

- prospectively study, *Hum. Reprod.* (in press)
- 34 Eklund, A. (1997) **The effect of early experience on MHC-based mate preferences in two B10.W strains of mice (*Mus domesticus*)**, *Behav. Genet.* 27, 223–229
- 35 Paterson, S. and Pemberton, J.M. (1998) **No evidence for major histocompatibility complex-dependent mating patterns in a free-living ruminant population**, *Proc. R. Soc. London Ser. B* 264, 1813–1819
- 36 Ober, C. *et al.* (1997) **HLA and mate choice in humans**, *Am. J. Hum. Genet.* 61, 497–504
- 37 Hedrick, P.W. and Black, F.L. (1997) **HLA and mate selection: no evidence in South Amerindians**, *Am. J. Hum. Genet.* 61, 505–511
- 38 Wedekind, C. *et al.* (1995) **MHC-dependent mate preferences in humans**, *Proc. R. Soc. London Ser. B* 260, 245–249
- 39 Hedrick, P.W. and Loeschcke, V. (1996) **MHC and mate selection in humans?** *Trends Ecol. Evol.* 11, 24
- 40 Wedekind, C. and Furi, S. (1997) **Body odour preferences in men and women: do they aim for specific MHC combinations or simply heterozygosity?** *Proc. R. Soc. London Ser. B* 264, 1471–1479
- 41 Singer, A.G., Beauchamp, G.K. and Yamazaki, K. (1997) **Volatile signals of the major histocompatibility complex in male mouse urine**, *Proc. Natl. Acad. Sci. U. S. A.* 94, 2210–2214
- 42 Kaufman, J. and Wallny, H.J. (1996) **Chicken MHC molecules, disease resistance and the evolutionary origin of birds**, *Curr. Top. Microbiol. Immunol.* 212, 129–141
- 43 von Schantz, T. *et al.* (1996) **MHC genotype and male ornamentation: genetic evidence for the Hamilton–Zuk model**, *Proc. R. Soc. London Ser. B* 263, 265–271
- 44 Hedrick, P.W. and Kim, T.J. **Genetics of complex polymorphisms: parasites and maintenance of MHC variation**, in *Genetics, Evolution and Society* (Singh, R.S. and Krimbas, C.K., eds), Harvard University Press (in press)
- 45 Boyce, W.M. *et al.* (1997) **Genetic variation of major histocompatibility complex and microsatellite loci: a comparison in bighorn sheep**, *Genetics* 145, 421–433
- 46 Satta, Y. *et al.* (1994) **Intensity of natural selection at the major histocompatibility complex loci**, *Proc. Natl. Acad. Sci. U. S. A.* 91, 7184–7188
- 47 Black, F.L. and Hedrick, P.W. (1997) **Strong balancing selection at HLA loci: evidence from segregation in South American families**, *Proc. Natl. Acad. Sci. U. S. A.* 94, 12452–12456
- 48 Jin, K., Speed, T.P. and Thomson, G. (1995) **Tests of random mating for a highly polymorphic locus: application to HLA data**, *Biometrics* 51, 1064–1076
- 49 Potts, W.P. and Slev, P.R. (1995) **Pathogen-based models favoring MHC genetic diversity**, *Immunol. Rev.* 143, 181–197
- 50 Trowsdale, J. (1995) **‘Both bird and man and beast’: comparative organization of MHC genes**, *Immunogenetics* 41, 1–17
- 51 Richman, A.D. and Kohn, J.R. (1996) **Learning from rejection: the evolutionary biology of single-locus incompatibility**, *Trends Ecol. Evol.* 11, 497–502
- 52 Satta, Y. *et al.* (1993) **The synonymous substitution rate at major histocompatibility complex loci in primates**, *Proc. Natl. Acad. Sci. U. S. A.* 90, 7480–7484
- 53 Edwards, S.V. *et al.* (1997) **Ancestral polymorphism of MHC class II genes in mice: implications for balancing selection and the mammalian molecular clock**, *Genetics* 146, 655–668

The future as the key to the past for palaeobotany?

D.J. Beerling

Two factors have provided a strong impetus for international experimental and modelling programmes on plant responses to global environmental change¹ (GEC): the threat of future increases in the concentration of atmospheric CO₂ and associated climatic change; and the central role of terrestrial plants and vegetation in the global carbon cycle. Revised predictions by the Intergovernmental Panel on Climate Change² indicate an atmospheric CO₂ concentration by the year AD 2100 of between 450 ppm and >800 ppm. These upper and lower limits are based on assumptions of economic growth, population growth and fossil fuel supply that are either low or moderate, respectively. The upper limit is not new to terrestrial vegetation and ecosystems, which have evolved and survived under such CO₂ concentrations (or higher) for at least the past 250 million years, with the exception of the short-lived fluctuations in the Quaternary period^{3,4}. Consequently, results from CO₂-enrichment experiments

Continued increase in the concentration of atmospheric CO₂ and its possible effects on global climate has generated intense research interest on the likely responses of terrestrial plants and vegetation. Results from this new research provide quantitative information on plant function and growth in an environment with a high CO₂ concentration, but are also relevant to understanding plant growth in the distant past and to the techniques employed by palaeobotanists for reconstructing past climates from fossil plant remains. Experimental CO₂ enrichment of plants has demonstrated direct effects on leaf physiognomy, the tolerance of plants to low temperature and the relationship between tree rings, CO₂ and climate; it therefore signals the need for caution in interpreting palaeoclimates from fossils.

