

22. G. J. Demaison, E. T. Moore, *Am. Assoc. Petrol. Geol. Bull.* **8**, 1179 (1980).
23. Sediments were demineralized with mixtures of HCl (1N) and hydrofluoric acid (10%). Acid-soluble OM was recovered after removal of paramagnetic metals and desalting as described [Y. Gélinas, J. A. Baldock, J. I. Hedges, *Org. Geochem.* **32**, 677 (2001)].
24. Solid-state  $^{13}\text{C}$  NMR is well suited for probing the bulk composition of sedimentary OM. When rigorous care is taken with spectral acquisition techniques [P. Kinches, D. S. Powlson, E. W. Randall, *Eur. J. Soil Sci.* **46**, 125 (1995)],  $^{13}\text{C}$  NMR can provide a representative estimate of all OC forms in a sample.
25. P. N. Nelson, J. A. Baldock, P. Clarke, J. M. Oades, G. J. Churchman, *Aust. J. Soil Res.* **37**, 289 (1999). Biochemical compositions and an application of the model can be found in Hedges et al. [*Nature* **409**, 801 (2001)]. For this work, however, oleic acid was used as the lipid component rather than stearic acid, and the calculated fraction of OC present in protein structures was not constrained by the N:C ratio of the sample.
26. Surface areas were obtained by Brunauer-Emmett-Teller adsorption isotherms using  $\text{N}_2$  as the adsorbent.
27. M. J. Bock, L. M. Mayer, *Mar. Geol.* **163**, 65 (2000).
28. R. S. Ganeshram, S. E. Calvert, T. F. Pedersen, G. L. Cowie, *Geochim. Cosmochim. Acta* **63**, 1723 (1999).
29. A. Lückge, M. Bousafir, E. Lallier-Vergès, R. Littke, *Org. Geochem.* **24**, 437 (1996).
30. S. M. Henrichs, in *Organic Geochemistry*, M. H. Engel, S. A. Macko, Eds. (Plenum, New York, 1993), pp. 101–117.
31. B. Dauwe, J. J. Middelburg, P. M. J. Herman, C. H. R. Heip, *Limnol. Oceanogr.* **44**, 1809 (1999). Spiked samples were hydrolyzed (with 6N HCl at 150°C for 70 min in  $\text{N}_2$ ). Amino acids were then reacted with o-phthalaldehyde and analyzed by reverse-phase high-performance liquid chromatography.
32. V. Salmon, S. Derenne, E. Lallier-Vergès, C. Largeau, B. Beaudouin, *Org. Geochem.* **31**, 463 (2000).
33. R. G. Keil, D. B. Montluçon, F. G. Prahl, J. I. Hedges, *Nature* **370**, 549 (1994).
34. R. J. Smernik, J. O Skjemstad, J. M. Oades, *Aust. J. Soil Res.*, **38**, 665 (2000).
35. The nonhydrolyzable component was obtained after demineralization and sequential hydrolyses to remove carbohydrates (with 2N to 6N trifluoroacetic acid at 100°C in  $\text{N}_2$ ) and proteins (with 6N HCl at 150°C in  $\text{N}_2$ ).
36. M. A. Wilson, *NMR Techniques and Applications in Geochemistry and Soil Chemistry* (Pergamon, Oxford, 1987).
37. We thank R. Keil, S. Wakeham, the University of Washington Marine Organic Geochemistry and CSIRO groups, and two anonymous reviewers for their inputs into this manuscript. Supported by NSF grants to J.I.H. and a Canadian NSERC fellowship to Y.C.

8 May 2001; accepted 24 August 2001

# Late Holocene Climate and Cultural Changes in the Southwestern United States

Victor J. Polyak\* and Yemane Asmerom

Columnar stalagmites in caves of the Guadalupe Mountains during the late Holocene record a 4000-year annually resolved climate history for the southwestern United States. Annual banding, hiatuses, and high-precision uranium-series dating show a present day–like climate from 4000 to 3000 years ago, following a drier middle Holocene. A distinctly wetter and cooler period from 3000 to 800 years ago was followed by a period of present day–like conditions, with the exception of a slightly wetter interval from 440 to 290 years before the present. The stalagmite record correlates well with the archaeological record of changes in cultural activities of indigenous people. Such climate change may help to explain evidence of dwelling abandonment and population redistribution.

