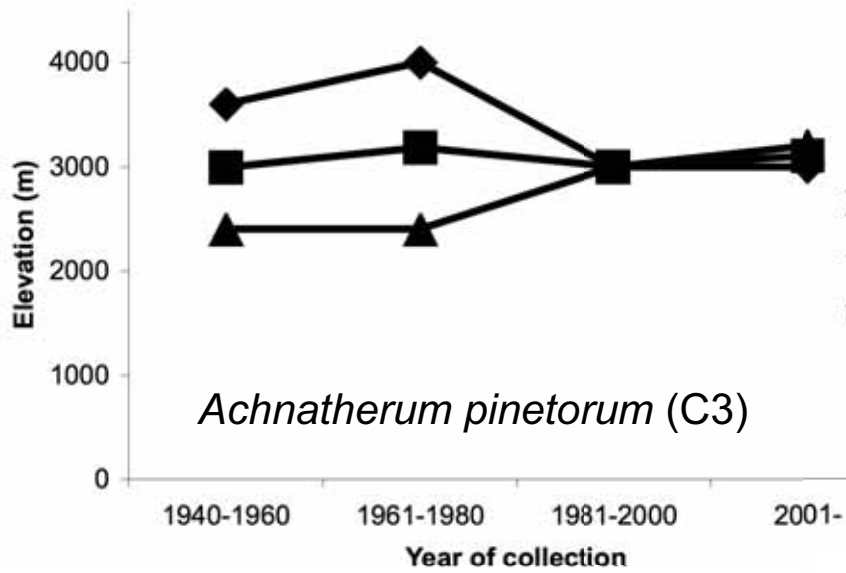


Archival atmospheric CO<sub>2</sub> data for Mauna Loa, Hawaii and growing season (June, July and August) air temperature data for Barcroft field station (3780 m) in California's White Mountains



Average decadal atmospheric CO<sub>2</sub> (open circles with solid line) and temperature (solid diamonds with dashed line) relative to initial observations made during the late 1950s.

Growing season temperatures appear to be increasing faster than atmospheric CO<sub>2</sub>.



Herbarium records for four graminoid species from seven mountainous counties in central eastern California. Consortium of California Herbaria (<http://ucjeps.berkeley.edu/consortium/>); accessed Sept 2007

Only *M. richardsonis* (C4) appears to be moving upslope.

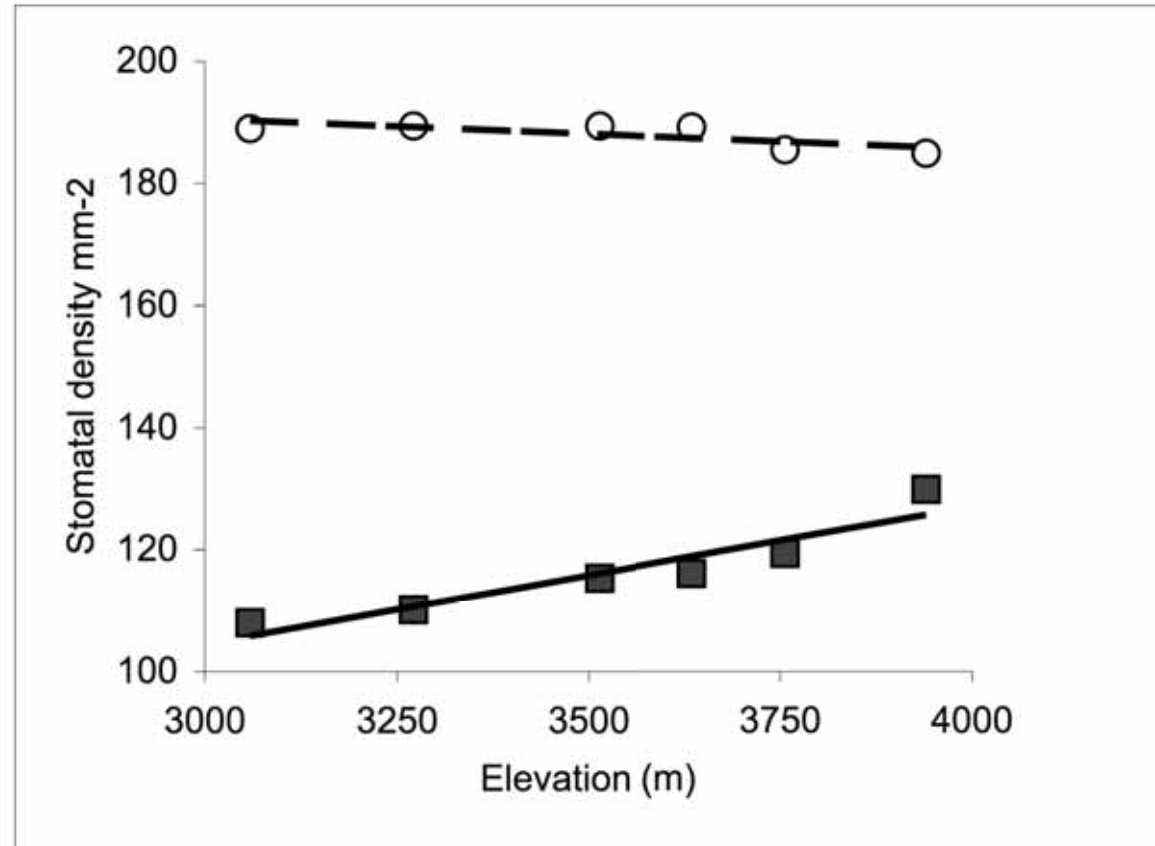
Leaf character	Lowland plants (500-600 m)	Alpine plants (2500-3000 m)
Stomatal density (mm <sup>-2</sup> )	80	101
Leaf nitrogen (% dry mass)	2.1	3.0
Leaf $\delta^{13}\text{C}$ (‰)	-29.0	-26.5

Representative values for several leaf characteristics associated with photosynthetic function in C3 plant species taken from plants in different elevation classes. (Data adapted from Körner 2003).

