Adaptive role of leaf habit in extinct polar forests

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SUMMARY

Fossils provide clear evidence of forests covering the Arctic and Antarctic throughout most of the past 250 million years. Ancient polar forests experienced the extreme seasonality of high latitude daylength, but flourished in a warm, temperate climate. For the past 50 years, it has been argued that deciduous trees in these ecosystems conserved carbon by avoiding the respiration required to sustain an evergreen leaf canopy during the continuous darkness of a warm winter. However, only recently have experiments been designed to test this argument by measuring the winter carbon balance of 'living fossil' trees in a simulated warm polar climate. Results of these experiments show clearly that the carbon cost of annually shedding leaves in deciduous trees greatly exceeds the cost of respiration for an evergreen canopy. Simulations with a mathematical model support this finding for mature forests growing across a wide latitudinal range, ending a century-long debate concerning the adaptive role of leaf habit in extinct polar forests.

Keywords: arctic, Antarctic, leaf habit, deciduous, respiration, fossil plants

INTRODUCTION

> "the moraine was obviously so interesting that when we had advanced some miles and got out of the wind, I decided to camp and spend the rest of the day geologising."
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> Robert Falcon Scott.
> Diary entry dated 8 February 1912.
> Beardmore Glacier, Antarctica (82ºS).

When the bodies of Scott and his polar party were found in 1913, a precious cargo of plant fossils from the Beardmore Glacier was discovered with their sledge. Later examination by the Cambridge palaeobotanist Albert Seward showed these to be the 250 million-year-old Permian remains of *Glossopteris*, an early gymnosperm already known from India, Australia and South Africa. This finding was to become an important piece in the jigsaw of evidence for Alfred Wegener's 1915 theory of 'continental drift', supporting the existence of Gondwanaland, a giant southern continent long since broken into pieces by movement of the Earth's crust. Sadly, the scientific world of 1915 was not yet ready for Wegener's radical ideas and, in the absence of a plausible mechanism for continental movement, it was forgotten until the 1950s when mounting evidence for plate tectonics revolutionised our view of the Earth.

But the significance of Scott's fossils did not end there. For in his 1914 report on the plant remains, Seward makes an important recognition; that ancient *Glossopteris* forests on Antarctica may have grown in an environment unlike any on Earth today, characterised by a warm, temperate climate, but the same extreme seasonality of polar daylight. At latitudes of 82ºS, forests would be plunged into winter darkness for 20 weeks and experience an equal period of continuous daylight during summer. In Seward's view, this would have presented few problems for an ancient forest, irrespective of whether it was made up of deciduous or evergreen species. He writes:

> "It may be assumed that in the days when Glossopteris and other genera flourished on Antarctica the climatic conditions, at least regards temperature, were more favourable than now, but we lack experimental data to give us a clue to the nature and extent of the influence of a prolonged sunless period. There is no serious difficulty in the way of Arctic or Antarctic plants surviving the winter months either in a condition similar to that of deciduous trees in a European winter, or even as evergreens living at low pressure on the surplus food manufactured in the course of the prolonged period of sunshine "
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> Seward, A.C. (1914)
> *British Museum Natural History Report. Geology* 1, p.41.

Seward's later work on Cretaceous fossil forests from Greenland reiterates this opinion and, for the remainder of his career, his ideas were not contested. Yet for the last 50 years the opposite view has prevailed; that the fossil forests of the Arctic and Antarctica were predominantly deciduous, and must have been so, as an adaptation to the warm darkness of an ancient polar winter. Proponents of this view argued that an evergreen forest could not be a viable or competitive option in a warm polar climate – the metabolic costs of keeping a leaf canopy alive during a dark winter were simply too great. And the sheer 'impossibility' of sustaining an evergreen canopy at warm high latitudes has been evoked to support geological theories of moving continents and astronomical shifts in the Earth's axis. This paper begins with a selective history of the 'deciduous view' of ancient polar forests, where it may have started, and how it was propagated through the scientific literature. It then goes on to discuss experimental data, recognised by Seward as being vital for the story, but not available in his lifetime. These data, together with emerging new evidence from palaeobotany and simulation modelling, are finally proving him right all along.

