stimulate growth, at least temporarily, even under serious nutrient shortage (*29, 37*).

Another concern raised by our results is that the deleterious levels of starch produced in leaves in the top of canopies under elevated CO_2 levels may cause alterations in dominance relations in plant communities as CO_2 rises. Accumulation of TNC appears to be a result of a specific local dissipation problem at the cellular or chloroplast level because we see no obvious reason for reduced sink activity or long-distance transport problems in the ecosystems with high CO_2 levels. This was indicated by significant increases in the allocation of carbon to the rhizosphere (Tables 1 and 4) and a lack of TNC concentration gradients in stem tissue in plants growing under elevated CO_2 (*14*).

Finally, our results challenge thinking about the biological effects of a doubling of atmospheric CO_2 levels. Observed over long periods, natural ecosystems are believed to have a nearly balanced carbon budget, with photosynthetic uptake equal to respiratory release of CO_2 (*38*). As a result, the ecosystem CO_2 compensation point should be close to ambient CO_2 levels, as was found in the arctic tundra (*39*). It is uncertain how rapidly ecosystem CO_2 compensation points will adjust to rising CO_2 levels. If ecosystem compensation points have not tracked the rapid increases in atmospheric CO_2 levels over the past 100 years, present ambient levels may already represent a massive CO_2 overload to some ecosystems. Our data indicate that elevated CO_2 may not necessarily lead to greater carbon sequestering by terrestrial ecosystems, but that it will likely result in greater carbon turnover.