Widely proposed explanations for these general observations;

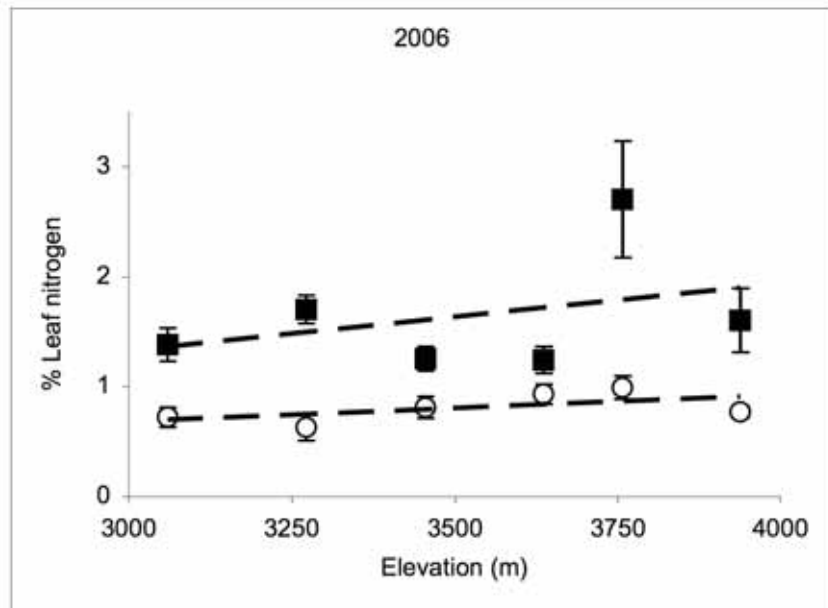
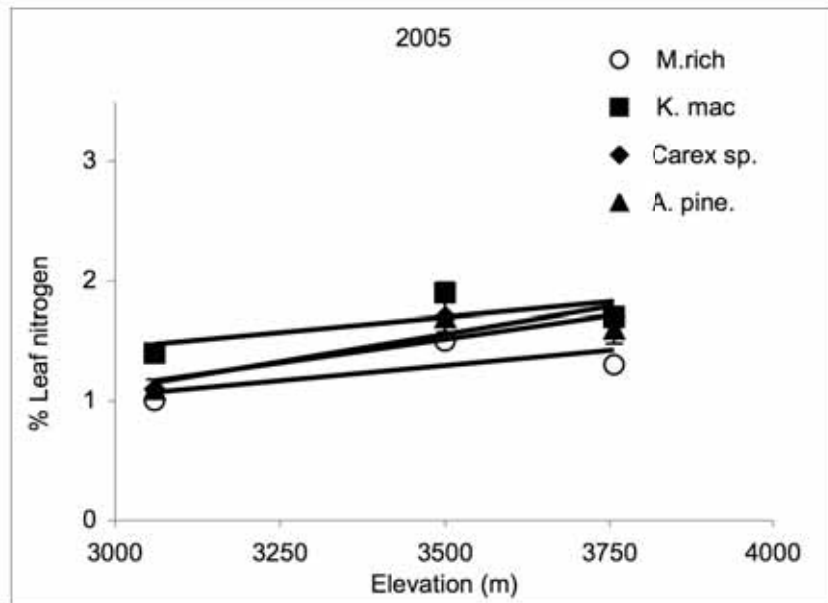
- Increases in stomatal density help compensate for diffusion-limited photosynthesis at high elevations
- Increases in leaf N represent increases in photosynthetic enzymes to help compensate for diffusion-limited photosynthesis at high elevations
- Increases in leaf  $\delta^{13}\text{C}$  indicate that photosynthesis remains diffusion-limited at high elevations

C4 photosynthesis should not be diffusion-limited in these low- $\text{pCO}_2$  atmospheres. These foliar traits are expected to be insensitive to elevation in *M. richardsonis*.



Stomatal density summed for both leaf surfaces in *Muhlenbergia richardsonis* (open circle) and *Koeleria macrantha* (square) from six sites, for the 2006 growing season. (Other species were not amenable to this analysis but the observed changes for *Koeleria macrantha* are common for C3 species.)

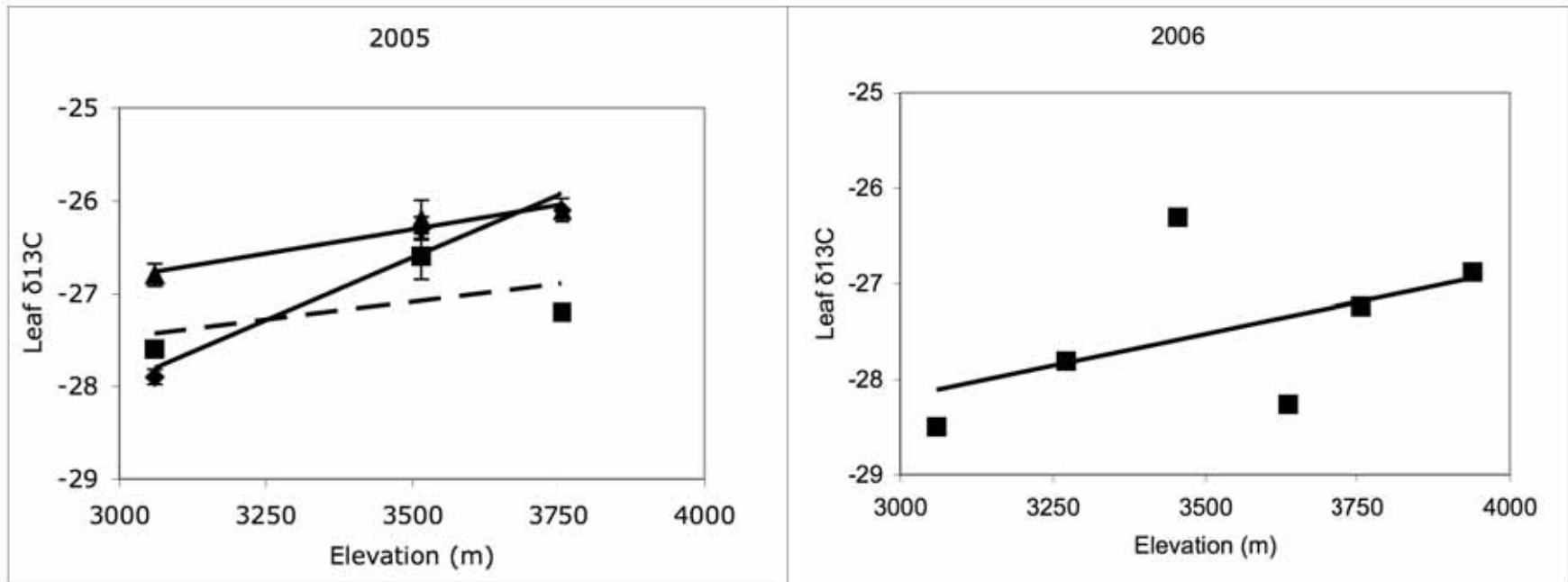
Elevation dependent changes in SD in C3 spp but not in C4 spp.