THE DECIDUOUS VIEW

Problems of a warm winter

The idea of the deciduous habit of ancient forests being an adaptation to winter darkness can be traced to two papers from a 1946 Botanical Society of America symposium on the evolution of floristic regions. Before the acceptance of plate tectonics, geologists debated whether polar fossils were evidence of a warm ancient climate, in which forests thrived at high latitudes, or were temperate plants whose remains had moved polewards as a consequence of 'continental drift' or the action of ocean currents. University of California Berkley palaeobotanist Ralph Chaney argued for the former, noting that genera such as *Pinus* and *Picea* known from ancient Canadian Arctic floras remain within today's polar region, and clearly tolerate extreme seasonality of daylength. Moreover, he proposed the deciduous habit as an adaptation to warm, dark winters.

> "Recent discovery by Wan-Chun Cheng of a living relative of Sequoia in central China, a tree which sheds its leafy twigs during the winter, provides a possible basis for explaining the occurrence of this now warm temperate plant in Grinnell Land. For without leaves, Sequoia and Taxodium might both be expected to survive a dark winter which was not cold"
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> Chaney, R.W. (1947)
> *Ecological Monographs* 17 (2), p. 145.

The recent discovery to which Chaney refers was of wild extant *Metasequoia*, a 'living fossil' conifer known as an Arctic fossil since 1878, but misidentified as *Sequoia*.

In the same symposium another Berkley palaeobotanist, Herbert Mason, developed the argument that warm dark conditions would present substantial problems for evergreen plants by promoting high rates of respiration and therefore carbon loss during winter. However, he disagreed with his former supervisor Chaney, concluding that the occurrence of any forests in such an environment was impossible.

> "… we must conclude that no tropical, warm temperate, or even temperate forest flora, could possibly live and develop in high arctic latitudes. It would be too cold on the one hand and too dark on the other hand. To raise the temperature in such an area and not change the long periods of darkness would only aggravate the situation because the increased temperature in such an area would increase the respiration rate to the point that in evergreen species the reserve food supply would soon be depleted and deciduous species would be forced out of dormancy before adequate light returned and they too would dissipate their food reserves through rapid respiration."
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> Mason, H.L. (1947)
> *Ecological Monographs* 17 (2), p. 207.

Mason also took an opposing viewpoint in his interpretation of the fossil evidence, suggesting the occurrence of continental drift or a change in the tilt (obliquity) of the Earth's axis relative to the Sun, leading to less pronounced seasonality in daylength. The obliquity explanation was expounded the following year by US plant physiologist H.A. Allard, who found the presence of Arctic fossil genera difficult to reconcile with the photoperiodic responses of their relatives confined to today's warm temperate regions. Only a change to more uniform daylength could allow these plants to survive at high latitudes, he argued.

In the following 30 years, mounting data about the positions of fossil-bearing landmasses finally laid the debate on continental drift to rest. The conclusive data were based upon inferences of the ancient Earth's magnetic field relative to the land surface, as preserved in the orientation of the magnetic field of iron minerals in rocks. They showed that, although the continents have moved during the intervening period, most landmasses bearing ancient forests were located at high palaeolatitudes.

The obliquity debate

The possibility of changing obliquity remained, however, and gained favour during the early 1980s when an emerging picture of warm ancient polar climates saw renewed interest in high latitude forests and further development of the 'deciduous view'. Jack Wolfe of the US Geological Survey argued that darkness or low light in winter would exclude evergreens from warm high latitude environments by favouring respiration over photosynthesis, thereby causing significant 'fuel consumption' and net carbon loss from leaves (Wolfe, 1980). To reconcile this hypothetical exclusion mechanism with clear fossil evidence of evergreen forests at polar palaeolatitudes in the Eocene (40 Ma), he favoured a shift of the Earth's axis to eliminate continuous winter darkness. On the other side of the world, Australians Douglas and Williams reached the same conclusion about the mixed evergreen-deciduous flora of Antarctica in the Early Cretaceous (145–100 Ma), also evoking the presence of evergreens as evidence of reduced obliquity. Leo Hickey of Yale University preferred a botanical explanation, suggesting that the large leaves of these ancient trees were a growth response to continuous summer light in the Arctic. Like Wolfe, he proposed adaptive significance for the deciduous habit, but argued that greater carbon loss in evergreens during warm dark winters gave them a competitive disadvantage, rather than excluding them outright. Palaeoecologist Daniel Axelrod of the University of California at Davis developed a similar perspective from an extensive review of the climatic and photoperiodic responses of modern plants; the deciduous habit was pre-adapted to warm winter darkness, but evergreens were perfectly viable (Axelrod, 1984). While each author placed his own emphasis on its ecological and geological significance, the idea that deciduous leaves saved carbon in winter was therefore firmly established in the literature by this point. However, it remained entirely speculative, without direct experimental evidence in its favour.