D.J. Beerling is at the
Dept of Animal and Plant Sciences,
University of Sheffield, Sheffield, UK S10 2TN
(d.j.beerling@sheffield.ac.uk).

should be of interest to palaeobotanists: they provide information relevant to understanding plant function during episodes of high CO₂ concentration in the geological past (e.g. the ‘greenhouse world’ of the mid-Cretaceous and mid-Eocene); and they are beginning to provide new insights into the effects of CO₂ on the relationship between plants and climate.

Past climates from plant fossils

Three aspects of the relationship between plants and their environment are used by palaeobotanists to give a signal of terrestrial climate from the fossils: leaf physiognomic characters⁵; the present climatic association of the ‘nearest living relatives’ (NLR) to the fossil^{6,7} (a concept including the use of climatic response surfaces developed from Quaternary palynological studies⁸); and the character of tree rings in fossilized woods⁹. Each aspect has largely been developed with the specific aim of extracting information about the climate from the fossils. A neglected element, but one that is difficult to include in these studies, is an adequate consideration

of the possible direct effects of high CO₂ concentration¹⁰. Results from GEC research provide new considerations for each of these techniques.

CO₂ effects on leaf physiognomy

The main approach for estimating a suite of terrestrial climatic parameters from a wide range of angiosperm fossil-leaf floras has been to seek correlations between modern leaf physiognomy and climate⁵. About 30 leaf characters, scored from modern samples collected in North and Central America, have been analysed in relation to corresponding climatic data obtained from the meteorological stations nearest each collection site. Multivariate analysis of both datasets is then used to establish correlations between modern leaf characters and climatic features using a computer program termed CLAMP (Climate–Leaf Analysis Multivariate Program). The correlations are considered to represent an optimization by the plants between carbon gain, water loss, structural support and climate¹¹. These same correlations are then applied to character traits measured from fossil-leaf assemblages to estimate terrestrial climates at the time of growth. However, even without any consideration of the direct effects of CO₂ concentration, possible errors associated with the application of this technique to fossil leaves seem likely¹².

Application of CLAMP to fossil-leaf assemblages assumes that leaf shape is ‘fixed’ and evolved in response to climate, and that phenotypic effects, arising from differences in soil nutrient status, herbivore pressure, atmospheric CO₂ and taphonomic bias in the assemblages themselves¹³, are unimportant⁵. Because the majority of CLAMP applications have been on Cretaceous and Tertiary fossil floras (when the atmospheric CO₂ concentration was several times above that of the present and climates were generally more equable than now³), it is important that some assessment is made of the possible bias on leaf phenotype from the effects of CO₂ concentration and temperature. Evidence for CO₂ effects on leaf shape and thickness¹⁴ is now beginning to emerge across

a range of different plant types. Madsen¹⁵ showed that the leaves of tomato plants grown with CO₂ enrichment exhibited strong morphological modifications, particularly leaf rolling and petiole length. More recently, CO₂-enrichment effects on leaf shape have been demonstrated in three herbaceous species, *Taraxacum officinale*, *Plantago major* and *Rumex crispus*, grown at concentrations of 350 and 700 ppm CO₂ for five months¹⁶. Allometric comparisons of leaves between the two CO₂ concentrations were made to distinguish changes specifically between the direct effects of CO₂ on leaf shape from those possibly correlated with altered leaf size or developmental order. The leaves of CO₂-enriched *T. officinale* had significantly ($p < 0.0001$) more pronounced dentition along the lamina margin than the leaves of unenriched *T. officinale* (Fig. 1). Changes in leaf shape were also observed in parallel experiments with *P. major* and *R. crispus*, where increased concentrations of CO₂ altered the allometric relationships between leaf length and width, and between leaf area and petiole length, respectively¹⁶.

The significance of changes in leaf shape of the oak *Quercus alba* grown in an elevated CO₂ atmosphere for three years has been specifically assessed to determine how the characters scored by CLAMP are affected¹⁷. Leaves of *Q. alba* that had developed in ambient (350 ppm), ambient + 150 ppm CO₂, and ambient + 300 ppm CO₂ were scored for the 29 characters required by CLAMP. The results showed large variations in several character traits between replicate CO₂ chambers. Increasing CO₂ concentration had a significant effect on only one leaf character, leaf:width ratio, which increased. The implication is that microsite variation has a greater effect on leaf shape than does CO₂, at least for this deciduous angiosperm tree. Increasing the concentration of CO₂ from ambient levels also affects leaf size in woody angiosperm species – a total of three out of 11 genera showed a significant change¹⁷ (although no changes in leaf size were reported when CO₂ levels were decreased). Extrapolation of this finding (to three out of 22 species whose leaf physiognomy is affected by CO₂), in each of two early Oligocene fossil floras, allowed some quantification of its impact on CLAMP climatic estimates. The results showed that modification of the physiognomic scores of these floras to allow for observed effects of CO₂ concentration introduced a maximum error of 1°C for estimates of mean annual temperature (MAT), which is comparable to the 1.5°C standard error (SE) of CLAMP. However, an SE estimate of 20 cm for growing season precipitation exceeds the CLAMP SE of 16 cm. Recent work indicates that the level of certainty of MATs derived from CLAMP is greater than previously realized and probably lies within the SE range 1.7–2.5°C for the modern dataset and 3–5°C for fossil floras¹² (with the additional consideration of the CO₂ effects mentioned previously on top of this). The potentially greater impact of the between-microsite variation of leaf phenotype in CLAMP estimates remains unexamined.

