

sections must extend deeper than this (R. S. Yeats, personal communication). Unusually low heat flow observed within the basin<sup>15</sup> and anomalously deep earthquakes beneath the basin<sup>16</sup> suggest substantial cooling due to downward advection of cool material, which is more compatible with the second model. We believe the deep earthquakes are due to loading of the basin and are unrelated to the faults slipping at the margins of the basin. More detailed future GPS measurements will place additional constraints on the extent and orientation of the sub-surface structures.

Slip on the modelled faults would cause strain to accumulate on the shallow locked sections—a process expected to result in earthquakes<sup>17</sup>. At present we do not know what fraction of the deformation associated with loading on these ramping structures is taken up seismically, as some of the deformation is clearly associated with active folding. A rupture dimension of  $5 \times 20$  km, characteristic of the near-surface faults currently being loaded by the slipping sections, and an average stress drop of 60 bar (2 m of slip), would yield an earthquake of up to moment magnitude  $M_w \approx 6.4$  (ref. 18). A moment magnitude  $M_w \approx 7.5-8$  would result if the deep faults were locked rather than slipping. Using geology alone, it is difficult to determine which of these alternatives is more likely. Our space geodetic observations, combined with models of elastic strain accumulation, suggest that the deep faults are slipping, with only the near-surface accumulating strain, so a  $M_w \approx 7.5-8$  event is unlikely. But the Santa Clara River Valley (within the Ventura basin) is densely popu-

lated, and a  $M_w \approx 6$  earthquake is still large and potentially damaging. □

Received 22 April; accepted 4 October 1993.

1. Donnellan, A., Hager, B. H., King, R. W. & Herring, T. A. *J. geophys. Res.* **98** (in the press).
2. Yeats, R. S. *J. geophys. Res.* **88**, 569–583 (1983).
3. Huftile, G. J. & Yeats, R. S. *J. geophys. Res.* (submitted).
4. Feigl, K. et al. *J. geophys. Res.* **98** (in the press).
5. Eberhart-Phillips, D., Lisowski, M. & Zoback, M. D. *J. geophys. Res.* **95**, 1139–1153 (1990).
6. Namson, J. & Davis, T. *Geology* **16**, 675–679 (1988).
7. Levi, S. & Yeats, R. S. *Tectonics* **12**, 688–702 (1993).
8. Jackson, J. & Molnar, P. *J. geophys. Res.* **95**, 22073–22087 (1990).
9. Molnar, P. Technical report (Southern California Earthquake Center, Univ. Southern California, Los Angeles, 1993).
10. Yeats, R. S. & Huftile, G. J. *EOS* **73**, 590 (1992).
11. Suppe, J. & Medwedeff, D. A. *Ecol. geol. Helv.* **83**, 409–454 (1990).
12. Webb, T. H. & Kanamori, H. *Bull. seism. Soc. Am.* **75**, 737–757 (1985).
13. Larsen, S. C., Agnew, D. C. & Hager, B. H. *J. geophys. Res.* **98**, 2119–2133 (1993).
14. Larson, K. M. & Webb, F. H. *Geophys. Res. Lett.* **19**, 1491–1494 (1992).
15. DeRito, R. F., Lachenbruch, A. H., Moses, T. H. & Munroe, R. J. *J. geophys. Res.* **94**, 681–699 (1989).
16. Bryant, A. S. & Jones, L. M. *J. geophys. Res.* **97**, 437–447 (1992).
17. Davis, T. L., Namson, J. & Yerkes, R. F. *J. geophys. Res.* **94**, 9644–9664 (1989).
18. Kanamori, H. & Anderson, D. L. *Bull. seism. Soc. Am.* **65**, 1073–1096 (1975).
19. Stein, R. S. & Yeats, R. S. *Sci. Am.* **260**(6), 48–57 (1989).