REFERENCES AND NOTES

1. F. I. Woodward, G. B. Thompson, I. F. McKee, *Ann. Bot.* **67**, 23 (1991).
2. B. R. Strain and J. D. Cure, Eds., *Direct Effects of Increasing Carbon Dioxide on Vegetation* (Publ. ER-0238, U.S. Department of Energy, Washington, DC, 1985).
3. F. A. Bazzaz and E. D. Fajer, *Sci. Am.* **266**, 68 (1992).
4. P. G. Jarvis, *Philos. Trans. R. Soc. London Ser. B* **324**, 369 (1989).
5. H. A. Mooney, B. G. Drake, R. J. Luxmoore, W. C. Oechel, L. F. Pitelka, *Bioscience* **41**, 96 (1991).
6. N. E. Grulke *et al.*, *Oecologia* **83**, 485 (1990).
7. J. D. Cure, in (*2*), pp. 99–116.
8. P. S. Curtis, B. G. Drake, P. W. Leadley, W. J. Arp, D. F. Whigham, *Oecologia* **78**, 20 (1989).
9. D. Eamus and P. G. Jarvis, *Adv. Ecol. Res.* **19**, 1 (1989).
10. C. Körner, in *Vegetation Dynamics and Global Change*, H. Shugart and A. Solomon, Eds. (Chapman & Hall, New York, in press).
11. S. P. Long, *Plant Cell Environ.* **14**, 729 (1991).
12. The 43 plants per house making up the experimental ecosystems were the tree and shrub species *Cecropia peltata* (Cecropiaceae), *Ficus benjamina* (Moraceae), *Theobroma cacao* (Sterculiaceae), and *Piper tiliaefolium* (Piperaceae); the climbing vines *Monstera dubia* (Araceae), *Piper nigrum* (Piperaceae), and *Tetrastigma voinerianum* (Vitaceae); the ground creepers *Ficus pumila* (Moraceae) and *Philodendron scandens* (Araceae); and the herbaceous monocots *Hedychium coccineum, Elettaria cardamomum* (Zingiberaceae), *Ctenanthe lubbersiana* (Marantaceae), *Heliconia humilis* (Musaceae), *Areca lutescens* (Arecaceae), and *Aechmea mexicana* (Bromeliaceae). Except for *T. cacao*, which was raised from seed, all plants of the same species were propagules of the same clone.
13. T. Kira and K. Yoda, in *Tropical Rain Forest Ecosystems*, H. Lieth and M. J. A. Werger, Eds. (Elsevier, Amsterdam, 1989), pp. 55–71.
14. C. Körner and J. A. Arnone III, data not shown.
15. L. H. Ziska *et al.*, *Oecologia* **86**, 383 (1991).
16. R. M. Gifford, *Aust. J. Plant Physiol.* **4**, 99 (1977).
17. F. A. Bazzaz, J. S. Coleman, S. R. Morse, *Can. J. For. Res.* **20**, 1479 (1989).
18. I. Nijs *et al.*, *Planta* **177**, 312 (1989).
19. The LAI was measured with a Licor LI-2000 Canopy Analyzer (electronic fisheye sensor) (Lincoln, Nebraska) calibrated at the harvest against actual leaf areas measured by a photoplanimeter. LI-2000 readings were corrected for background values, and the data presented here are corrected and calibrated values.
20. T. W. Sasek, E. H. DeLucia, B. R. Strain, *Plant Physiol. Suppl.* **75** (abstr. 26) (1984).
21. S.-C. Wong, *Photosynth. Res.* **23**, 171 (1990).
22. R. D. Wulff and B. R. Strain, *Can. J. Bot.* **60**, 1084 (1982).
23. T. W. Sasek, E. H. DeLucia, B. R. Strain, *Plant Physiol.* **78**, 619 (1985).
24. M. Stitt, *Plant Cell Environ.* **14**, 741 (1991).
25. R. B. Thomas and B. R. Strain, *Plant Physiol.* **96**, 627 (1991).
26. J. Masl, G. D. Farquhar, R. M. Gifford, *Aust. J. Plant Physiol.* **17**, 465 (1990).
27. R. J. Norby, E. G. O'Neill, R. J. Luxmoore, *Plant Physiol.* **82**, 83 (1986).
28. W. J. Arp, *Plant Cell Environ.* **14**, 869 (1991).
29. R. J. Norby and E. G. O'Neill, *New Phytol.* **117**, 515 (1991).
30. H. Poorter, S. Pot, H. Lambers, *Physiol. Plant.* **73**, 553 (1988).
31. J. W. Raich and K. J. Nadelhoffer, *Ecology* **70**, 1346 (1989).
32. R. J. Norby, R. J. Luxmoore, E. G. O'Neill, D. G. Weller, *Environmental Sciences Division Publication 2318* (Oak Ridge National Laboratory, Oak Ridge, TN, 1984).
33. Soil xylanase and protease activities were determined by F. Schinner (personal communication).
34. E. T. Elliott, H. W. Hunt, J. K. Detling, J. C. Moore, D. E. Reuss, *Bull. Ecol. Soc. Am.* **71**, 147 (1990).
35. E. G. Reekie and F. A. Bazzaz, *Oecologia* **79**, 212 (1989).
36. J. P. E. Anderson and K. H. Domsch, *Soil Biol. Biochem.* **10**, 215 (1978).
37. R. J. Luxmoore, R. J. Norby, E. G. O'Neill, in *Forest Plants and Forest Protection*, 18th International Union of Forestry Research Organizations (IUFRO), World Congress, Div. 2, 1987) (IUFRO Secretariate, Vienna,1987), vol. 1, pp. 178–183.
38. P. G. Jarvis, *Tree Physiol.* **2**, 347 (1986).
39. D. T. Tissue and W. C. Oechel, *Ecology* **68**, 401 (1987).

40. We thank our colleagues in the Department of Botany for their assistance during this study, especially W. Hilti for quantifying canopy development, M. Würth for the determination of TNC, W. Flückiger and S. Braun for chemical analysis of soils and water, and E. Schreier for artwork. H. Lambers, R. Norby, B. Schmid, and M. Diemer provided helpful comments on an earlier version of this manuscript.

27 April 1992; accepted 9 July 1992

The Present Is Not the Key to the Past: A Polar Forest from the Permian of Antarctica

Edith L. Taylor,* Thomas N. Taylor, N. Rubén Cúneo

An in situ Upper Permian fossil forest in the central Transantarctic Mountains near the Beardmore Glacier includes 15 permineralized trunks in growth position; the paleolatitude of the site was approximately 80° to 85° south. Numerous leaves of the seed fern *Glossopteris* are present in the shale in which the trunks are rooted. The trunks are permineralized and tree rings reveal that the forest was a rapidly growing and young forest, persisting in an equable, strongly seasonal climate—a scenario that does not fit with some climate reconstructions for this time period.