How applicable these findings are to a wider range of plant taxa is unknown. Eleven taxa are too few to draw any general conclusions, and the effect of higher temperatures with CO₂ enrichment is an additional consideration that has not been investigated sufficiently to infer any secure conclusions. One mechanism potentially affecting leaf growth and shape at high concentrations of CO₂ is the activity of a widely distributed enzyme, xyloglucan endotransglycosylase, which is responsible for catalysing cutting and splicing of the xyloglucan molecules that span adjacent cell wall microfibrils¹⁸. High CO₂ levels stimulate the activity of this enzyme, via a signal transduction pathway to the inside of the leaves, increasing epidermal cell-wall extensibility and hence leaf

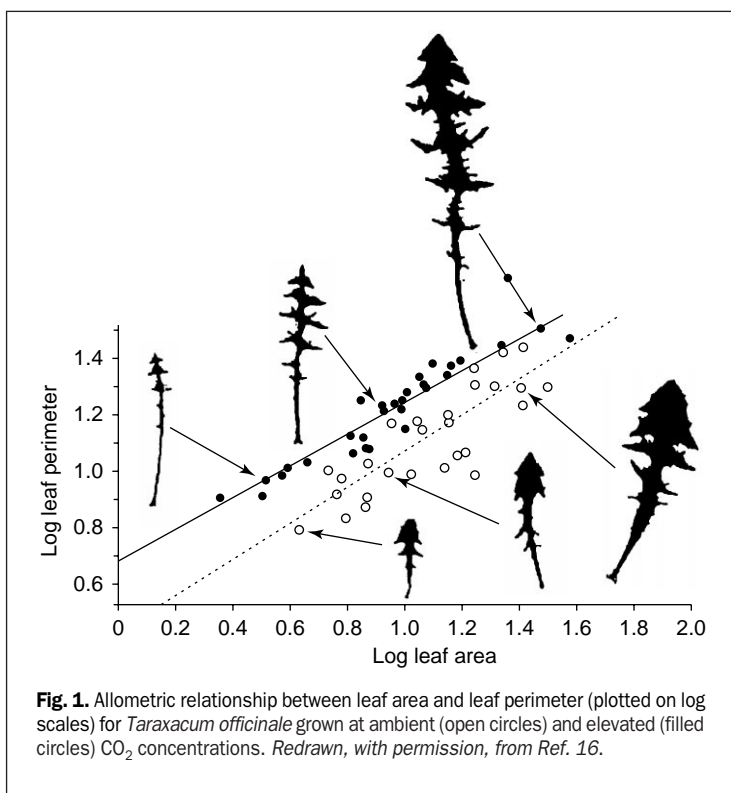


Fig. 1. Allometric relationship between leaf area and leaf perimeter (plotted on log scales) for *Taraxacum officinale* grown at ambient (open circles) and elevated (filled circles) CO₂ concentrations. Redrawn, with permission, from Ref. 16.

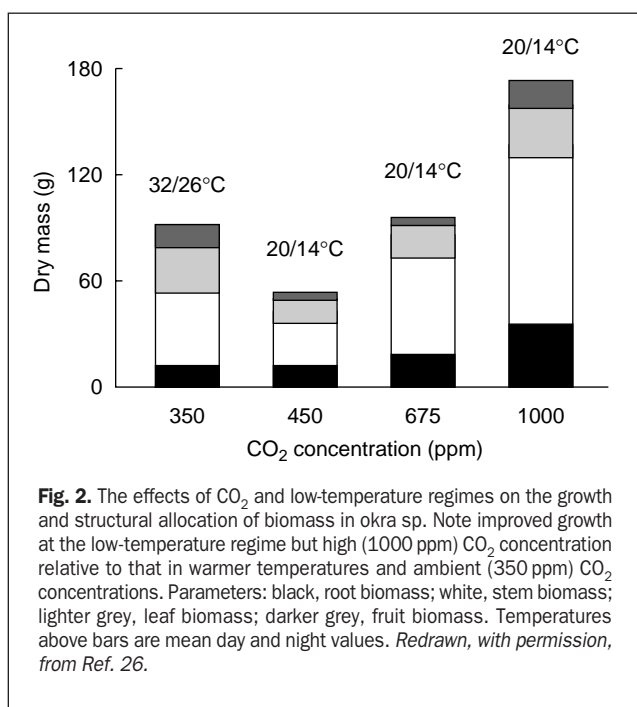


Fig. 2. The effects of CO₂ and low-temperature regimes on the growth and structural allocation of biomass in okra sp. Note improved growth at the low-temperature regime but high (1000 ppm) CO₂ concentration relative to that in warmer temperatures and ambient (350 ppm) CO₂ concentrations. Parameters: black, root biomass; white, stem biomass; lighter grey, leaf biomass; darker grey, fruit biomass. Temperatures above bars are mean day and night values. Redrawn, with permission, from Ref. 26.

expansion. Although incomplete, the experimental evidence indicates the potential for high concentrations of CO₂ to affect leaf phenotype. Whether these phenotypic changes in leaf shape could become 'fixed' genetically will depend upon the selective advantage conferred to the plant and, of course, on the duration of the high CO₂ concentration. Palaeoclimatic parameters derived by CLAMP from fossil-leaf assemblages believed to have grown in a high-CO₂ environment are therefore potentially erroneous to some degree.