Leaf nitrogen concentration at different elevations in graminoid species from the White Mountains in 2005 (a) and 2006 (b).

Sampled species in 2005 were C3 plants *Achnatherum pinetorum* (triangle), *Carex* sp. (diamond) *Koeleria macrantha* (square), and the C4 plant *Muhlenbergia richardsonis* (open circle). Sampled species in 2006 were *Koeleria macrantha* and *Muhlenbergia richardsonis*. All linear fits were significant for 2005 (Table 2) but not for 2006 (Table 3). The lines that best describe the association between elevation and leaf nitrogen for 2005 are given as; leaf nitrogen =  $0.0003 \times \text{elevation} - 1.123$  ( $R = 0.631$ ) for *A. pinetorum*, leaf nitrogen =  $0.0003 \times \text{elevation} - 1.686$  ( $R = 0.817$ ) for *Carex* sp., leaf nitrogen =  $0.0002 \times \text{elevation} - 0.129$  ( $R = 0.587$ ) for *K. macrantha*, and leaf nitrogen =  $0.0001 \times \text{elevation} - 0.294$  ( $R = 0.613$ ) for *M. richardsonis*.

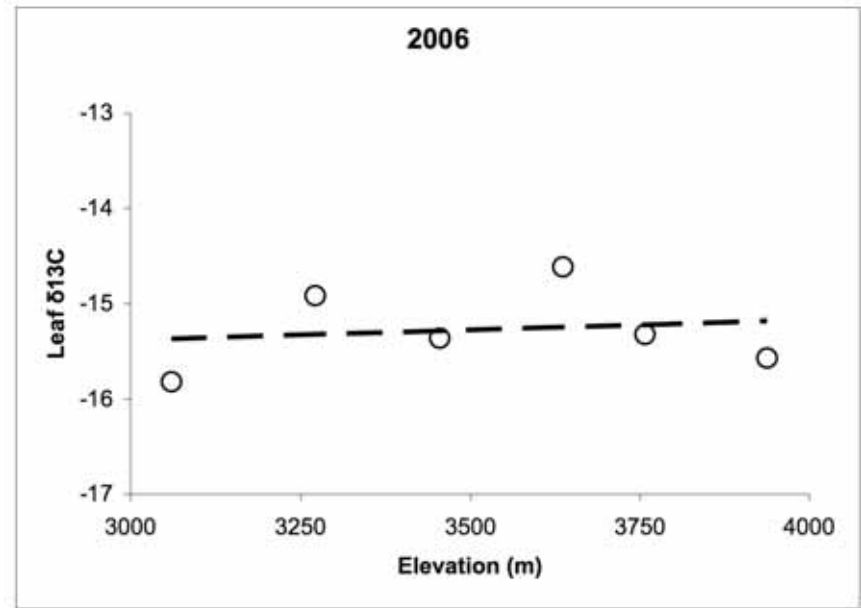
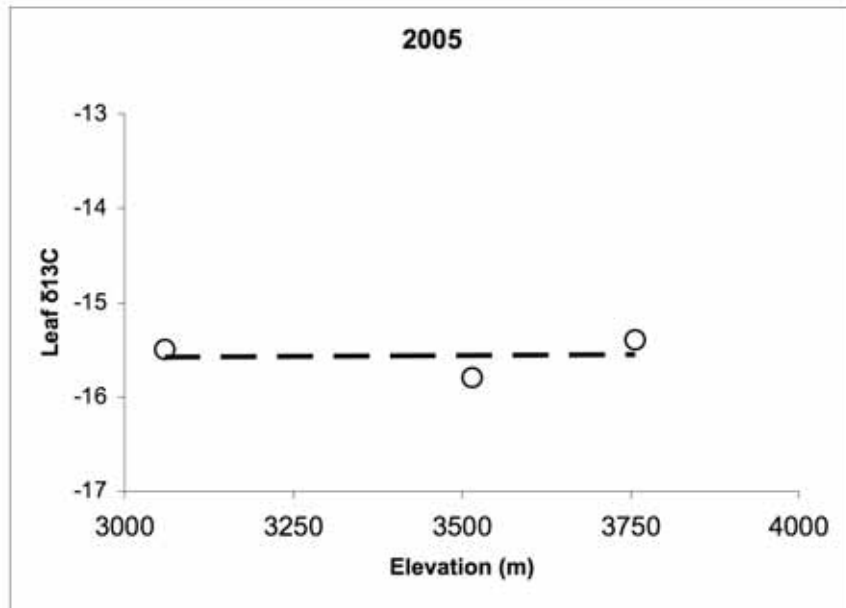
Elevation dependent changes in %N differed between years but was similar for both photosynthetic types.



Leaf  $\delta^{13}\text{C}$  at different elevations in C3 graminoid species from the White Mountains in 2005 (a) and 2006 (b).

Sampled species in 2005 were C3 plants *Achnatherum pinetorum* (triangle), *Carex* sp. (diamond), and *Koeleria macrantha* (square). Among the C3 species, only *Koeleria macrantha* was sampled in 2006. All linear fits were significant or marginally significant (*K. macrantha* in 2005) in 2005 (Table 2) and 2006 (Table 3).

Elevation dependent change in isotopic composition seen in C3 spp...



Leaf  $\delta^{13}\text{C}$  at different elevations in *Muhlenbergia richardsonis* (C4) from the White Mountains in 2005 (a) and 2006 (b).