Fossil forests represent an important data source that can be utilized to reconstruct past climates. High-latitude fossil forests are rare, with instances known from Cretaceous deposits on Alexander Island (Antarctic peninsula) (*1*) and Paleocene-Eocene sediments on Axel Heiberg Island (Canadian Arctic) (*2*). These sites provide an opportunity to examine forest density and productivity at high-latitude sites in the past. The preservation of the wood also allows for an analysis of tree ring data. When combined with data from compression-impression floras, vegetation reconstruction is greatly enhanced. This biological input represents an important parameter that can be used to calibrate climate models based primarily on physical data.

During our 1991 to 1992 field season, we examined an in situ fossil forest on a flat bench at the top of the northward extending ridge of Mount Achernar (Fig. 1). The forest is exposed over an area of about 20 by 12 m (84°22′23″S, 164°37′56″E; Buckley Island Quadrangle) (*3*). Fifteen stumps are preserved in growth position and occur within shaley floodplain deposits (*4*) in the upper part of the Buckley Formation. Based on palynomorphs recovered at nearby sites (*5*), the age of this deposit is considered to be Late Permian.

E. L. Taylor and T. N. Taylor, Byrd Polar Research Center and Department of Plant Biology, Ohio State University, Columbus, OH 43210.
N. R. Cúneo, Museo Paleontológico Egidio Feruglio, 9 de Julio 655 (9100) Trelew, Chubut, Argentina.

*To whom correspondence should be addressed.

The stumps range from 9 to 18 cm in diameter and are generally preserved close to ground level. They are permineralized by silica so that wood cells are preserved. The largest aboveground segment preserved is approximately 20 cm high (Fig. 2), but a portion of the rooting zone of many stumps is also preserved. The trunks are rooted in a shale and siltstone that contains *Glossopteris* leaf impressions and a few specimens of the rooting structure of the glossopterids, *Vertebraria*. The mean distance between the stumps is 1.95 m, which would imply a high mean density if extrapolated for a large forest (~2000 individuals per hectare).

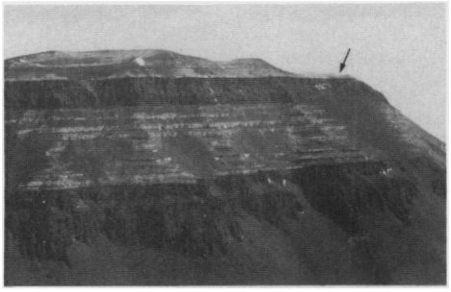


Fig. 1. Eastern face of Mount Achernar, central Transantarctic Mountains. Fossil forest occurs on flat bench at upper right (arrow).

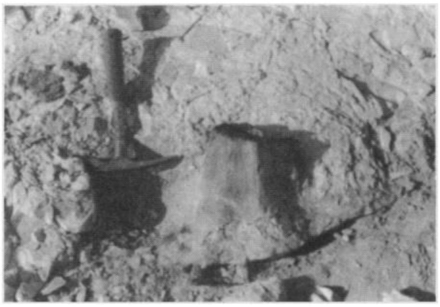


Fig. 2. Stump preserved in situ (slightly flattened to one side). Rock hammer is 28 cm. long.

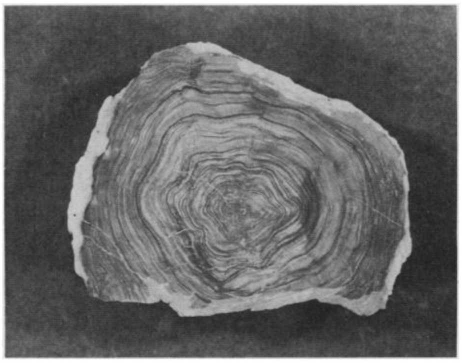


Fig. 3. Cross section of etched block of fossil wood showing distinct rings and extensive crushing. There are only seven true growth rings in this specimen; the remainder are false rings. Width of specimen is 9.5 cm.