We present high-resolution late Holocene climate reconstruction for the southwestern United States on the basis of variations in annual band thickness, growth–no growth records, differences in mineralogy, and high-precision uranium-series (U-series) dating of stalagmites. These stalagmites, from Carlsbad Cavern and Hidden Cave, Guadalupe Mountains, New Mexico (Fig. 1), show evidence of primary features such as aragonite layers, well-preserved delicate fossils, and growth banding, indicating a lack of diagenetic alteration. Aragonite layers in calcitic stalagmites generally form at the typically low cave temperature (i.e., 20°C) under conditions of higher-than-normal evaporation from already elevated Mg/Ca in cave waters, and can therefore be regarded (in comparison to calcite layers) as indicators of more evaporative conditions in caves (1–4). Changes in species of well-preserved fossil

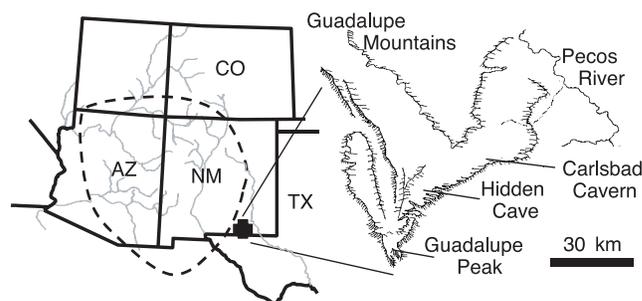
mites and other microarthropod parts may also be broad indicators of climate change (5). Annual growth banding in stalagmites, documented elsewhere by only a few reports (3, 6–9), has the potential to reveal highly resolved climate change. In this semi-arid region with seasonal-dependent precipitation, stalagmite growth is moisture limited, and with relative humidity of 75 to 95% in these caves, the stalagmites—although not yet useful for stable isotope work (10), unlike other settings (2, 11)—preserve well-defined, climate-revealing, annual bands.

Layers of altering clear and inclusion-rich

calcite [couplets (8, 9)] define annual banding in the stalagmites, which can be detected by optical microscopy (Fig. 2). Our darker inclusion-rich portions of each couplet appear to consist of a mixture of water and organics probably formed by a dry-seasonal deposition of microflora. The clear portion of each band represents faster growth during seasonal periods of increased drip rates. To establish that the bands constitute annual deposition of calcite, we measured thicknesses of >1600 bands (from a possible ~2000 bands,  $2796 \pm 88$  to  $835 \pm 25$  years B.P.) in stalagmite BC2. The average measured band thickness equals  $0.106 \pm 0.002$  mm/year, and the growth rate derived from U-series dating equals  $0.100 \pm 0.006$  mm/year, which are within their  $2\sigma$  errors (12, 13). There are no apparent hiatuses in this segment of stalagmite BC2, and it is clear that the bands represent annual deposition of calcite, and that band thickness represents the growth rate. This agreement was strengthened by supporting data from all five stalagmites (13). It is also apparent that decreased annual precipitation usually results in thinner bands, aragonite layers, or no-growth scenarios. For instance, a sequence of thinner bands in stalagmite BC2 was deposited coeval with aragonite layers in stalagmites 89029 and 89037. In our climatic setting, thicker calcite bands are therefore interpreted as relative indicators of increased annual precipitation like that reported by Brook et al. (9).

A significantly cooler, wetter climate in the

**Fig. 1.** Location of Carlsbad Cavern, Hidden Cave, and the Guadalupe Mountains in relation to the puebloan Southwest (dashed line). Samples from Carlsbad Cavern came from the entrance to Bat Cave near the commercial trail. Collection location of Hidden Cave samples is given in (5).



Department of Earth and Planetary Sciences, University of New Mexico, 200 Yale Boulevard, Albuquerque, NM 87131, USA.