Linear fits were not significant for either 2005 or 2006.

...but not in the C4 spp.

- Is there any advantage to being C4 in these low CO<sub>2</sub> atmospheres at high elevations?

1. Which is increasing faster in the mountains, growing season temperature (which might favor Alpine C4 photosynthesis) or pCO<sub>2</sub> (which might favor Alpine C3 photosynthesis)?

Temperature is changing faster implying that high elevation conditions are becoming increasingly favorable for C4 species.

2. Is there evidence for differential upslope migration of *M. richardsonis* and co-occurring C3 plants in recent years?

Limited evidence from herbarium records suggest that *M. richardsonis* is moving upslope which was not true for the reference C3 species.

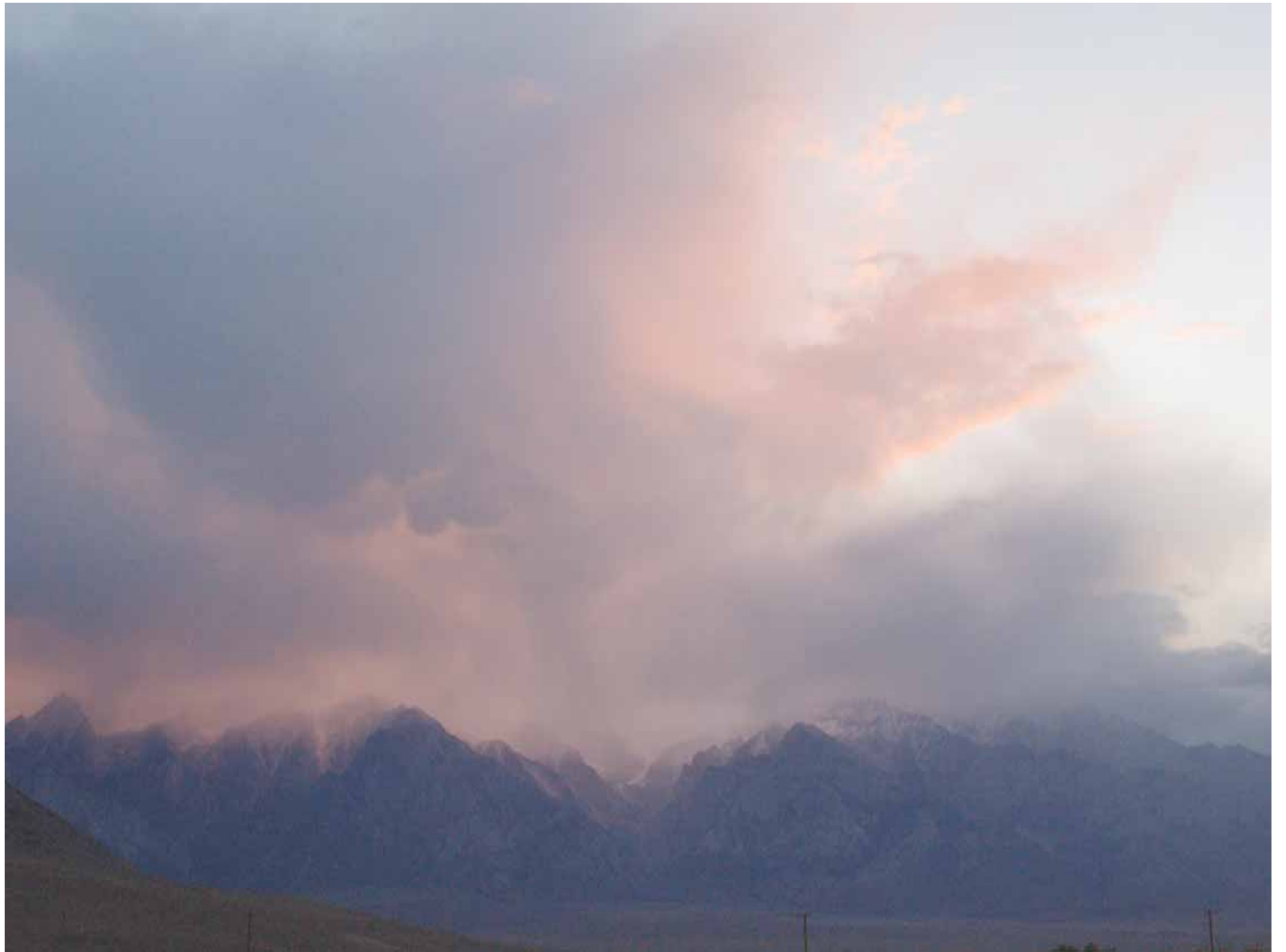
3. Do C4 leaves respond to changing elevations differently from C3 plants?

Elevation effects on SD and  $\delta^{13}\text{C}$  differed between *M. richardsonis* and the reference C3 species suggesting that these are indeed CO<sub>2</sub> diffusion effects in C3 plants. Elevation effects on leaf %N were the same for C3 and C4 plants alike suggesting that this response reflects other elevation variables (e.g. temperature) which affects C3 and C4 species similarly.

C4 species appear to be pre-adapted to the low  $p\text{CO}_2$  conditions of high altitudes and are probably absent from contemporary Alpine communities due to low temperatures.

C4 species are predicted to become more frequent in high-elevation vegetation as temperature rise.