CO₂ effects and nearest living relatives

Extrapolation of the climatic tolerance of a fossil plant from that of its nearest living relative is based on the assumption that the current plant-climate relationship remained unaffected over the time in question^{6,7}. This is termed the 'nearest living relative' (NLR) approach. The validity of the approach depends upon the taxonomic level at which the comparisons are made and decreases with increasing age of the flora. NLR-based climatic inferences can be unreliable because lineages have evolved to occupy different climatic conditions. Errors of this type can be reduced by restricting comparisons to the distribution of similar functional types, such as frost-sensitive plant groups¹⁹ (e.g. palms, gingers and cycads). At the global and local scale, palm distribution is strongly controlled by temperature because they are especially vulnerable to frost – they have a single massive apical growing point, the death of which invariably leads to the death of the whole plant. Irrespective of evolutionary 'drift' in the climatic tolerance of NLRs, a high level of CO₂ in the atmosphere could fundamentally alter plant-climate relationships through direct effects on water economy: CO₂ enrichment typically increases whole-plant water-use efficiency²⁰ and extends net photosynthesis to higher temperatures²¹. As a consequence, species currently limited in their geographical distribution by drought might have spread into more arid regions under a higher CO₂ concentration in the atmosphere of the geological past. Episodes of low CO₂ concentration (e.g. during past glaciations) would also have affected species distributions because of parallel ecophysiological considerations⁸.

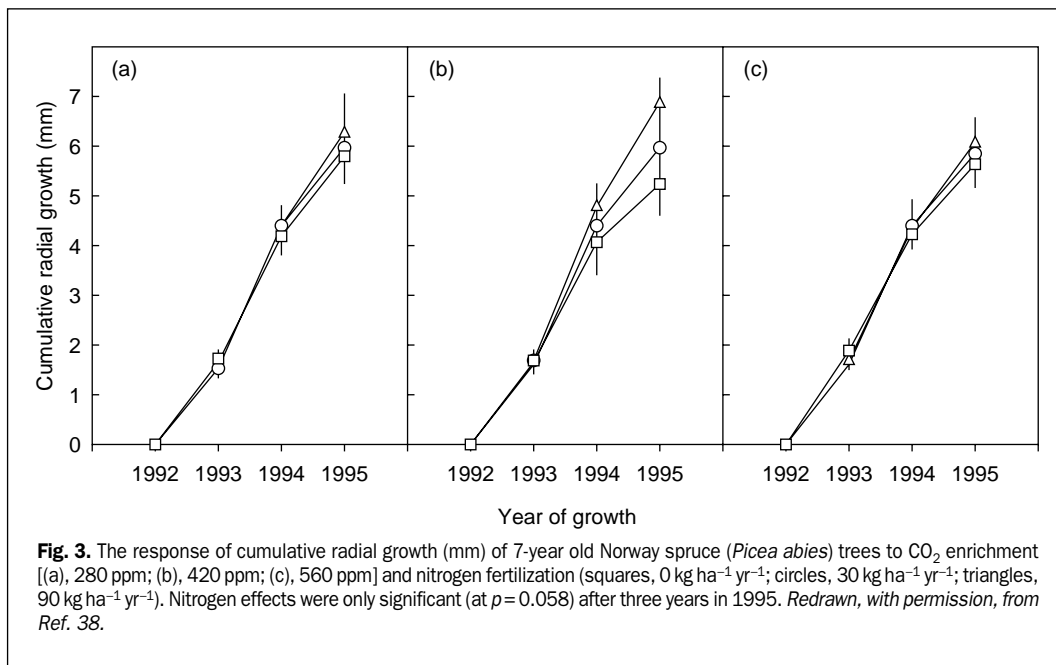
Application of frost-sensitive NLRs to the fossil record, extending back at least 250 million years, requires some

appreciation of the possible effects of CO₂ concentration on low-temperature tolerance. Several experiments have shown that chilling injury in herbaceous plants (with the C₃ and C₄ photosynthetic pathway) and conifers can be ameliorated by CO₂ enrichment^{22–25}. Sionit *et al.*²⁵ found that at ambient CO₂ concentrations okra (*Abelmoschus esculentus*) grew best at high temperatures, but that elevated CO₂ concentrations caused increased growth, survival and reproduction at lower temperatures (Fig. 2). Effectively, therefore, elevated CO₂ concentrations would have allowed okra to persist under temperature regimes that it could not have survived under previously²⁶. Amelioration of mild chilling stress (via high CO₂ concentrations) might involve the release of abscisic acid (ABA)²⁷, suggesting a general mechanism that is potentially applicable to a wide range of plant taxa.