ACKNOWLEDGEMENTS. We thank everyone who assisted us with the GPS field observations; the Ohio State University, Scripps Institution of Oceanography and the University NAVSTAR Consortium (UNAVCO) who lent us receivers; the land owners, agencies and oil companies who allowed us access to private or restricted land; K. Feigl, D. Dong and T. Herring who contributed to the processing of the GPS data; and R. Yeats, J. Suppe and J. Shaw for comments on the manuscript. The research described in this paper was carried out under a National Research Council postdoctoral fellowship (to A.D.), at the NASA Goddard Space Flight Center, the Seismological Laboratory and Jet Propulsion Laboratory, California Institute of Technology, and the Massachusetts Institute of Technology under contracts with NASA, the US Geological Survey, and the US National Science Foundation.

## Forest disequilibrium caused by rapid Little Ice Age cooling

Ian D. Campbell\* & John H. McAndrews

Department of Botany, University of Toronto, and Department of Botany, Royal Ontario Museum, Toronto, Ontario, Canada M5S 2C6

GLOBAL climatic change may alter species' ranges as well as restructuring ecosystems<sup>1–3</sup>. Models simulating forest growth predict that the area covered by different forest types may be affected<sup>2</sup>, which may in turn further affect climate<sup>3</sup>. In the mixed forests of southern Ontario, pollen analyses have demonstrated that after AD 1400, *Fagus* (beech), the formerly dominant warmth-loving species, was replaced first by oak (*Quercus*) and subsequently by pine (*Pinus strobus*). Although these changes had been attributed to aboriginal forest clearance<sup>4–6</sup>, they have also been seen in areas unaffected by aboriginal farming, and are now thought to reflect Little Ice Age cooling<sup>7</sup>. Although modelling suggests that some forests may take several centuries to reach equilibrium after a climatic change<sup>8,9</sup>, a real forest showing this behaviour has not previously been identified. Here we model the Little Ice Age by a 2 °C decrease in mean annual temperature from AD 1200 to 1850, and show that the changes predicted by a forest simulator derived from FORET<sup>10</sup> match those seen in southern Ontario. These forests thus appear to have remained in disequilibrium with the prevailing climate for more than 650 years.

The FORET-derived model uses an annual time step in which individuals (of 52 species in this case) are allowed to grow, compete and die. Growth is constrained by species-specific responses to aspects of the environment (such as growing degree-days or the absence of exposed mineral soil for seedbed), limits of the species itself (such as maximum growth rate or maximum height), and by competition with each other (modelled primarily as mutual shading). FORET and similar models have been used with great success in a wide variety of applications, including

simulating the effects of a pathogen, post-glacial forest development and the dynamics of several forest types around the world<sup>10</sup>. This simulated succession is converted to a pollen diagram through regression equations relating the relative abundance of each tree species to the relative abundance of its pollen<sup>11–13</sup> (Fig. 3). The converted simulation results mimic actual pollen records from the region<sup>14</sup>. Hence we can use this