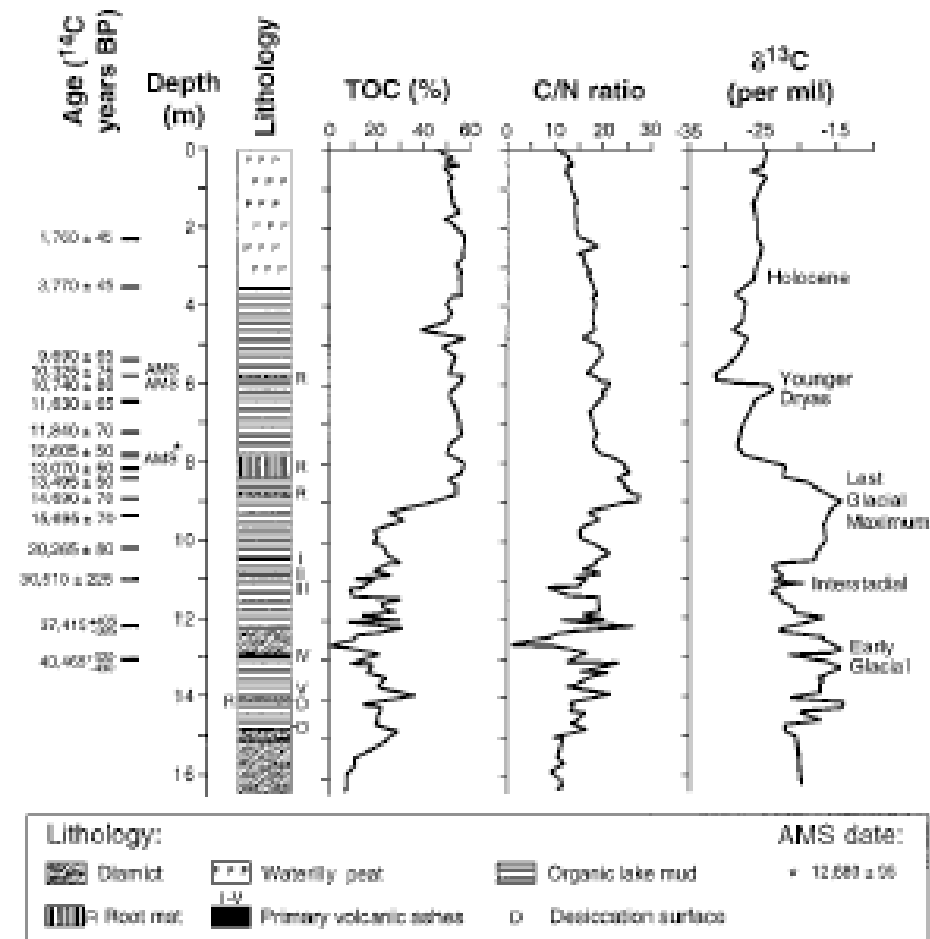
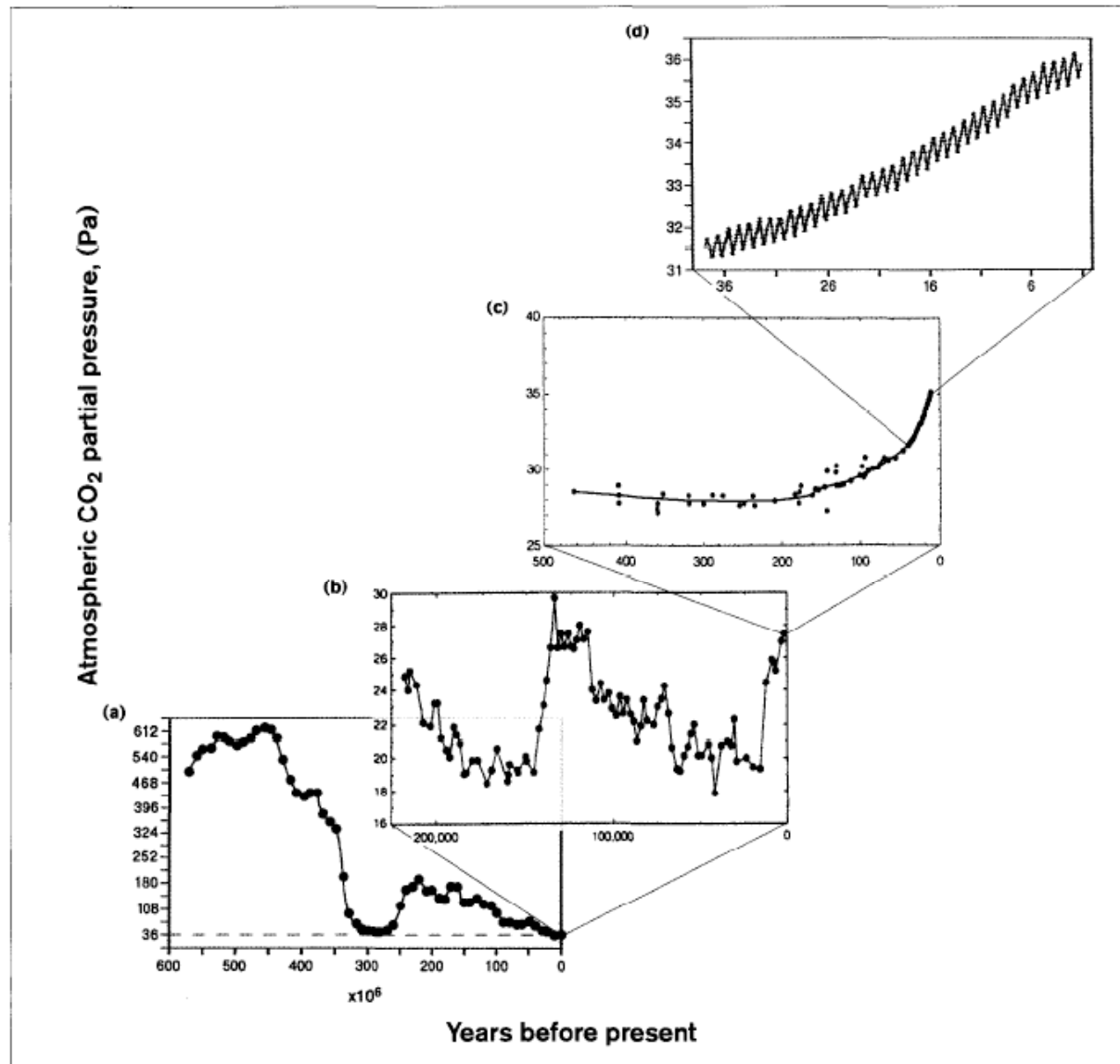