For ring analysis the wood was cut and cellulose acetate peels of the surfaces were made after etching in concentrated hydrofluoric acid and neutralizing in sodium bicarbonate. The Mount Achernar wood contains distinct growth rings that indicate a marked seasonality in the climate (Fig. 3). Mean ring width is 4.5 mm, and the largest ring observed was 11.38 mm wide. The rings consist primarily of earlywood with a small proportion of latewood (Fig. 4). No frost rings were evident, even in those areas where they would be expected most commonly (that is, at the beginning and end of annual rings). However, a large number of false rings are present. These consist of areas in which the tracheid walls are thicker and thus appear denser than in the normal wood (Fig. 4). They occur at various levels throughout the year's growth, that is, they do not appear to be confined to one particular part of the ring.

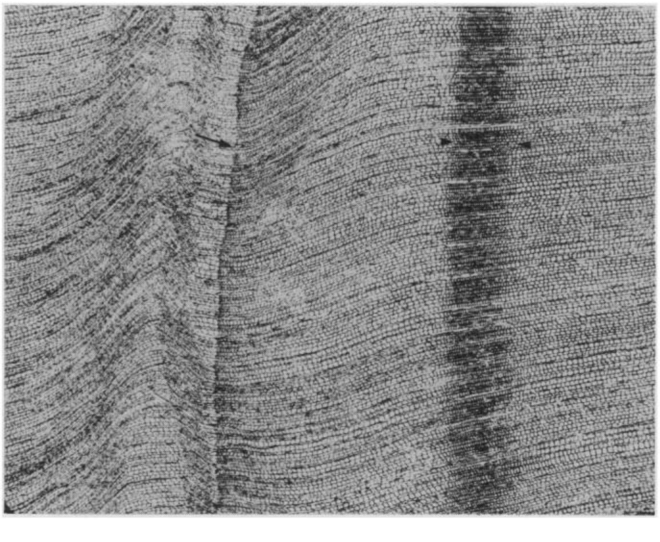
The largest number of rings preserved in a single specimen is 15. The small number of rings, combined with the high density of individuals and the large size of some of the rings, suggests that the Mount Achernar deposit represents a young, rapidly growing forest. The plants may have been growing so rapidly in some seasons (11.38 mm of tracheid production in a single season) that the tracheid walls may have been insufficiently lignified. Such rapid growth could account for the preservation of many of the tracheid files, some of which are collapsed into a zigzag pattern (Fig. 4). Because there are few rings and extensive evidence of crushing, it is not possible to cross date the specimens.

The structure of the individual rings, with a large amount of earlywood and little (one to three cells) latewood, is comparable to that seen in other high-latitude forests. Doubtless the Permian forest was adapted to a similar light regime (24 hours of light in the growing season; 24 hours of dark during the winter), and we assume that the growth rings represent annual rings. Unlike the northern boreal forest today, however, this Permian forest was probably deciduous. *Glossopteris* leaves have been found in large mats in many localities throughout Antarctica and the rest of Gondwana, including varved sedimentary rocks (*6*), relations that clearly indicate the deciduous nature of these plants. As pointed out by several authors (*7*), warm polar climates favor the development of deciduous forests because the winter (dark) respiration rate would be high in evergreen plants and would cause depletion of stored food reserves. In addition, desiccation during winter can also be severe in plants that retain their leaves. The presence of deciduous forests at high latitudes suggests that the climate at this time was warm. Other evidence for the warmth of the Late Permian climate is the absence of frost rings and the large size of some of the growth rings.

The reason for the large number of false rings in these specimens is uncertain. Some extant plants growing in arid habitats develop false rings, and these cases reflect the alternation of wet and dry seasons. Because the Mount Achernar *Glossopteris* forest was growing in a floodplain environment, it likely was subjected to fluctuating water levels. The geologic evidence suggests that the environment changed over time from lacustrine to a floodplain and eventually to a marshy environment (*3*).