Results from experiments on chilling injury and CO₂ enrichment are contradictory. Frost resistance in cereals is considerably greater at 700 ppm CO₂ than at 350 ppm (Ref. 24), and saplings of Scots pine (*Pinus sylvestris*) grown with CO₂ enrichment (550–600 ppm) showed a transient hardening of needles in response to low temperature during the first year of exposure²³. In contrast, growth of seedlings of the conifer *Picea mariana* under elevated CO₂ concentrations actually increased their susceptibility to frost damage²⁸, although growth of six-year old Norway spruce (*Picea abies*) trees for two years in a CO₂-enriched atmosphere had no effect on frost damage either in the autumn after hardening or during spring dehardening²⁹. The differences in treatment responses between these two conifer studies might be related to the experimental protocol – in the study of *P. mariana*, CO₂ enrichment was applied only towards the end of the growing season rather than continuously.

There is also a strong possibility that the combination of warmer temperatures and high CO₂ concentrations could alter the phenological development of plants. Experimental investigations of CO₂ enrichment on phenology in tropical ecosystems is still to be done³⁰. Reich³¹, however, suggests that the phenology of tropical rain forests would be relatively insensitive to changes in CO₂ concentration, temperature and precipitation, whereas that of dry tropical forests would be strongly sensitive. In these systems, if stand transpiration was reduced through increased water-use efficiency, elevated CO₂ levels might delay the onset of leaf shedding and stimulate a longer lifespan.

For plants in ancient climates characterized by high atmospheric CO₂ concentrations and shallow equator-to-pole temperature gradients (e.g. those of the mid-Cretaceous and mid-Eocene), these data suggest the possibility of significant effects of CO₂ concentrations on the ability to tolerate low temperatures. Application of the NLR approach to the Eocene¹⁹ suggested that climate models for this epoch³² simulated absolute minimum temperatures for continental interiors that were too cold, zero to –10°C, considering the global distribution of fossil palms, cycads and gingers, which, based on current tolerances for these groups, indicated temperatures of between 2 and –2°C. However, during the mid-Eocene these plants probably grew in atmospheric CO₂ concentrations of 600–900 ppm (Ref. 3), which is possibly enough to ameliorate low-temperature stress and allow greater tolerance of colder conditions than now²⁶. This could introduce a bias into estimates of past terrestrial-temperature ranges based on the plant fossil record that has not been previously appreciated. Experimental approaches aimed at quantifying such effects will need careful selection of populations from suitable geographical locations to avoid possible 'strains' of frost-tolerant or frost-sensitive plants from the more northern and southern edges of their ranges,



indicates that the expected large 'fertilization' effect of CO₂ (at high concentrations) on the stem growth of trees is not a ubiquitous property of all species. In many cases, no effects of CO₂ enrichment on wood growth rings have been reported³⁷⁻³⁹. The growth of *Q. alba* for four years at elevated CO₂ levels in open-top chambers showed no direct CO₂ effects on stem-wood growth rate³⁷. Similarly, the growth of four- to seven-year old Norway spruce trees with CO₂ enrichment (560 ppm for three years) did not increase the stem radial increment³⁸. The lack of responsiveness of tree ring widths to CO₂ enrichment in natural ecosystems might result from down-regulation of the photosynthesis-related enzymes and changes in the leaf-area indices of whole stands of trees. In addition to an influence on carbon partitioning in trees, CO₂ concentration affects interactions between trees and soil nutrients and mycorrhizas, which could subsequently alter the relationship between climate, CO₂ concentration and tree-ring width³⁹. The effects of the interactions between nitrogen and CO₂ on growth-ring widths have been well illustrated by Hattenschwiler *et al.*³⁸ – no significant effects on cumulative radial-stem growth of seven-year old Norway spruce was found between trees grown at 280, 420 and 560 ppm CO₂, but there was a significant (at $p = 0.058$) nitrogen-fertilization effect after three years (Fig. 3).

Fig. 3. The response of cumulative radial growth (mm) of 7-year old Norway spruce (*Picea abies*) trees to CO₂ enrichment [(a), 280 ppm; (b), 420 ppm; (c), 560 ppm] and nitrogen fertilization (squares, 0 kg ha⁻¹ yr⁻¹; circles, 30 kg ha⁻¹ yr⁻¹; triangles, 90 kg ha⁻¹ yr⁻¹). Nitrogen effects were only significant (at $p = 0.058$) after three years in 1995. Redrawn, with permission, from Ref. 38.

respectively (in the Northern Hemisphere). At this stage, however, it is not possible to quantify and correct for the effects of CO₂ concentration, but the results from CO₂-enriched growth experiments point to the need for caution when interpreting palaeobotanical data in this manner.

CO₂ and climatic effects on tree rings

Analysis of the secondary xylem characteristics (wood) of trees potentially indicates the seasonality of climate by the presence or absence of growth rings and the conditions of growth by the width of the rings^{7,9}. Fossil tree stumps first appear in the geological record in the Devonian (about 370 million years ago)⁷, but the majority of detailed studies on ring-width variations in fossilized woods have focused on Mesozoic and Tertiary materials³³⁻³⁶.

Climatic inferences are based on the premise that tree-ring width reflects an integrated response by the tree to seasonality in light, temperature, water availability and atmospheric CO₂ concentration. It is assumed that warm temperatures and high CO₂ concentrations, with adequate rainfall, contribute to wider ring widths, which are in turn a direct indication of the higher productivity of the tree – but how robust is this assumption? Evidence from experiments

Numerous attempts have been made to detect the expected CO₂ fertilization effect on tree growth caused by the increasing concentration of atmospheric CO₂ over the past two centuries⁴⁰⁻⁴³. All approaches, so far, have failed to detect such effects unambiguously, even when sensitivity to CO₂ concentration is maximized by sampling trees growing at high altitude and, therefore, at reduced partial pressures of CO₂ (Ref. 40). Instead, increases in the width of growth rings, where they have been recorded, have been attributed to climatic variations⁴¹, although given the interdependence of climate and atmospheric CO₂ such a conclusion may be unwarranted³⁹. In addition, appropriate statistical analyses of the time-series data are required to prevent autocorrelation between unrelated variables. As these have frequently been omitted in such studies, any fertilization effects of increased concentrations of CO₂ would have been further obscured³⁹.