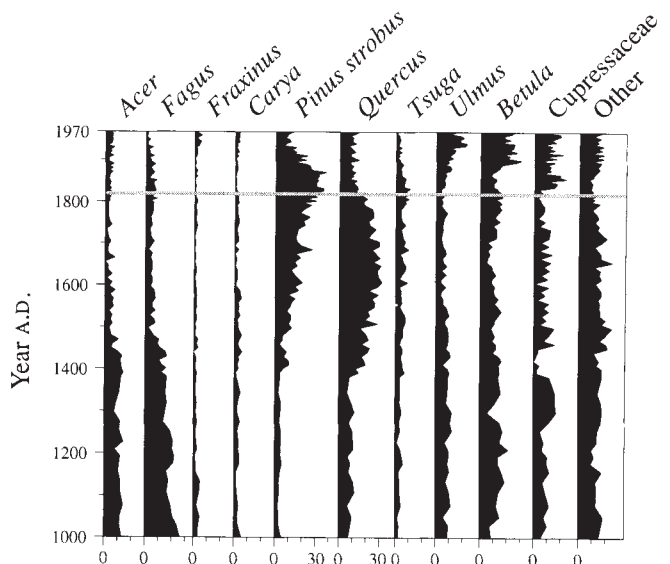
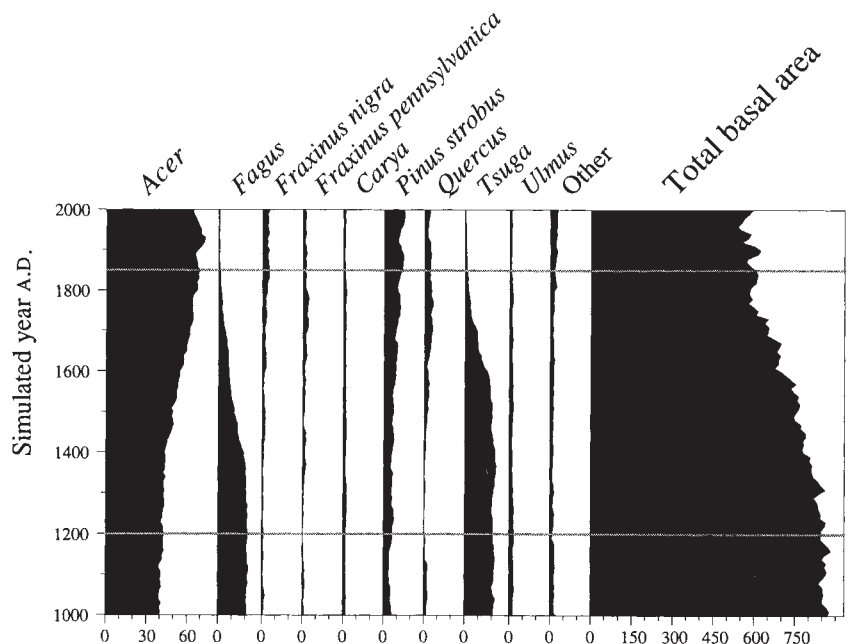


FIG. 1 Relative abundance pollen diagram of selected taxa from Crawford Lake, the most detailed pollen diagram of the last millennium available for southern Ontario. A rapid decline in *Fagus* begins ~AD 1450, leading to a succession of first *Quercus* then *Pinus strobus*. The horizontal line after AD 1800 indicates the first signs of European disturbance. The horizontal axis is per cent of total pollen (10 per cent per unit).

\* Present address: Forestry Canada, 5320–122 Street, Edmonton, Alberta, Canada T6H 3S5.

FIG. 2 Simulated forest succession shows a decrease in *Fagus grandifolia* starting immediately with the onset of cooling; it is followed by increases in *Quercus rubra*, *Pinus strobus*, *Fraxinus nigra* and *Acer saccharum*; *Tsuga canadensis* declines later than *Fagus*. The total basal area also declines, indicating a more open forest containing less biomass. The simulation climate was monotonically cooled by 2 °C from AD 1200 to 1850, as suggested by proxy data for the Little Ice Age from nearby Michigan<sup>23</sup>. The horizontal axis is per cent basal area (10 per cent per unit) except for the total basal area, which is m<sup>2</sup>ha<sup>-1</sup>.



simulation to examine the dynamics of this period of southern Ontario's forest history.

The most important feature of the simulation results is the decline in total basal area (Fig. 2), initiated immediately after the start of cooling (~AD 1200). By AD 1850, basal area reaches a value of less than 70% of the pre-cooling mean, implying at least a one-third reduction in total biomass per hectare. It is significant that this decrease starts at the same time as the first decline in *Fagus* abundance, suggesting that the premature death of dominant *Fagus* trees, rather than a failure of *Fagus* regeneration (as saplings of other species would take the place of the *Fagus* saplings), is initially implicated in this basal area decrease.

Furthermore, although *Quercus* and *Pinus strobus* do increase dramatically in both the real and simulated pollen records, this is due largely to their strong pollen production and dispersal; their simulated basal areas increase only slightly. Rather, the co-dominant *Acer saccharum*, which produces only a moderate quantity of pollen, is the species which eventually most benefits from the decline in *Fagus* in the simulation.