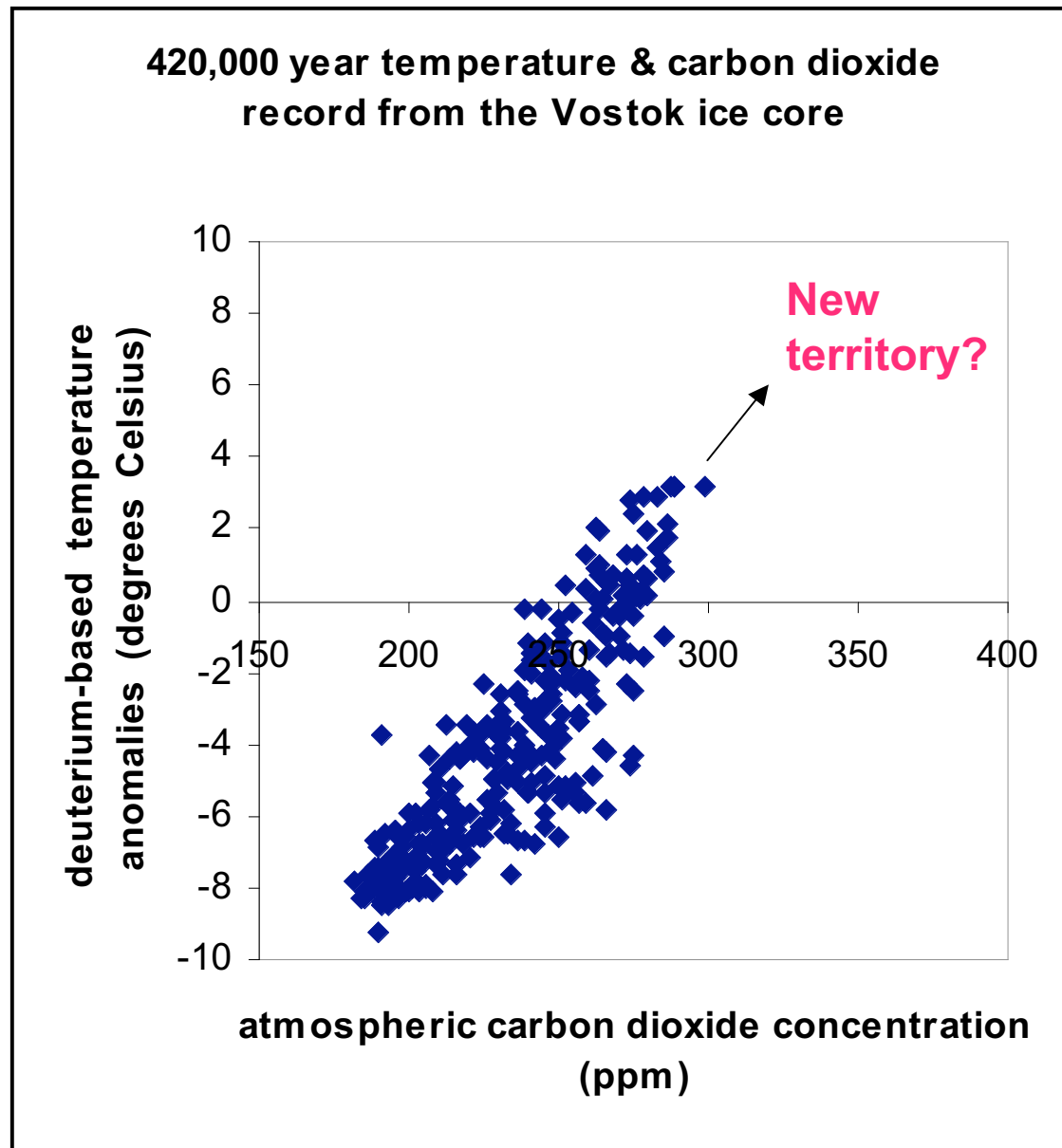
Fig. 1. Stratigraphy and bulk sediment properties of core SL1, Sacred Lake, Mount Kenya. The  $^{14}\text{C}$  dates older than 30,000 years B.P. are probably minimum ages.