During the Permian the Mount Achernar forest was at approximately 80° to 85°S latitude. By comparison, an in situ fossil forest described from the Late Cretaceous of Alexander Island in the Antarctic peninsula area (*1*) was considered to be 65° to 75°S latitude. These trees produced growth rings up to 9.5 mm in width. The Paleocene-Eocene fossil forests from the Canadian

Fig. 4. Cross section of peel preparation showing growth ring boundary (arrow) and false ring (between arrowheads). Magnification, ×27.



Arctic (*2*) also exhibited high growth rates and have been placed at approximately 75° to 80°N paleolatitude (*8*). These deposits had ring widths averaging 3.0 to 5.0 mm with a maximum of 10 mm (based on field measurements). In the Arctic today, trees are capable of producing a growth ring in as little as one month. Cambial activity in many of these trees ceases even though light levels still appear to be adequate for photosynthetic activity. This growth pattern suggests that modern high-latitude trees are limited by temperature; the narrow size of their rings (1.0 mm or less) supports this interpretation. Temperature does not appear to have been a limiting factor to forest growth during the Late Permian in Antarctica. The deciduous nature of the *Glossopteris* forest, combined with the relatively large size of the growth rings, suggests that the climate was more favorable to tree growth than that which occurs today at latitudes 10° to 15° lower. On the basis of the rate of tree growth, the Permian polar climate is more comparable to Paleocene-Eocene climates in the Arctic.

As is true of temperate trees today, there was a clear cessation of cambial activity each year in these Permian trees. The small proportion of latewood suggests that cambial activity suddenly ceased at the end of the growing season, which otherwise appeared to be quite favorable for growth. In the absence of frost rings, we suggest that latewood production and the subsequent cessation of cell divisions in the vascular cambium were a response to decreasing light levels in the autumn. Basinger (*2*) has proposed that minimal latewood development in the Paleocene Arctic woods indicates a lack of winter hardening in these plants. He suggested that these trees experienced only short periods of freezing weather, if any.

Some models, based primarily on physical parameters, have suggested that winter temperatures averaged −30° to −40°C and summer temperatures 0°C for this region [for example (*8*)]. However, the biological evidence suggests that this was not the case. Clearly, Permian forests were present at latitudes where no vascular plants can survive today. Growth in these forests could be extremely fast, as evidenced by growth ring data. A lack of latewood development in the tree rings and the absence of frost rings suggests that temperatures rarely went below freezing.

Biological input to physical climate models is of primary importance in limiting the range of past climatic interpretations and can provide increased resolution when integrated with such models. More importantly, these data provide important information that can be applied to expand our knowledge of possible changes in plant growth and distribution as a result of current climate changes.

REFERENCES AND NOTES

1. T. H. Jefferson, *Palaeontology* **25**, 681 (1982).
2. J. E. Francis, *Arctic* **41**, 314 (1988); J. E. Francis, *Geol. Surv. Can. Bull.* **403**, 29 (1991); J. F. Basinger, *ibid.*, p. 39.
3. J. L. Isbell, thesis, Ohio State University (1990). The site was first noted by Isbell during the 1985 and 1986 field season. The sedimentology of Mount Achernar and other Buckley Formation sites in the central Transantarctic Mountains are discussed in this thesis.
4. N. R. Cúneo, J. L. Isbell, E. L. Taylor, T. N. Taylor, *C. R. XII Int. Congr. Carb. and Permian Geo. Strat.*, Buenos Aires, Argentina, 22 to 27 September 1991, S. Archangelsky, Ed., Buenos Aires (in press).
5. M. J. Farabee, E. L. Taylor, T. N. Taylor, *Rev. Palaeobot. Palynol.* **69**, 353 (1991).
6. G. J. Retallack, *Bull. Geol. Surv. New South Wales* **26**, 384 (1980); B. M. Gunn and R. I. Walcott, *N. Z. J. Geol. Geophys.* **5**, 407 (1962).
7. R. A. Spicer and J. L. Chapman, *Trends Ecol. Evol.* **5**, 279 (1990); J. A. Wolfe, *Paleobiology* **13**, 215 (1987); D. I. Axelrod, *Evolution* **20**, 1 (1966).
8. E. Irving and P. J. Wynne, *Geol. Surv. Can. Bull.* **403**, 209 (1991).
9. T. J. Crowley, W. T. Hyde, D. A. Short, *Geology* **17**, 457 (1989); J. E. Kutzbach and R. G. Gallimore, *J. Geophys. Res.* **94**, 3341 (1989).
10. This work was supported in part by the National Science Foundation (DPP-8815976 to T.N.T. and E.L.T. and DPP-9109448 to E.L.T.) and by an Ohio State University Byrd Fellowship to N.R.C. We thank J. L. Isbell and J. W. Collinson for helpful comments on the manuscript and J. L. Isbell for field assistance. E.L.T. also thanks the members of the Laboratory of Tree-Ring Research, University of Arizona, Tucson, for assistance with tree-ring analysis techniques and helpful discussions. Contribution no. 810 of the Byrd Polar Research Center.