Modern viewpoint

The current consensus is that Earth's obliquity remains relatively stable through geological time, and therefore high latitude forests must have experienced extreme photoperiodic seasonality. Polar regions basked in a warm 'greenhouse' climate associated with elevated atmospheric CO_2, and forests were a major biome in the Arctic and Antarctic for more than 200 Myr, the interval linking Scott's Permian Glossopteris (250 Myr ago, Ma), with Chaney's Tertiary conifers (40 Ma). Many of their important genera have modern representatives: *Sequoia*, *Metasequoia*, *Taxodium*, *Ginkgo*, *Picea* and *Pinus* from the Arctic; and *Araucaria*, *Agathis*, *Nothofagus* and *Podocarpus* from the Antarctic. Until recently, the deciduous view of these plants has held sway, with evergreens kept as underdogs through their wasteful consumption of carbon in warm conditions. Although many of the modern representatives of these genera are evergreen, examples such as *Quercus* and *Magnolia*, where evergreen and deciduous plants are congeneric, and species like *Quercus ithaburensis*, where leaf shedding is facultative, remind us that leaf habit is not immutable. Rather, it seems to be a plant trait that switches readily during evolution. Thus genera which today are evergreen may have been deciduous in the distant past.

Fossil forests have been discovered at palaeolatitudes of up to 82ºN and S, and independent isotopic evidence indicates a high CO_2 ancient greenhouse climate, with mean winter temperatures remaining above 5ºC despite a dark period of up to 20 weeks. The fossils of crocodiles and turtles from high latitude forests confirm this interpretation; since their living relatives are confined to the topics and sub-tropics, unable to survive freezing winter temperatures. Ancient polar forests therefore have no modern analogue because, although Siberian forests reach 72ºN, they experience average winter temperatures of -30ºC and absolute minima of -60ºC, literally freezing their metabolism and preventing carbon loss by respiration. With no way of going back in time, how then can we test the deciduous view of polar forests, that shedding leaves in winter saves carbon reserves?

Carbon loss hypothesis

A rigorous quantitative test requires a precise formulation of the problem. To meet this requirement, we have formalised the deciduous view as the 'carbon loss hypothesis', summarised by Box 1.

At face value, the hypothesis seems entirely reasonable. The rate of plant respiration in modern plants near doubles with each 10ºC rise in temperature – surely this would have spelled trouble for evergreen leaves in a warm climate during an extended period of darkness? And did these leaves really retain chlorophyll through weeks on end where no photosynthesis was possible? However, even in 1985, when support for the carbon loss hypothesis was at its height, University of London palaeobotanists Geoff Creber and Bill Chaloner were urging caution (Creber and Chaloner 1985). They drew attention to experiments with modern plants demonstrating acclimation of respiration to temperature, such that seasonal responses to warming are much less sensitive than immediate responses. So what was to stop ancient evergreens down-regulating their metabolism in a similar fashion, and over-wintering in a near-dormant state? And despite seasonality in daylength at high latitudes, the annual influx of solar energy was similar to that at lower latitudes. So what stood in the way of ancient trees achieving high productivities even at high latitudes?

Of course, the most direct way to really know how evergreen trees respond to warm dark periods is through

BOX 1 *The carbon loss hypothesis for trees growing in a high latitude environment with a warm winter*

Deciduous		**Evergreen**
Carbon content of leaf litter *(large cost)* + Carbon loss through respiration of bare branches during winter darkness *(small cost)*	*is less than*	Carbon loss through respiration of leaves and branches during winter darkness *(large cost)* + Carbon content of leaf litter *(small cost)*

experimental tests. In 1988 botanist Jennifer Read and palaeobotanist Jane Francis were the first to try these at the University of Tasmania, using a range of genera with close taxonomic affinity to Antarctic fossils (Read and Francis, 1992). The plants were kept in the dark for 10 weeks at either warm (15ºC) or cool (4ºC) temperatures, with controls exposed to a natural day-night regime. Fourteen of sixteen species survived the warm treatment with no loss of chlorophyll, and leaf damage in darkness was greatest in the plants with small carbon storage reserves, being more pronounced in warm conditions. Despite their clear conclusion that the majority of evergreens tested did survive protracted darkness, these experiments have been variously interpreted as supporting or conflicting with the carbon loss hypothesis. Further unequivocal experimental tests were clearly required.