During the Little Ice Age, increased canopy opening after the death of *Fagus* would have allowed *Quercus*, *Fraxinus* and *Pinus strobus* to expand, and eventually reduced competition for *Acer saccharum*. *Tsuga canadensis*, however, reproduces poorly under an open canopy<sup>15</sup>, and its eventual decline may result from canopy opening as much as from climate cooling. Thus the sequence of events observed in the pollen records of this region was essentially a combination of seral and climatic successions initiated by a rapid climate cooling.

In this simulation, climate cooling was stopped at AD 1850. The forest succession continues, however, to the end of the simulation run at AD 2000, and presumably would continue beyond, so that even 150 years after the end of the climate cooling the forest would not yet have reached equilibrium with the prevailing climate.

In the actual pollen record the succession is truncated by logging and land clearance in the mid-1800s. Although the Little Ice Age was coming to an end at this time, it seems likely that the forest had not yet reached equilibrium with the climate, as the model suggests seral succession would have continued in the absence of further cooling. Although many ecologists, palaeo-ecologists, and park managers use the pre-clearance vegetation as their baseline 'equilibrium' forest, our results show that as early as AD 1450, the forest composition and structure were in disequilibrium with the prevailing climate. Although many

authors have considered the possibility of a lag between change and forest response, due to the time needed for soil development<sup>16</sup>, species migration<sup>17</sup>, or simply for mature stems to die and be replaced by different species<sup>18</sup>, few have considered the possibility of a rapid climate change triggering a seral type of succession.

Although a similar forest simulator was used to demonstrate the possibility of a disequilibrium forest resulting from Little Ice Age cooling<sup>8</sup>, such a forest has not previously been identified, and remained until now a theoretical construct.

Although the wild forest of southern Ontario, now largely cleared, is no longer a major carbon reserve, disequilibrium dynamics have been simulated for global warming scenarios in other forest types<sup>19</sup>. The implications for future climate change are significant. First, a transient decrease in forest biomass may result from rapid climate change. Tree death on a massive scale

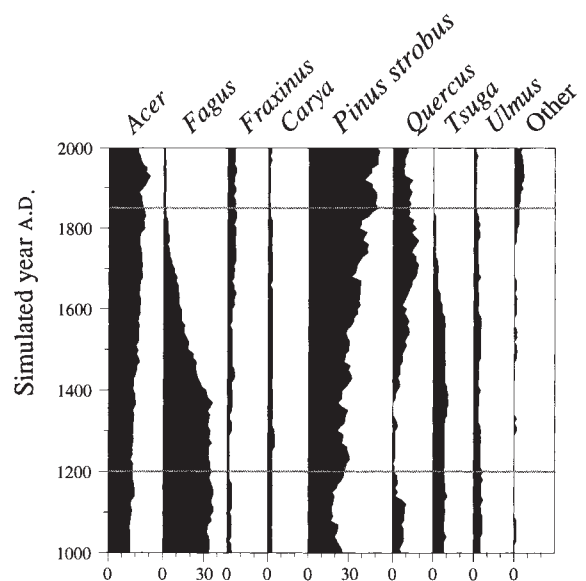


FIG. 3 Simulated pollen record created by applying pollen/biomass regression equations to the simulated forest succession. The simulated pollen record strongly resembles actual pollen records from the region<sup>14</sup>. The horizontal axis is per cent pollen (10 per cent per unit).

would produce a large fuel supply for wildfire, and would in any event result in a flux of stored carbon into the atmosphere. The opening of the forest canopy would also increase the albedo of the landscape, leading to cooling of the land surface<sup>3</sup>. Either effect has serious implications for future climate change. Furthermore, although there is still some dispute over the potential migration rates of tree species in response to climate change, forest equilibrium is not only a matter of species presence, but also of forest structure<sup>20,21</sup>. Even with all relevant species and suitable soils present, it may nevertheless take several centuries for a forest to equilibrate with climate because of the lags inherent in seral succession; this has been simulated for northern Michigan mixed forest under future climate change scenarios<sup>9</sup>.