\*To whom correspondence should be addressed. E-mail: polyak@unm.edu

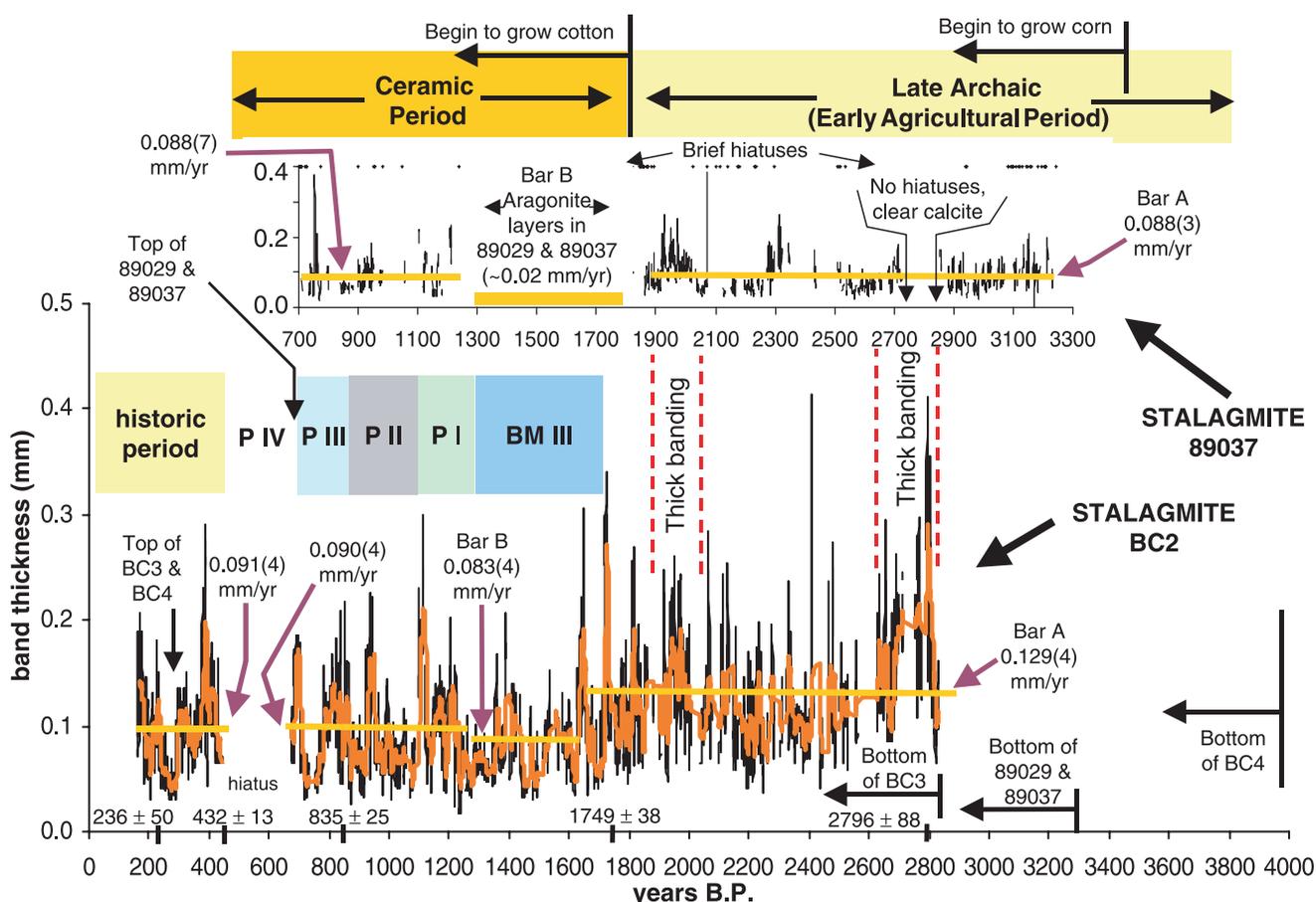
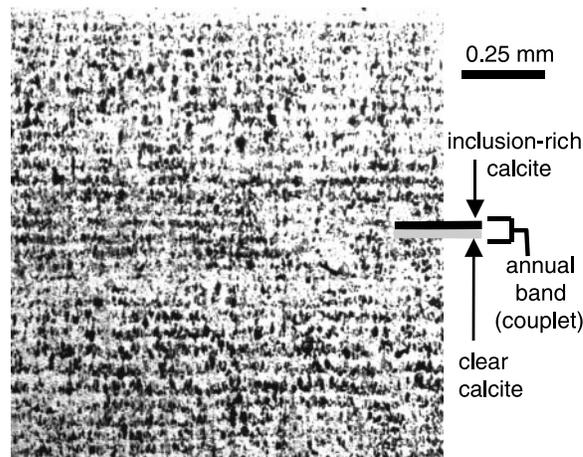
## REPORTS