Figure 1

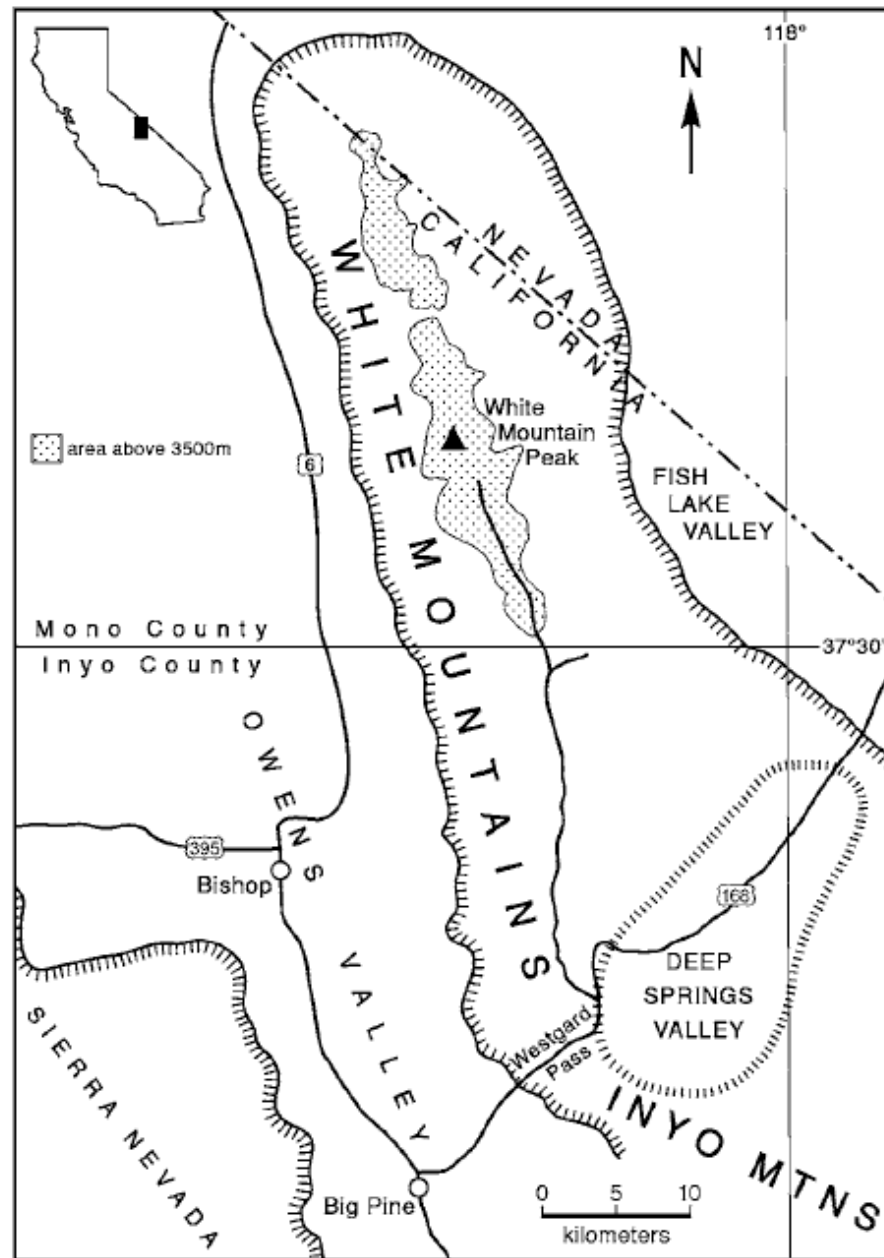


Atmospheric CO<sub>2</sub> levels over geological time. (a) Partial pressure for the last 600,000,000 years, modeled from the geochemical global carbon cycle of Berner [1] (estimated error is  $\pm 50\%$ ). (b) Atmospheric CO<sub>2</sub> during the last two major glacial periods (220,000 years) measured from

ice core bubbles [2]. (c) CO<sub>2</sub> during the last 500 years, also measured from ice core bubbles [3]. (d) Direct atmospheric measurements of CO<sub>2</sub> levels from the top of Mauna Loa volcano in Hawaii made since 1957 [4]. The dips correspond to summer in the Northern hemisphere.



Source: Petit, J.R., et al., 2001, Vostok Ice Core Data for 420,000 Years, IGBP PAGES/World Data Center for Paleoclimatology Data Contribution Series #2001-076. NOAA/NGDC Paleoclimatology Program, Boulder CO, USA.

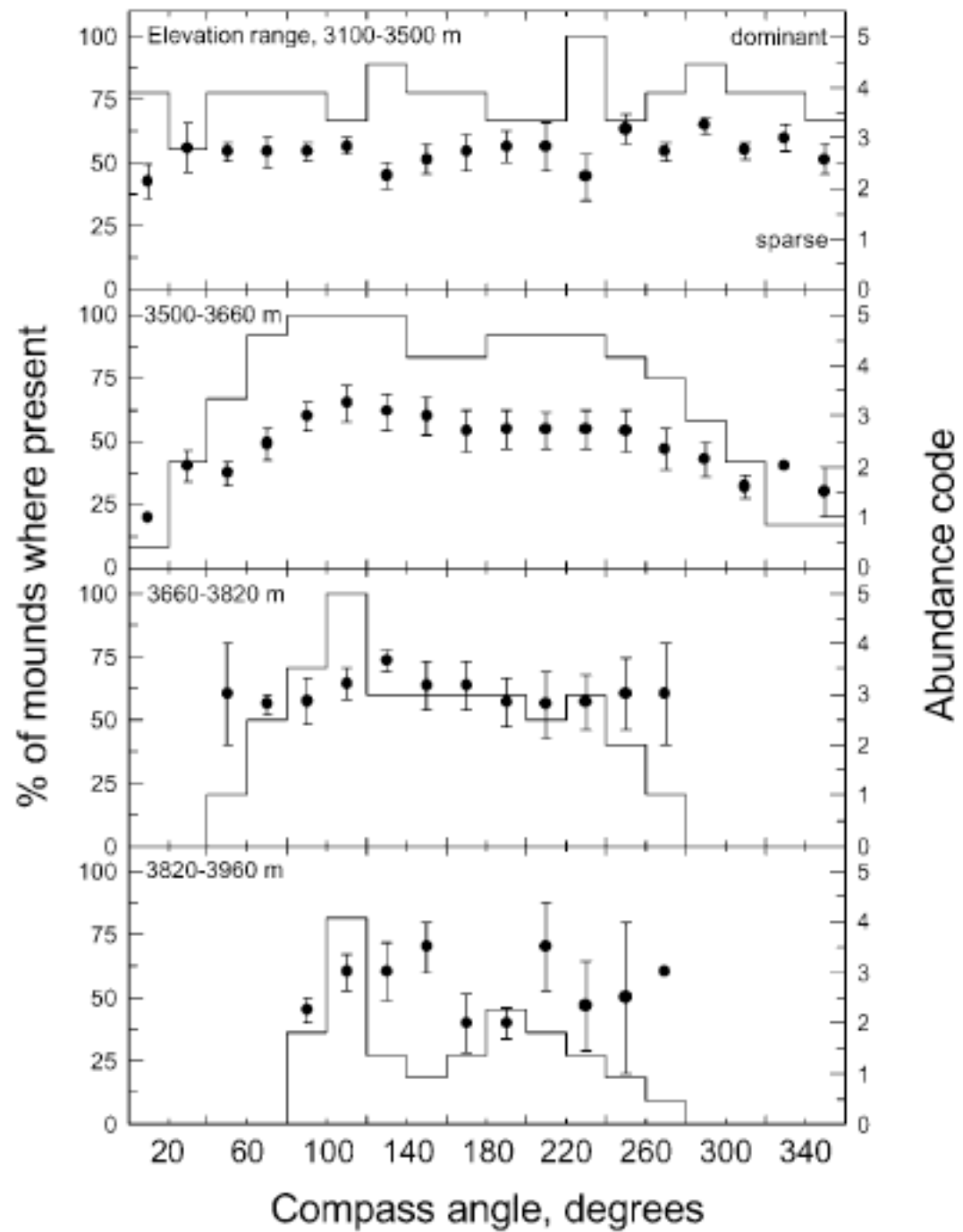


**FIGURE 1.** Regional location of the White Mountains in eastern California and adjacent Nevada. Alpine habitats over 3500 m elevation are shown by the stippled area.