In other regions, a succession such as this might not be observed in the pollen record. In southern Ontario, its prominence is due to several factors, including the high pollen representation of some of the species involved in the succession, the ecotonal nature of the region, the long lifespans of many of the tree species, and the infrequent prehistoric fire regime<sup>22</sup> which allowed a long seral succession to develop. Although a similar disequilibrium probably occurred in other regions, the absence of any one of these factors would render it nearly unobservable in the pollen record. □

Received 5 April; accepted 8 September 1993.

1. Melillo, J. M., Callaghan, T. V., Woodward, F. I., Salati, E. & Sinha, S. K. in *Climate Change*:

- The IPCC Scientific Assessment* (eds Houghton, J. T., Jenkins, G. J. & Ephraums, J. J.) 283–310 (Cambridge University Press, New York, 1990).
- Pastor, J. & Post, W. M. *Nature* **334**, 55–58 (1988).
  - Bonan, G. B., Pollard, D. & Thompson, S. L. *Nature* **359**, 716–718 (1992).
  - McAndrews, J. H. in *Vegetation History* (eds Huntley, B. & Webb, T. III) 673–697 (Kluwer, New York, 1988).
  - McAndrews, J. H. & Boyko-Diakonow, M. in *Quaternary Geology of Canada and Greenland* (ed. Fulton, R. J.) 528–530 (Geological Survey of Canada, Ottawa, 1989).
  - Burden, E. T., McAndrews, J. H. & Norris, G. *Can. J. Earth Sci.* **23**, 43–54 (1986).
  - Campbell, I. D. & McAndrews, J. H. *Can. J. Bot.* **69**, 1719–1730 (1991).
  - Davis, M. B. & Botkin, D. B. *Quat. Res.* **23**, 327–340 (1985).
  - Solomon, A. M. & Bartlein, P. J. *Can. J. For. Res.* **22**, 1727–1738 (1992).
  - Shugart, H. H. *A Theory of Forest Dynamics* (Springer, New York, 1984).
  - Davis, M. B. *Am. J. Sci.* **261**, 897–912 (1963).
  - Delcourt, P. A., Delcourt, H. R. & Webb, T. III *Atlas of Mapped Distributions of Dominance and Modern Pollen Percentages for Important Tree Taxa of Eastern North America* (Am. Ass. Stratigraphic Palynologists, Dallas, 1984).
  - Bradshaw, R. H. W. & Webb, T. III *Ecology* **66**, 721–737 (1985).
  - Campbell, I. D. thesis, Univ. Toronto, 1992.
  - Godman, R. M. & Lancaster, K. in *Silvics of North America vol. 1: Conifers* (eds Burns, R. M. & Honkaia, B. H.) 604–612 (United States Department of Agriculture Forest Service Handbook 654, Washington DC, 1990).
  - Pennington, W. *Vegetatio* **67**, 105–118 (1986).
  - Davis, M. B. *Ecology* **50**, 312–332 (1969).
  - Bryson, R. A. *Quat. Res.* **15**, 143–159 (1981).
  - Solomon, A. M. *Oecologia* **68**, 567–579 (1986).
  - Davis, M. B. in *Community Ecology* (eds Diamond, J. & Case, T. J.) 269–284 (Harper and Row, New York, 1986).
  - Delcourt, H. R., Delcourt, P. A. & Webb, T. III *Quat. Sci. Rev.* **1**, 153–175 (1983).
  - Johnson, E. A. *Fire and Vegetation Dynamics: Studies from the North American Boreal Forest* (Cambridge Univ. Press, New York, 1992).
  - Bernabo, J. C. *Quat. Res.* **15**, 143–159 (1981).

ACKNOWLEDGEMENTS. We thank M. Apps, E. Hogg and S. Zoltai for comments on the manuscript.