Analyses of contemporary tree-ring sequences covering the more recent past, for which we have direct instrumental records of atmospheric CO₂ and terrestrial temperatures⁴⁴, provide an alternative source of information about the climatic effects on tree growth through time. Short-term (several decades) sequences of tree rings show that variations in ring width and maximum late-wood density of trees from the Northern Hemisphere correspond with temperature⁴⁴. This work appears to provide a good basis for extrapolating inferences about climate from fossil woods. New data, however, obtained from trees across a wider range of sites in the Northern Hemisphere, now indicate that ring widths and maximum late-wood density do not correspond with

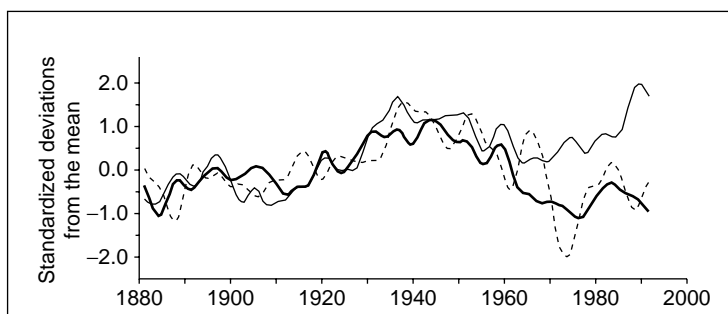


Fig. 4. Twenty-year smoothed plot of variations in tree-ring width (broken line), maximum late-wood density (bold line) and Northern Hemisphere growing season temperatures (solid line) from 1880 to 1996. The y-axis units are deviations from the mean growth-ring thickness, maximum late-wood density and temperature from 1881 to 1940. Trees were sampled from a network of Northern Hemisphere sites and each parameter standardized to a common baseline. Redrawn, with permission, from Ref. 45.

temperature recorded since about 1950 (Fig. 4)^{45,46}. This indicates a difference in the climatic 'forcing' of tree growth in recent decades. The anomaly is also apparent in tree-ring records from a subcontinental network of sites, suggesting that it is a real feature of the response of trees rather than an artefact of data processing. This unusual response indicates a shift in the relationship between tree growth, climate and atmospheric CO₂ concentration, which was not seen in the previous 70–80 years, and raises more concerns about the use of subfossil and fossil woods to reconstruct past climates. Other features of the environment, apart from temperature, have also changed in recent years, including atmospheric CO₂ concentration, UV-B radiation and nitrogen deposition – these cannot be excluded as the explanation for the lack of correlation between tree growth and temperature. Nevertheless, the possibility exists that tree–climate–atmosphere relationships are not constant through time, as previously assumed, and extrapolation of climatic inferences from analyses of fossil woods remains an uncertain science until the causal mechanism is identified.

Prospects

Given the value of plant fossils, it is important that current methods of palaeoclimatic interpretation from these sources are constrained as new ecophysiological data become available. Results from growth experiments on plants with CO₂ enrichment, and CO₂ enrichment combined with climatic warming, suggest some surprises may be in store for palaeobotanists. Similar experiments are required for more ancient taxa that evolved under much higher CO₂ concentrations than now. Correlations between climate and plant growth appear to be less certain than previously assumed. Future research on plant responses to CO₂ promises to develop greater refinements of palaeoclimatic reconstructions from the plant fossil record. There remains, however, a need to develop new methods of terrestrial climate reconstruction based on a more reliable (i.e. mechanistic) understanding of plant responses to the environment. Developments determining the causes of variation in stable isotopes of carbon, hydrogen and oxygen of subfossil and fossil plant remains show potential in this direction.