southwestern United States during the late Pleistocene (14) produced massively large stalagmites in caves of the Guadalupe Mountains [some of the world's largest (15)], whereas virtually no speleothem growth in these caves has been reported during the drier Holocene. Growth of the small columnar stalagmites during the late Holocene, although minute in com-

parison, marks the beginning of increased annual precipitation at ~4000 years B.P. (13). The apparent lack of stalagmite growth before 4000 years ago (4 ka) supports a drier middle Holocene for the southwestern United States, consistent with other published reports (16–19). Some packrat midden studies show the increasing spread of the American deserts after

5 ka, which seems to imply an overall decrease in effective moisture from the early to late Holocene (20, 21). However, intervals of increased moisture during the late Holocene in the southwestern United States are reported by numerous studies (5, 22–30) and seem to support an interpretation favoring greater effective moisture at least during the core of the late Holocene. Geologic and archaeological evidence for the Colorado Plateau indicates several drier and wetter intervals for the last 2000 years (22). A wetter period from 4 to 2.2 ka for the northern Chihuahuah Desert, west of the Guadalupe Mountains, was reported on the basis of stable isotopes and soil geomorphology (27). A neopluvial at 3370 <sup>14</sup>C years B.P. in the Guadalupe Mountains region from the aeolian record was also reported (28). In addition, fossil northern or highland mammals from Pratt Cave sediment at 2560 <sup>14</sup>C years B.P., and Honest Injun Cave sediment at 3 to 1 ka in the Guadalupe Mountains, indicated more mesic conditions than at present (29, 30). Somewhat similar results have been reported elsewhere in the southwestern United States. High lake levels at Cloverdale Lake, southwestern New Mexico (between 5

**Fig. 2.** Micrograph showing examples of typical well-formed annual banding preserved in small columnar stalagmites.



**Fig. 3.** Comparison of annual band data for stalagmites BC2 (Carlsbad Cavern) and 89037 (Hidden Cave) as band thickness versus age. The two time scales are synchronized. These data are compared to the archaeological record for the southwestern United States. The orange curve (stalagmite BC2) is 5-year smoothed data. BM III is Basketmaker III; P I,

II, III, IV are the Pueblo I, II, III, and IV periods of the Pecos classification. The colored boxes indicate the approximate chronologic occurrence and duration of these periods (33, 34). Bars A and B, which designate average growth rate, enhance correlations between important sequences within the two stalagmites.

## REPORTS

and 2 ka); expansion of ponderosa pines near Chaco Canyon, New Mexico [at 2.2 ( $^{14}\text{C}$ ) ka]; increase in lake levels at Potato Lake, central Arizona (by 3 ka); and increased effective moisture at Bear Lake, northwestern Arizona (after 4 ka) were all reported after a drier middle Holocene (23–26).