## Nitrate respiration in the hydrothermal vent tubeworm *Riftia pachyptila*

U. Hentschel & H. Felbeck

Marine Biology Research Division 0202, Scripps Institution of Oceanography, University of California San Diego, La Jolla, California 92093-0202, USA

THE vestimentiferan tubeworm *Riftia pachyptila* is found around hydrothermal vent areas in the deep sea. Intracellular bacterial chemoautotrophic symbionts use the oxidation of sulphide from the effluent of the vents as an energy source for CO<sub>2</sub> fixation. They apparently provide most or all of the nutritional requirements for their gutless hosts<sup>1–5</sup>. This kind of symbiosis has since been found in many other species from various other phyla from other habitats<sup>6–9</sup>. Here we present results that the bacteria of *R. pachyptila* may cover a significant fraction of their respiratory needs by the use of nitrate in addition to oxygen. Nitrate is reduced to nitrite, which may be the end product (nitrate respiration)<sup>10</sup> or it may be further reduced to nitrogen gas (denitrification)<sup>11</sup>. This metabolic trait may have an important role in the colonization of hypoxic habitats in general by animals with this kind of symbiosis.

Because the symbionts cannot be cultured<sup>12</sup> we used physically purified bacteria<sup>13</sup> for our experiments which were incubated under anaerobic conditions in the presence of nitrate. Nitrite appeared in the medium at a linear rate (0.91 ± 0.07 nmol per mg protein per min, *n* = 3) for at least 90 min (Fig. 1) and was independent of the nitrate concentration between 50 μM and 1 mM. Nitrite was not formed without nitrate (*n* = 3), with plume tissue containing no symbionts (*n* = 1), when the bacteria were boiled (*n* = 3), or when cyanide was added (*n* = 2). When the concentration of nitrate dropped below 20 μM (Fig. 1), nitrite was reduced as well, indicating that nitrite can be respired further. There was no indication that the symbionts can respire nitrate to ammonium. Nitrate respiration was stimulated by sulphide with maximal rates at 500 μM sulphide (Fig. 2), but not by thiosulphate. This supports previous results<sup>14,15</sup> that the sym-

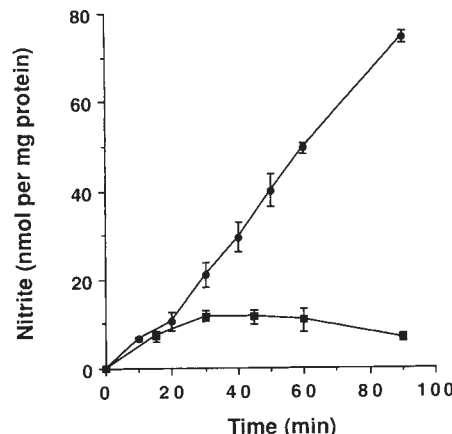


FIG. 1 Production of nitrite by purified symbionts from *R. pachyptila*. Live tubeworms were collected in temperature-insulated containers from the Genesis vent site at 2,638 m depth at 12° 48.675' N, 103° 56.386' W on the East Pacific Rise. Symbionts were purified under anaerobic conditions<sup>13</sup> from crude homogenates of trophosome<sup>17</sup>, the tissue containing the bacteria. Isolated symbionts were incubated anaerobically in 10 ml *Riftia* saline<sup>24</sup> containing 500 μM sulphide and 1 mM (●) or 50 μM nitrate (■). The concentration was adjusted to about 2 mg symbiont protein ml<sup>-1</sup>. The incubations were done at 15 °C and stirred continuously. To maintain anaerobic conditions, each incubation chamber was closed with a rubber septum and a nitrogen gas stream was introduced through a needle 15 min before and during the experiment. At 10 min intervals, 1.5 ml aliquots were drawn through a syringe and centrifuged for 5 min in a Fisher table-top centrifuge. The concentration of nitrite in the supernatant of the samples (nmol per mg symbiont protein) was determined after removal of sulphide<sup>25</sup>. Data points represent means ± s.e., *n* = 3.

bionts are sulphide specialists.

Because denitrification is usually a trait found in bacteria from anaerobic environments, the influence of oxygen on the reduction of nitrate by the symbionts had to be assessed. The only measurements of oxygen consumption by purified *R. pachyptila*