CHALLENGING THE DECIDUOUS VIEW

Experiments simulating an ancient polar environment

In spring 2000 we established an experiment designed specifically to test the impacts of warm polar conditions on ancient tree genera (Beerling and Osborne, 2002). Our experiment utilised controlled environment growth rooms at the University of Sheffield to simulate an ancient warm polar climate and high CO_2 atmosphere. Air conditioning units ensured that temperatures never fell below freezing, and warmed the climate in growth rooms to 5ºC above the air outside. Mean annual temperature was 15ºC and mean temperature of the coldest month 8ºC, matching the warmest estimates for ancient high latitude environments, and therefore providing a stiff test for the carbon loss hypothesis by maximising winter respiration rates. To investigate the impacts of an elevated CO_2 atmosphere on plant carbon balance, we imposed two CO_2 treatments replicated (n =4) across different growth rooms. The first enriched CO_2 to 800 ppm, more than twice today's value of 370 ppm, but a conservative estimate for the period when forests flourished at the poles. The second was an un-enriched control. We were interested in the extent to which high CO_2 might modify plant carbon balance, by stimulating photosynthesis and suppressing respiration, as reported previously by researchers investigating current anthropogenic global change. Daylength in the blacked-out growth rooms was controlled using water-cooled artificial lighting, set using timers to reproduce the seasonality in photoperiod at latitudes of 69ºN. Plants therefore experienced six weeks of continuous light in summer and six weeks complete darkness in winter.

'Living fossil' plant species were selected for the experiment and grown in pots from one-year-old saplings. Each has close taxonomic and morphological affinity with polar fossils: *Metasequoia glyptostroboides* (Dawn Redwood / deciduous), *Taxodium distichum* (Swamp Cypress / deciduous), *Ginkgo biloba* (Maidenhair Tree / deciduous), *Sequoia sempervirens* (Coastal Redwood / evergreen) and *Nothofagus cunninghamii* (Cunningham Beech / evergreen). All plants survived three winters in experimental conditions, in agreement with the previous findings of Read and Francis, and maintained a normal rhythm of leaf expansion and abscission.

Plant carbon balance

To test the carbon loss hypothesis (Box 1), plants were sealed within custom-built chambers throughout a complete 24-hour period, and whole-plant CO_2 fluxes determined using gas exchange analysis, measuring changes in the CO_2 concentration of an air stream passed through the chamber (Royer *et al*. 2003). As predicted by the hypothesis (Box 1), respiration rates of evergreen plants holding onto leaf canopies during the 6-week dark period were higher than those of the leafless deciduous plants for two consecutive winters (2001–2002 and 2002–2003). Over the entire winter dark period in 2002–2003, young evergreen trees lost an average of eight times more carbon through respiration than their deciduous counterparts. There was no effect of CO_2 concentration on respiration in these plants. The production of leaf litter represents an additional carbon cost (Box 1), and this was significantly greater in deciduous than evergreen species for both years of our experiment. In 2002–2003 the deciduous plants shed an average of twenty times more carbon in leaf litter than their evergreen counterparts. As with respiration, there was no effect of CO_2 on this pattern. However the critical test of the carbon loss hypothesis came when carbon losses from respiration and leaf litter were added together (Box 1). The result came as somewhat of a surprise, with the carbon costs of leaf litter production far outweighing those of respiration. As a consequence, the total respiratory and litter carbon costs for evergreens were a mere ninth of the total cost for deciduous trees, a finding that was completely at odds with the carbon loss hypothesis. The hypothesis had therefore been overturned at its first direct experimental test.

However, a number of issues remained unresolved. Would this experimental finding in young trees hold for mature forests? And would the apparent disadvantage of the deciduous habit at 69ºN hold at higher latitudes, where the winter is three times longer, and the costs of respiration correspondingly higher? We addressed the first question by scaling our experimental findings from young trees to mature forest, accounting for the larger leaf canopy in older trees and the higher fraction of leaves lost each year in mature compared with young evergreens. The scaling procedure had two important effects: first it magnified the carbon cost of winter respiration and leaf litter production in evergreen and deciduous trees; and secondly it increased the cost of leaf litter production in evergreens relative to their deciduous counterparts. The net effect of scaling was to diminish the difference in carbon cost between leaf habits. But our main experimental conclusion remained intact – the deciduous habit incurred a winter carbon cost that was 1.5 to 2 times greater than the cost for evergreens. The carbon loss hypothesis still did not add up.