Our stalagmite record (five stalagmites) consistently provides a century- and annually resolved history of climate. Growth of stalagmites from 4 to ~3 ka lacks good representation but suggests at least intervals of slightly greater effective annual moisture than at present. Thicker annual bands in four of the five stalagmites from ~3000 to 1700 years B.P. indicate significantly greater effective annual moisture than at present (average growth rate represented by Fig. 3, bar A). A 200-year period of thicker bands at 2800 to 2600 years B.P. in these stalagmites appears to depict the wettest interval of the late Holocene for this region. This is synchronous with a reported abrupt change to cooler and wetter conditions in Europe, and globally in temperate and boreal zones, at ~2650 years B.P. (31). Another period of thicker bands represents sizable increased effective moisture around 2000 years B.P. This is followed by a distinctly drier interval from ~1700 to 1300 years B.P. defined by thinner bands in stalagmite BC2 and BC4 and aragonite layers in the Hidden Cave stalagmites (Fig. 3, bar B) (13). Stalagmite growth during this period indicates that the climate was near its present-day conditions, but overall slightly wetter. Termination of growth of three of the five stalagmites near 700 to 800 years B.P. (hiatuses just above the following dates:  $835 \pm 25$ ,  $819 \pm 82$ , and  $888 \pm 144$  years B.P.) and thinner bands in stalagmite BC4 starting at this time define the beginning of a period of decreased annual precipitation equal to or drier than at present. Our results show that this period of near-present-day climate extends to the present and is interrupted by a brief <300-year period of slightly increased precipitation, as shown by the continued growth of the Bat Cave stalagmites. This growth in stalagmite BC2 is best represented by a continuous sequence of 292 bands and two U-series dates ( $432 \pm 13$  and  $236 \pm 50$  years B.P.), with the thickest banding from 440 to 290 years B.P. The top of stalagmite BC2 is ~170 years B.P. Interpolated ages for the tops of stalagmites BC3 ( $336 \pm 86$  years B.P.) and BC4 ( $250 \pm 56$  years B.P.) are at or soon after the abrupt thinning of banding at ~290 years B.P. in stalagmite BC2. This interval of stalagmite growth from 440 to 290 years B.P. occurred during a brief period of global cooling referred to as the Little Ice Age (32). Comparably, the period of the Little Ice Age was defined by a study of stalagmites from Madagascar as 425 to 230 years B.P. (9) and was reported as beginning at 450 years B.P. on the basis of stalagmites from Nepal (2).

Our overall interpretation is that the climate

in the southwestern United States from the mid- to late Holocene became wetter at ~4 ka and comparable to or slightly wetter than the present climate until ~3 ka. The most significant period of increased moisture occurred from ~3 to 1.7 ka, with distinct pulses at 2.8 and 2.0 ka. Greater than present-day wetness persisted until ~800 years B.P., after which conditions became as dry as or drier than present-day conditions. A ~300-year period of slightly greater than present-day moisture occurred between 460 and 170 years B.P., with the most notable increase in annual precipitation during the interval from 440 to 290 years B.P.

The stalagmite record shows changes in annual precipitation at an annual to decadal resolution, allowing for comparison of the archaeological records with the Pecos classification of cultural periods for the southwestern United States (Fig. 3). Earliest evidence for the growth of corn by ancestral Americans in the southwestern United States (33) is coeval with the beginning of the late Holocene wet period defined by our data. This is also when the Late Archaic period is reported to begin in most areas (33, 34). Evidence from Pendejo Cave in the adjacent Sacramento Mountains shows the use of corn from 2950 to 1665 years B.P. (35), which coincides with our wettest interval. Ceramics and cotton appeared at the same time that we report a slight decrease in effective moisture around 1700 years B.P. (33). These somewhat drier conditions lasted from ~1700 to ~1300 years B.P., which overlaps with the Basketmaker III period (33, 34). Population increases during the last 2000 years in areas of the Colorado Plateau that are currently very dry have been interpreted as indicators of periods of increased annual precipitation (22). An apparent increase in effective moisture at 1250 years B.P. that lasted until 1100 years B.P. (Fig. 3) marks a time of population expansion on the Colorado Plateau (22) and is coeval with the Pueblo I period for most areas of the southwestern United States, when cultures moved from pithouses to above-ground dwellings (33). Population redistribution from higher elevations and population growth of lower elevation areas took place during the Pueblo II period (33, 34), corresponding to a drying trend in our record at 1100 years B.P. that becomes increasingly wetter up to 900 years B.P. and drier again by 850 years B.P. The Pueblo III period represents a higher elevation population redistribution at ~850 years B.P. and a lower elevation redistribution around 750 to 700 years B.P. (33, 34), which compares well with our data showing a wetter period from ~850 to 800 years B.P. followed by abrupt drying conditions. Timing of the onset of significantly drier conditions, represented by no stalagmite growth from ~670 to 460 years B.P., is also coincident with the Pueblo IV period of significant abandonment of higher elevation dwellings and population redistribution to river areas (22, 33, 34). The historic period starts

near the beginning of the Little Ice Age (~500 years B.P.). Climate change, although not the sole reason, is an important underlying explanation for cultural shifts and evolution in the arid southwestern United States during the late Holocene.