Source: Rundel et al., 2005

**Fig. 1** White Mountains study site, showing the location of the Nello Pace lab (*arrow*), the summit of Mt. Barcroft (*dark arrowhead*), and numerous study mounds (*white arrowheads*). The peak in the background is White Mountain Peak (4,342 m)

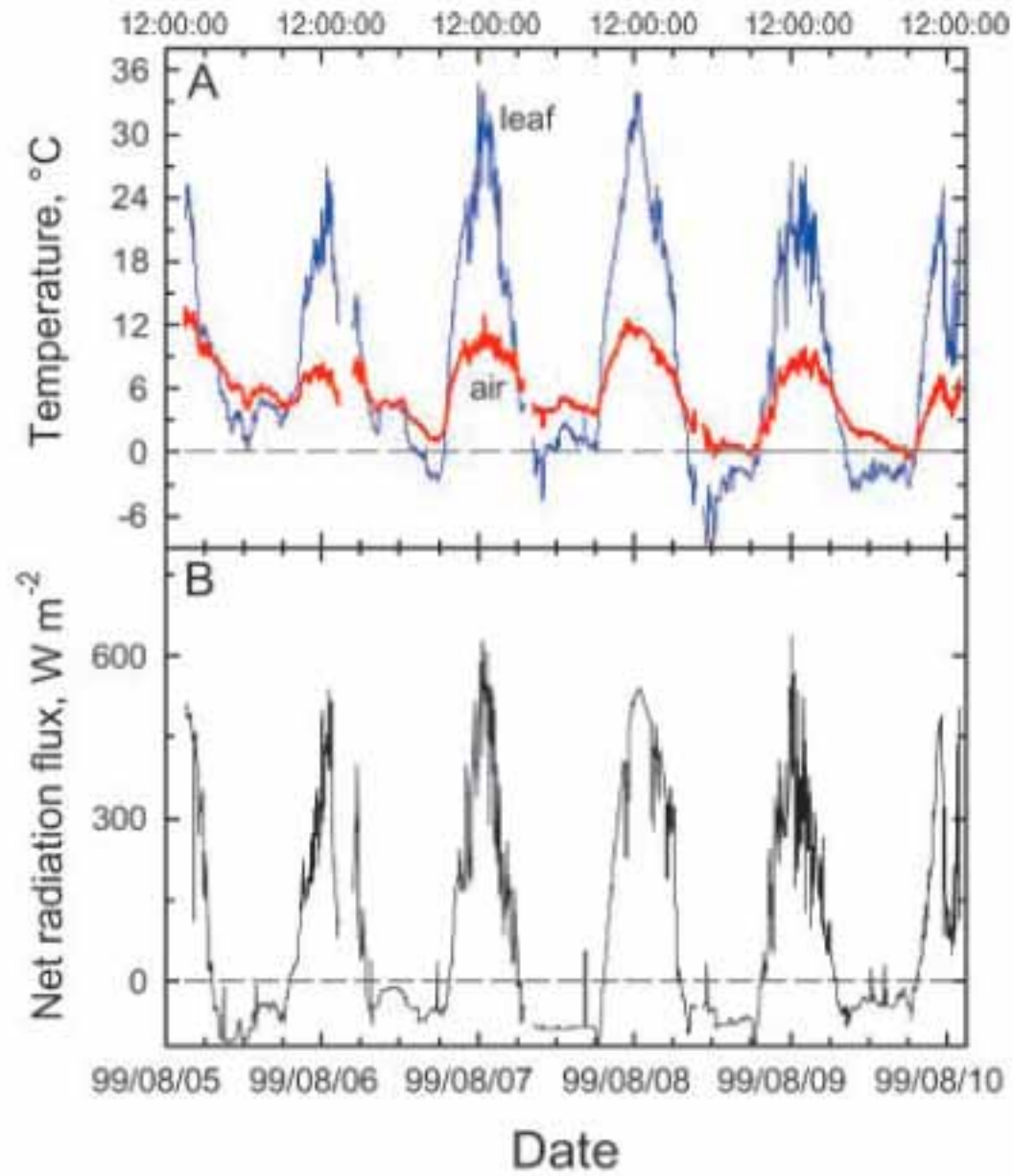




Source: Sage, 2002

**Fig. 2** View of the prostrate growth form of *Muhlenbergia richardsonis* (in foreground, indicated by the letter "M") and the bunch grass morphology of *Koeleria macrantha* (indicated by arrows). Elevation is approximately 3,800 m





Source: Sage, 2002

**Table 1** Height and leaf temperature of *Muhlenbergia richardsonis* and *Koeleria macrantha* in the alpine zone of the White Mountains, California, in August 1998 (mean  $\pm$ SD,  $n=5-10$ ). Superscripts indicate statistically significant groups at a measurement site at  $P<0.05$  by Student's  $t$ -test

Location and time (hours)	Canopy height (mm)		Leaf temperature ( $^{\circ}$ C)	
	<i>Muhlenbergia</i>	<i>Koeleria</i>	<i>Muhlenbergia</i>	<i>Koeleria</i>
Open flats, 3,800 m, 1230	21 $\pm$ 3 <sup>a</sup>	59 $\pm$ 7 <sup>b</sup>	30 $\pm$ 13 <sup>a</sup>	18 $\pm$ 4 <sup>b</sup>
Open flats, 3,800 m, 1300	25 $\pm$ 6 <sup>a</sup>	56 $\pm$ 10 <sup>b</sup>	27 $\pm$ 2 <sup>a</sup>	15 $\pm$ 3 <sup>b</sup>
Rocky enclosure, 3,800 m, 1330	21 $\pm$ 5 <sup>a</sup>	49 $\pm$ 7 <sup>b</sup>	34 $\pm$ 2 <sup>a</sup>	23 $\pm$ 3 <sup>b</sup>
Open flats, 3,750 m, 1400	37 $\pm$ 7 <sup>a</sup>	58 $\pm$ 16 <sup>b</sup>	25 $\pm$ 4 <sup>a</sup>	15 $\pm$ 2 <sup>b</sup>
All sites	25 $\pm$ 8 <sup>a</sup>	55 $\pm$ 10 <sup>b</sup>	29 $\pm$ 4 <sup>a</sup>	18 $\pm$ 4 <sup>b</sup>