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References

- Steffen, W.L. *et al.* (1992) *Global Change and Terrestrial Ecosystems: the Operational Plan (The International Geosphere Biosphere Program)* (Report 21), ICSU, IGBP Secretariat, the Royal Swedish Academy of Sciences
- Houghton, J.T. *et al.* (1996) *Climate Change 1995. The Science of Climate Change*, Cambridge University Press
- Berner, R.A. (1997) **The rise of plants and their effect on weathering and atmospheric CO₂**, *Science* 276, 544–546
- Beerling, D.J. and Woodward, F.I. (1997) **Changes in land plant function over the Phanerozoic: reconstructions based on the fossil record**, *Bot. J. Linn. Soc.* 124, 137–153
- Wolfe, J.A. (1995) **Paleoclimatic estimates from Tertiary leaf assemblages**, *Annu. Rev. Earth Plan. Sci.* 23, 119–142
- Boulter, M.C. and Fisher, H.C., eds (1994) *Cenozoic Plants and Climates of the Arctic (NATO ASI Series I: Global Environmental Change)* (Vol. 27), Springer-Verlag
- Chaloner, W.G. and Creber, G.T. (1990) **Do fossil plants give a climatic signal?** *J. Geol. Soc.* 147, 343–350
- Huntley, B. (1994) **The use of climate response surfaces to reconstruct palaeoclimate from Quaternary pollen and plant macrofossil data**, in *Palaeoclimates and their Modelling* (Allen, J.R. *et al.*, eds), pp. 7–16, Chapman & Hall
- Chaloner, W.G. and Creber, G.T. (1973) **Growth rings in fossil woods as evidence of past climates**, in *Implications of Continental Drift to the Earth Sciences* (Tarling, T.H. and Runcorn, S.K., eds), pp. 425–437, Academic Press
- Beerling, D.J. (1997) **The net primary productivity and water use of forests in the geological past**, *Adv. Bot. Res.* 26, 193–227
- Givnish, T.J. (1987) **Comparative studies of leaf form: assessing the relative roles of selective pressures and phylogenetic constraints**, *New Phytol.* 106, 131–160
- Jordan, G.J. (1997) **Uncertainty in palaeoclimatic reconstructions based on leaf physiognomy**, *Aust. J. Bot.* 45, 527–547
- Boyd, A. (1994) **Some limitations in using leaf physiognomic data as a precise method for determining paleoclimates with an example from the Late Cretaceous Pautūt flora of west Greenland**, *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 112, 261–278
- Pearson, M., Davies, W.J. and Mansfield, T.A. (1995) **Asymmetric responses of adaxial and abaxial stomata to elevated CO₂: impacts on the control of gas exchange by leaves**, *Plant Cell Environ.* 18, 837–843
- Madsen, E. (1973) **Effect of CO₂ concentration on the morphological, histological and cytological changes in tomato plants**, *Acta Agric. Scand.* 23, 241–246
- Thomas, S.C. and Bazzaz, F.A. (1996) **Elevated CO₂ and leaf shape: are dandelions getting toothier?** *Am. J. Bot.* 83, 106–111
- Gregory, K.M. (1996) **Are palaeoclimate estimates biased by foliar physiognomic responses to increased atmospheric CO₂?** *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 124, 39–51
- Ranasinghe, S. and Taylor, G. (1996) **Mechanism for increased leaf growth in elevated CO₂**, *J. Exp. Bot.* 47, 349–358
- Greenwood, D.R. and Wing, S.L. (1995) **Eocene continental climates and latitudinal temperature gradients**, *Geology* 23, 1044–1048
- Eamus, D. and Jarvis, P.G. (1989) **The direct effects of increase in the global atmospheric CO₂ concentration on natural and commercial temperate trees and forests**, *Adv. Ecol. Res.* 19, 2–55
- Long, S.P. (1991) **Modification of the response of photosynthetic productivity to rising temperature by atmospheric CO₂ concentrations: has its importance been underestimated?** *Plant Cell Environ.* 14, 729–739
- Potvin, C. (1985) **Amelioration of chilling effects by CO₂ enrichment**, *Physiol. Veg.* 23, 345–352
- Repo, T., Hänninen, H. and Kellomäki, S. (1996) **The effects of long-term elevation of air temperature and CO₂ on the frost hardiness of Scots pine**, *Plant Cell Environ.* 19, 209–216
- Veisz, O. *et al.* (1996) **Frost resistance in winter cereals as a function of atmospheric CO₂ concentration, temperature and soil moisture content**, *Novenytermeles* 45, 445–452
- Sionit, N., Strain, B.R. and Beckham, H.A. (1981) **Environmental controls on the growth and yield of okra. I. Effects of temperature and of CO₂ enrichment at cool temperature**, *Crop Sci.* 21, 885–888
- Hogan, K.P., Smith, A.P. and Ziska, L.H. (1991) **Potential effects of elevated CO₂ and changes in temperature on tropical plants**, *Plant Cell Environ.* 14, 763–778
- Ward, D.A. and Lawlor, D.W. (1990) **Abscisic acid may mediate rapid thermal acclimatization of photosynthesis in wheat**, *J. Exp. Bot.* 41, 309–314
- Margolis, H.A. and Vezina, L.P. (1990) **Atmospheric CO₂ enrichment and the development of frost hardiness in containerised black spruce seedlings**, *Can. J. For. Res.* 20, 1392–1398
- Wiemken, V., Kossatz, L. and Ineichen, K. (1996) **Frost hardiness of Norway spruce grown under elevated CO₂ and increased nitrogen fertilization**, *J. Plant Physiol.* 149, 433–438
- Lechowicz, M.J. and Koike, T. (1995) **Phenology and seasonality of woody plants: an unappreciated element in global change research**, *Can. J. Bot.* 73, 147–148
- Reich, P.B. (1995) **Phenology of tropical forests: patterns, causes and consequences**, *Can. J. Bot.* 73, 164–174
- Sloan, L.C. (1994) **'Equable' climates during the early Eocene: significance of regional palaeogeography for North American climate**, *Geology* 22, 881–884
- Creber, G.T. and Chaloner, W.G. (1985) **Tree growth in the Mesozoic and early Tertiary and the reconstructions of palaeoclimates**, *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 52, 35–60
- Francis, J.E. (1991) **The dynamic of polar forests: Tertiary fossil forests of Axel Heiberg Island, Canadian Arctic Archipelago**, *Geol. Surv. Canada* 403, 29–38