### References and Notes

1. J. W. Murray, *J. Geol.* **62**, 481 (1954).
2. R. F. Denniston, L. A. González, Y. Asmerom, R. H. Sharma, M. K. Reagan, *Quat. Res.* **53**, 196 (2000).
3. L. B. Railsback, G. A. Brook, J. Chen, R. Kalin, C. J. Fleisher, *J. Sediment. Res.* **A64**, 147 (1994).
4. At present, the collection areas in Hidden Cave (two stalagmites, BC2 and BC4) and Bat Cave–Carlsbad Cavern (two stalagmites, 89029 and 89037) are over-all dry and inactive, although we monitored some growth of calcite in Hidden Cave during the 1991–1992 El Niño season. Most of these small columnar stalagmites are currently dormant and may grow only during very wet years. Precipitation in the Carlsbad region is seasonal, with most rainfall coming in the summer; enhanced winter amounts occur from El Niño–Southern Oscillation (ENSO)–dominated precipitation. The growth–no growth pattern of many of these small columnar stalagmites in these less humid cave zones therefore corresponds to wetter than and drier than current climate conditions, respectively.
5. V. J. Polyak, J. C. Cokendolpher, R. A. Norton, Y. Asmerom, *Geology* **29**, 643 (2001).
6. A. Baker, P. L. Smart, R. L. Edwards, D. A. Richards, *Nature* **364**, 518 (1993).
7. Y. Y. Shopov, D. C. Ford, H. P. Schwarcz, *Geology* **22**, 407 (1994).
8. D. Genty, Y. Quinif, *J. Sediment. Res.* **66**, 275 (1996).
9. G. A. Brook, M. A. Rafter, L. B. Railsback, S. Sheen, J. Lundberg, *The Holocene* **9**, 695 (1999).
10. C. H. Hendy, *Geochim. Cosmochim. Acta* **35**, 801 (1971).
11. J. A. Dorale, R. L. Edwards, E. Ito, L. A. González, *Science* **258**, 1626 (1992).
12. U-series analysis for chronology was performed at the Radiogenic Isotope Laboratory at the University of New Mexico. Stalagmite powder was dissolved in  $\text{HNO}_3$  and spiked with a mixed  $^{229}\text{Th}$ – $^{233}\text{U}$ – $^{236}\text{U}$  spike. The use of a mixed spike eliminates propagation of weighing error into the age uncertainties. U and Th were coprecipitated with pure  $\text{FeOH}_3$  and subsequently separated in anion exchange columns in two steps. All isotopic ratios were measured on a Micromass Sector 54 thermal ionization mass spectrometer with a high-abundance sensitivity filter using an ion-counting Daly multiplier. The reported uncertainties in the ratios are  $2\sigma$  of the mean. Age uncertainties include uncertainties related to initial  $^{230}\text{Th}/^{232}\text{Th}$  correction ( $4.4 \times 10^{-6} \pm 50\%$ ). Decay constants are from H. Cheng *et al.* [*Chem. Geol.* **169**, 17 (2000)].
13. Additional growth rate and U-series data, along with photographs of the sample extraction sites of the five stalagmites, are available as supplementary material at Science Online ([www.sciencemag.org/cgi/content/full/294/5540/PAGE/DC1](http://www.sciencemag.org/cgi/content/full/294/5540/PAGE/DC1)).
14. G. I. Smith, F. A. Street-Perrott, in *Late-Quaternary Environments of the United States—The Late Pleistocene*, H. E. Wright Jr., Ed. (Univ. of Minnesota Press, Minneapolis, MN, 1983), pp. 190–212.
15. C. A. Hill, *Geology of Carlsbad Cavern and Other Caves in the Guadalupe Mountains, New Mexico and Texas* (New Mexico Bureau of Mines and Mineral Resources Bulletin 117, Socorro, NM, 1987).
16. E. Antevs, *Am. Antiq.* **20**, 317 (1955).
17. O. K. Davis, D. S. Shafer, *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **92**, 107 (1992).
18. V. T. Holliday, *Quat. Res.* **31**, 74 (1989).
19. S. A. Hall, *Geol. Soc. Am. Bull.* **88**, 1593 (1977).
20. J. L. Betancourt, K. A. Rylander, C. Peñalba, J. L. McVickar, *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **165**, 71 (2001).
21. T. R. Van Dender, T. L. Burgess, J. C. Piper, R. M. Turner, *Quat. Res.* **41**, 99 (1994).
22. R. C. Euler, G. J. Gumerman, T. N. V. Karlstrom, J. S. Dean, R. H. Hevly, *Science* **205**, 1089 (1979).