14 May 1992; accepted 22 July 1992

Structural Models for the Metal Centers in the Nitrogenase Molybdenum-Iron Protein

Jongsun Kim and D. C. Rees*

Structural models for the nitrogenase FeMo-cofactor and P-clusters are proposed based on crystallographic analysis of the nitrogenase molybdenum-iron (MoFe)-protein from *Azotobacter vinelandii* at 2.7 angstrom resolution. Each center consists of two bridged clusters; the FeMo-cofactor has 4Fe:3S and 1Mo:3Fe:3S clusters bridged by three nonprotein ligands, and the P-clusters contain two 4Fe:4S clusters bridged by two cysteine thiol ligands. Six of the seven Fe sites in the FeMo-cofactor appear to have trigonal coordination geometry, including one ligand provided by a bridging group. The remaining Fe site has tetrahedral geometry and is liganded to the side chain of Cys$^{\alpha 275}$. The Mo site exhibits approximate octahedral coordination geometry and is liganded by three sulfurs in the cofactor, two oxygens from homocitrate, and the imidazole side chain of His$^{\alpha 442}$. The P-clusters are liganded by six cysteine thiol groups, two which bridge the two clusters, α88 and β95, and four which singly coordinate the remaining Fe sites, α62, α154, β70, and β153. The side chain of Ser$^{\beta 188}$ may also coordinate one iron. The polypeptide folds of the homologous α and β subunits surrounding the P-clusters are approximately related by a twofold rotation that may be utilized in the binding interactions between the MoFe-protein and the nitrogenase Fe-protein. Neither the FeMo-cofactor nor the P-clusters are exposed to the surface, suggesting that substrate entry, electron transfer, and product release must involve a carefully regulated sequence of interactions between the MoFe-protein and Fe-protein of nitrogenase.

Reduction of dinitrogen to ammonia by the nitrogenase enzyme system requires two metalloproteins, the molybdenum-iron (MoFe)–protein and the iron (Fe)–protein [reviewed in (*1*)]. The MoFe-protein is an $\alpha_2\beta_2$ tetramer with total molecular mass of $\sim$240 kD, and the Fe-protein is a $\gamma 2$ dimer. Three distinct types of redox centers are associated with these proteins: The MoFe-protein contains two types of centers, the FeMo-cofactor [reviewed in (*2*)] and the P-clusters [reviewed in (*3*)], and the Fe-protein dimer contains one 4Fe:4S cluster whose structure is described in an accompanying article (*4*). Because the active site of nitrogenase is provided by the MoFe-protein, the redox centers of this protein have attracted considerable attention. The FeMo-cofactor, first identified by Shah and Brill (*5*), most likely represents the site of substrate reduction (*6*) and has the approximate composition of one Mo atom, six to eight Fe atoms, eight to nine S atoms, and one homocitrate group (1Mo:6-8Fe:8-9S:1 homocitrate) (*2, 7, 8*). The P-clusters are believed to contain two 4Fe:4S clusters in close proximity (*9–13*), although the detailed properties of this center are distinct from better characterized proteins that con-

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Division of Chemistry and Chemical Engineering 147-75CH, California Institute of Technology, Pasadena, CA 91125.

*To whom correspondence should be addressed.