- 35 Kumagai, H. *et al.* (1995) **Growth-ring analysis of early Tertiary conifer woods from the Canadian high Arctic and its palaeoclimatic interpretation**, *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 116, 247–262
- 36 Francis, J.E. and Hill, R.S. (1996) **Fossil plants from the Pliocene Sirius group, transarctic mountains: evidence for climate from growth rings and fossil leaves**, *Palios* 11, 389–396
- 37 Norby, R.J. *et al.* (1996) **Increased growth efficiency of *Quercus alba* trees in a CO₂ enriched atmosphere**, *New Phytol.* 131, 91–97
- 38 Hattenschwiler, S. *et al.* (1996) **Tree ring responses to elevated CO₂ and increased N deposition in *Picea abies***, *Plant Cell Environ.* 19, 1369–1378
- 39 Lloyd, J. and Farquhar, G.D. (1996) **The CO₂ dependence of photosynthesis, plant growth responses to elevated atmospheric CO₂ concentrations and their interactions with soil nutrient status. I. General principles and forest ecosystems**, *Funct. Ecol.* 10, 4–32
- 40 Graumlich, L.J. (1991) **Subalpine tree growth, climate and increasing CO₂: an assessment of recent growth trends**, *Ecology* 72, 1–11
- 41 D'Arrigo, R.D. and Jacoby, G.C. (1993) **Secular trends in high northern latitude temperature reconstructions based on tree rings**, *Climate Change* 25, 163–177
- 42 D'Arrigo, R.D. and Jacoby, G.C. (1993) **Tree growth-climate relationships on the northern boreal tree line of North America: evaluation of potential responses to carbon dioxide**, *Global Biogeochem. Cycles* 7, 525–536
- 43 Jacoby, G.C. and D'Arrigo, R.D. (1997) **Tree rings, carbon dioxide, and climatic change**, *Proc. Natl. Acad. Sci. U. S. A.* 94, 8350–8353
- 44 Briffa, K.R. *et al.* (1995) **Unusual twentieth-century summer warmth in a 1,000-year temperature record from Siberia**, *Nature* 376, 156–159
- 45 Briffa, K.R. *et al.* (1998) **Trees tell of past climates: but are they speaking less clearly today?** *Philos. Trans. R. Soc. London Ser. B* 353, 65–73
- 46 Briffa, K.R. *et al.* (1998) **Reduced sensitivity of recent tree growth to temperature at high northern latitudes**, *Nature* 391, 678–682

Benthic suspension feeders: their paramount role in littoral marine food webs

Josep-Maria Gili and Rafel Coma

The physical properties of seawater allow living creatures and particulate matter to remain in suspension, thereby creating a niche for suspension feeding – a trophic strategy that does not occur on land. Small cells (phytoplankton and microorganisms) predominate in such suspended (planktonic) communities. Suspension feeders have evolved mechanisms for capturing food that can be highly diluted within the water mass and, at the same time, be too small to be detected and captured individually. The possible mechanisms have been described by ‘aerosol filtration’ theory¹ (Box 1). The importance of this feeding strategy is particularly apparent in benthic marine communities, in which most animal groups have morphological structures capable of exploiting suspended particles as a potential food source.

For many species, suspension feeding involves food items that are either large enough to be individually seized or so small that they are only obtained in sufficient quantity by processing the surrounding water^{2,3}. Therefore, many benthic sessile suspension feeders employ a variety of foraging behaviours to enable them to feed in the typically stochastic environments they live in. They have also adopted appropriate feeding strategies for a wide spectrum of prey, as has been observed in zooplankton organisms⁴. Recent field

In recent years, particular attention has been paid to coupling and energy transfer between benthos and plankton. Because of their abundance, certain benthic suspension feeders have been shown to have a major impact in marine ecosystems. They capture large quantities of particles and might directly regulate primary production and indirectly regulate secondary production in littoral food chains. Suspension feeders develop dense, three-dimensional communities whose structural complexity depends on flow speed. It has been postulated that these communities can self-organize to enhance food capture and thus establish boundary systems capable of successfully exploiting a less structured system, namely, the plankton.

Josep-Maria Gili and Rafel Coma are at the Dept of Marine Biology, the Institut de Ciències del Mar (CSIC), Plaça del Mar s/n, 08039 Barcelona, Spain (gili@cucafera.icm.csic.es; coma@cucafera.icm.csic.es).

experiments investigating the natural diet of several species have provided new information suggesting that sessile suspension feeders feed on a wider spectrum of prey type and size than previous laboratory work pointed out^{5,6} (Box 2).

Sessile organisms tend to capture food items in bulk rather than individually because they are adapted to moving fluid environments⁷. This adaptation, combined with the low cost of active filtering⁸, means that benthic sessile suspension feeders could provide a prime example of optimal foraging in a marine context⁹ (Box 2). The development of dense populations and multispecies communities, which are composed mainly of suspension feeders in shallow environments, has been explained by different theories, which corroborate the important contribution of suspension feeders to benthic communities. These theories are based on aspects reflecting statements such as ‘the population density does not affect seston [i.e. the total particulate matter suspended in the water column] uptake or population growth’ or ‘sestonic food does not become limiting above a suspension feeding bed’¹⁰. They predict that the formation of colonies and clones (i.e. populations) is energetically more favourable than increasing the growth of an individual to its largest possible body size¹¹.