23. R. S. Anderson, *Quat. Res.* **40**, 351 (1993).
24. P. R. Krider, *Quat. Res.* **50**, 283 (1998).
25. L. D. McFadden, J. R. McAuliffe, *Geomorphology* **19**, 303 (1997).
26. C. Weng, S. T. Jackson, *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **153**, 179 (1999).
27. B. J. Buck, H. C. Monger, *J. Arid Environ.* **43**, 357 (1999).
28. D. E. Wilkins, D. R. Currey, *The Holocene* **9**, 363 (1999).
29. J. S. Applegate, in *Biological Investigations in the Guadalupe Mountains National Park, Texas*, H. H. Genoways, R. J. Baker, Eds. (U.S. National Park Service Transactions and Proceedings Series 4, 1979), pp. 159–166.
30. E. L. Lundelius Jr., in *Biological Investigations in the Guadalupe Mountains National Park, Texas*, H. H. Genoways, R. J. Baker, Eds. (U.S. National Park Service Transactions and Proceedings Series 4, 1979), pp. 239–258.
31. B. van Geel *et al.*, *Radiocarbon* **40**, 535 (1998).
32. H. H. Lamb, *Climatic History and the Future* (Princeton Univ. Press, Princeton, NJ, 1977).
33. L. Cordell, *Archaeology of the Southwest* (Academic Press, Boston, 1997).
34. D. E. Stuart, R. P. Gauthier, *Prehistoric New Mexico* (Univ. of New Mexico Press, Albuquerque, NM, 1996; reprint of 1984 ed.).
35. M. D. Tagg, *Am. Antiq.* **61**, 311 (1996).
36. We thank R. Turner and the Lincoln National Forest, D. Pate, J. Richards, S. Allison, B. Onac, P. Provencio, and Carlsbad Caverns National Park for field assistance and permission to collect samples. Supported in part by NSF grants ATM-9731138 and EAR-94-2048 (Y.A.).

22 May 2001; accepted 28 August 2001

# Constraint to Adaptive Evolution in Response to Global Warming

Julie R. Etterson\*† and Ruth G. Shaw

We characterized the genetic architecture of three populations of a native North American prairie plant in field conditions that simulate the warmer and more arid climates predicted by global climate models. Despite genetic variance for traits under selection, among-trait genetic correlations that are antagonistic to the direction of selection limit adaptive evolution within these populations. Predicted rates of evolutionary response are much slower than the predicted rate of climate change.

Plants have responded to historical climate change by migration and adaptation (1). However, habitat fragmentation is likely to impede migration in the future (2). Furthermore, migration may be slower than during the recession of the glaciers, because migration will depend on seedling establishment in occupied habitats (3). The persistence of populations thus hindered from spread into higher latitudes may depend more heavily on adaptive evolution.

Evolutionary response requires genetically based variation among individuals. However, even given this substrate for natural selection, evolution may be constrained by genetic correlations among traits that are not in accord with the direction of selection (4, 5), correlations termed “antagonistic.” For example, if selection favors high values of two traits but these traits are negatively genetically correlated, selection response can be inhibited (Fig. 1A).