Modelling extinct forests

Accounting for the differential effects of latitude was trickier, and required a more sophisticated mathematical modelling approach. We used a model that had been developed specifically for simulating the structure and function of ancient conifer forests (Osborne and Beerling 2002). As its starting point, it used the process-based approach developed for work on future climate change, but extended this by directly accounting for the effects of leaf habit on physiology and the structural properties of leaves. In turn, each of these had knock-on effects on canopy properties and ecosystem biogeochemical cycling. The resulting model was a blend of physiological routines representing photosynthesis, respiration and evapotranspiration, and growth schemes based on limitations by light, nutrients and water availability. It took climate and CO_2 input data, and produced outputs describing forest carbon exchange and structure that agreed closely with modern observations. By supplying the model with data generated by climate simulations for the Cretaceous (100 Ma), we were able to test the carbon loss hypothesis across a range of latitudes from the Arctic Circle (66ºN) to the northernmost limits of ancient polar forests (82ºN).

In keeping with the hypothesis, we found that as winter lengthened with latitude, so the penalty of respiration increased for evergreen forests. But compared with the carbon lost through leaf fall, this respiratory burden remained relatively small, and the total winter carbon cost for deciduous forests was 1.5 to 2 times greater than the equivalent cost for evergreens, agreeing with the independent data from experiments. We therefore rejected the carbon loss hypothesis on the basis of experimental and model results.

A PARADIGM SHIFT?

Our findings spell the end for the carbon loss hypothesis but raise another important issue. Fossils suggest that deciduous trees flourished in high latitude ecosystems. How did they become so successful if shedding leaves each year was so costly? The answer may lie in patterns of carbon uptake during the rest of the year. Measurements of plant carbon exchange in our experiment revealed distinct ‘pulses’ of carbon gain in deciduous trees during spring and autumn that were missing in evergreen species. The pulses were even larger in a CO_2-rich atmosphere, and allowed deciduous trees to ‘catch-up’ with evergreens in their annual carbon budgets, thereby compensating for their disadvantage in winter.

Surprisingly, neither deciduous nor evergreen trees were able to capitalise fully on the continuous light of the polar summer (Osborne and Beerling 2003). Six weeks of continuous illumination was simply too much of a good thing for photosynthesis, with plants swamped with carbon, and apparently limited by root nitrogen uptake. The result was acclimation of photosynthesis, caused by down-regulation of the enzyme systems used in carbon uptake, and a significant decline in leaf CO_2-uptake rates.

Integrated across the whole year, these distinct differences between winter, spring / autumn, and summer left deciduous and evergreen trees on an equal footing. Net annual primary production was similar across species with different leaf habits, with elevated CO_2 having a positive overall effect (Royer *et al*. 2003). So carbon balance may well be a red herring in the search for explanations about ancient polar forest function. An alternative view is now required, and it could emerge from new studies considering the lifespan (retention time) rather than the habit of leaves.

Leaf lifespan in evergreens varies from a few months in the rapidly cycling canopies of tropical forests, to a decade or more in ancient conifer genera like *Araucaria*. This variation has profound consequences for leaf structure and function – a long-lived leaf must be tough and unpalatable, but the costs of these traits are low protein content, high fibre content, and a correspondingly low photosynthetic rate (Wright *et al*. 2004). These trade-offs have major impacts at the ecosystem scale, slowing carbon exchange, nutrient cycling and evapotranspiration. And now palaeobotany has a new method for glimpsing these in the distant geological past. Falcon-Lang (2000) recently discovered that the lifespan of leaves is recorded in the anatomical properties of their wood. His technique remains in its infancy, but is being developed and applied to fossil woods by palaeobotanists Melise Harland and Jane Francis at the University of Leeds. Their reconstructions of leaf lifespan using Arctic and Antarctic fossil wood fragments may help piece together the workings of these extinct forests, giving us fresh insight into their carbon, nutrient and water relations. This approach signals a paradigm shift in the way we think about polar forests and, in time, may offer a new world view on the adaptive role of leaf lifespan and habit.

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