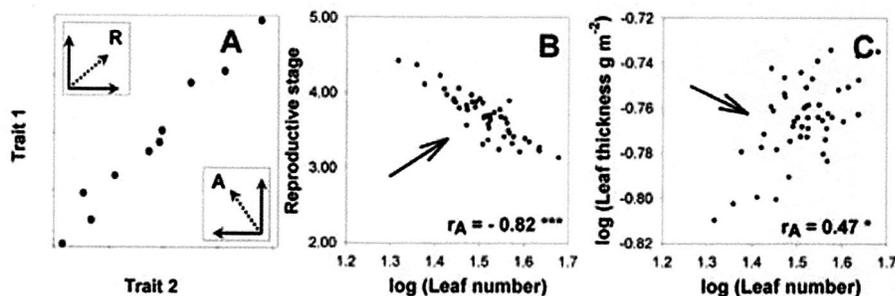
We evaluated the evolutionary potential of three populations of the native annual legume *Chamaecrista fasciculata*, which were sampled from an aridity gradient in tallgrass prairie fragments in the U.S. Great Plains (Fig. 2A) (6). Natural selection on phenotypic variation in *C. fasciculata* differs across this geographic range

(7). Field and common garden studies of Minnesota (MN), Kansas (KS), and Oklahoma (OK) populations of *C. fasciculata* demonstrated clinal variation and genetic divergence with respect to physiological and morphological traits (7). Greenhouse drought experiments also demonstrated adaptation of these populations to different water availability conditions; northern plants are less drought-tolerant than southern plants (7).

We used this spatial gradient in climate as a proxy for the temporal trend in climate predicted for northern populations with global warm-

ing. For example, one global climate model predicts that the MN population will experience soil moisture conditions similar to the current climate of KS by 2025–2035 (Fig. 2B) (8). To predict rates of adaptation to climate change, we estimated evolutionary trajectories for three populations reciprocally planted in three environments. The evolutionary trajectory of a northern population reared in progressively more southern sites provides insight into the population’s adaptive potential in the face of global warming.

We produced pedigreed seeds for MN, KS, and OK populations by controlled crosses in the greenhouse according to a standard quantitative genetic design (9). Progeny from these crosses were reciprocally planted into field sites in MN, KS, and OK (10). We measured traits subject to differing natural selection under distinct drought regimes (fecundity and leaf number) or varying clinally across the geographic range of this study (leaf thickness and the rate of phenological development) (7). In mid-summer we recorded the leaf number and reproductive stage of each plant (11) and collected the uppermost fully expanded leaf. At the natural end of the growing season, we recorded total pod number and seed counts from three representative pods; from these measures, we estimated total lifetime fecundity (12).



**Fig. 1.** Illustration of the influence of genetic correlations among traits on selection response. (A) Hypothetical positive genetic correlation ( $r_A$ ) between two traits (each point represents the joint breeding value for each of two traits). There are two selection scenarios. For R (reinforcing), selection is in the same direction on traits; the depicted  $r_A$  is in accord with the direction of selection, enhancing evolutionary response; thus, the genetic correlation is reinforcing. For A (antagonistic), selection is in the opposite direction for both traits;  $r_A$  is antagonistic to the direction of selection, inhibiting evolutionary response. (B) Scatter plot of MN population reproductive stage and leaf number breeding values (centered on the phenotypic mean), showing significant negative genetic correlation that is antagonistic to the positive vector of joint selection on these traits. (C) Scatter plot of the MN population leaf thickness and leaf number breeding values (centered on the phenotypic mean), showing significant positive genetic correlation that is antagonistic to the negative vector of joint selection.

University of Minnesota, Department of Ecology, Evolution and Behavior, Minnesota Center for Community Genetics, 1987 Upper Buford Circle, St. Paul, MN 55108, USA.

\*To whom correspondence should be addressed.  
 †Present address: University of Virginia, Department of Biology, Glomer Hall, Charlottesville, VA 22903, USA. E-mail: jre7e@virginia.edu