

Early Holocene Atmospheric CO₂ Concentrations

Wagner *et al.* (1) present a high-resolution record of leaf stomatal index (SI), from which they reconstruct the concentration of atmospheric CO₂ in the early Holocene (10,070 to 9,380 ¹⁴C-yr BP, 11,300 to 10,600 cal yr BP) (1, 2). The resulting record shows a CO₂ concentration of about 270 ppmv at 11,300 yr BP, a sharp increase to about 330 ppmv at 11,260 yr BP, and (with the exception of a dip to 300 ppmv at about 11 kyr BP) a rather constant CO₂ concentration at the high level of about 330 ppmv over the next 500 years.

Wagner *et al.* correctly state that the CO₂ record from the ice core of Taylor Dome (3, 4)—to date considered the most reliable and precise reconstruction of atmospheric CO₂ over the Holocene—has a low temporal resolution in the discussed time interval. There are, nevertheless, at least three overlapping data points (depending on the accuracy of the synchronization) from the Taylor Dome record that show CO₂ concentrations between 260 to 270 ppmv (60 to 80 ppmv lower than those suggested by Wagner *et al.*) (see Fig. 1). The elevated CO₂ concentrations of the SI-based CO₂ record are not found in the ice core record.

Ice-core CO₂ measurements are direct measurements on air that has been enclosed in bubbles. The occurrence of artefacts in earlier ice core records mainly from Greenland drill sites [enrichment of CO₂ due to chemical reactions in the ice; depletion of CO₂ due to fractionation during clathrate formation (5)] can be avoided by careful sample selection. In the Taylor Dome ice core we found no indications of chemical reactions producing additional CO₂, and no clathrates occur (3). This record clearly shows that an atmospheric CO₂ concentration from 260 to

280 ppmv was the rule during the preindustrial Holocene, including the early Holocene. We do not want to question the SI method, but we notice that there is a fundamental discrepancy between the record of Wagner *et al.* and the stomata density-based CO₂ record of Beerling *et al.* (6), who report largely scattering proxy CO₂ values from 225 to 310 ppmv between 9940 and 9600 ¹⁴C-yr.

Wagner *et al.* claim that the concept of relatively stable Holocene CO₂ concentrations of 270 to 280 ppmv until the Industrial Revolution is falsified by their results. We believe that this conclusion is not justified.

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References and Notes

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2. The preliminary age scale has been obtained with the use of the published ¹⁴C fixpoints that have been calibrated with Calib 4.1 software and the INTCAL98 calibration curve [M. Stuiver *et al.*, *Radiocarbon* **40**, 1041 (1998)], and interpolated with a cubic smoothing spline.

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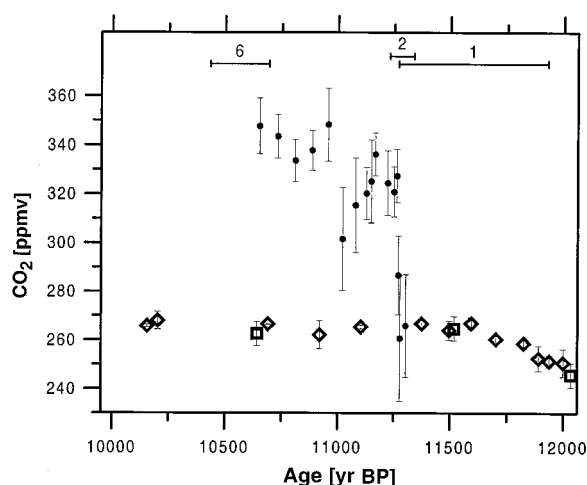
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Wagner *et al.* (1) report early Holocene (10,070 to 9,380 ¹⁴C yr BP) CO₂ concentrations—reconstructed from the stomatal index (SI) of fossil *Betula pubescens* and *B. pendula* leaves—of ca. 260 ppmv rising rapidly to values of around 330 to 340 ppmv, with one sample dipping to ca. 300 ppmv. These values conflict with previous CO₂ reconstructions that used stomatal density (SD) of fossil *Salix herbacea* leaves (2, 3), and with direct ice-core measurements from Taylor Dome (4) and other Antarctic ice cores (5). All of these data-sets are consistent with atmospheric CO₂ levels reconstructed or measured at ca. 260 to 280 ppmv over this time period.

Wagner *et al.* used a modern calibration set relating SI of leaves from one *Betula pendula* tree preserved over the recent (1952–1995) CO₂ rise from 312 to 360 ppmv (6), supplemented by some older herbarium and field material of *B. pubescens*. The reconstructed CO₂ values appear to have been made by comparison with the regression line through the calibration set, involving its extrapolation to SI values above those in the calibration set. The reconstruction should instead have been performed by inverse regression (7) of the calibration set, where CO₂ concentration is modeled as a function of SI for reconstruction purposes (8). Inverse regression has several important statistical properties (9), including minimizing the root mean squared error of prediction.

We also question whether the calibration set of Wagner *et al.* is of general applicability to *Betula pendula* and *B. pubescens* in the early Holocene. We have made SI measurements following Wagner *et al.*'s procedure on *Betula pubescens* leaves collected from 20 to 1100 m above sea level in southern Norway covering a pCO₂ gradient of 36.5 to 31.6 Pa, and from 37 herbarium specimens collected below 500 m above sea level in Norway and Finland between 1877 and 1978, corresponding to a range of atmospheric CO₂ levels of 290 to 335 ppmv. There was no statistically significant relationship of SI against CO₂ in the historical data-set, suggesting that genotype, environment, and perhaps the location of the trees have a greater influence on SI than pCO₂. The stomatal index in the altitudinal data-set increased significantly with altitude, but largely as a result of a slight, insignificant, decrease in SD and

Top: One sigma-calibrated age ranges for the ¹⁴C control points 1, 2 and 6 as an indicator of the possible age range of the CO₂ record reconstructed from stomatal frequency. The labels are the same as in Wagner *et al.* (1). **Center and Bottom:** Atmospheric CO₂ concentration reconstructed from stomatal index (●) (1) and direct measurements of CO₂ concentration of air enclosed in bubbles in the ice cores from Taylor Dome (◊) (3, 4) and Vostok (□) (7, 8).



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a large decrease in epidermal cell density (SI = SD × 100/SD + ED), such that epidermal cell density accounted for 76% of the variation in SI. These results suggest that SI varies more with individual genotype and habitat factors than with CO₂ concentration. A calibration set based largely on measurements from one tree growing on a peat bog may be misleading, and SI of *B. pubescens* and *B. pendula* is not sufficiently related to CO₂ concentration to allow reliable CO₂ reconstructions from fossil leaves of mixed origin.

Wagner *et al.*'s conclusion that "during the early Holocene, atmospheric CO₂ concentrations that were >300 ppmv could have been the rule rather than the exception" conflicts with other independent measurements or estimates of CO₂ concentrations (2–5). This anomaly may result from the deficiencies in their modern calibration set and the great variability in SI, SD, and epidermal cell density among *Betula* trees.

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Response: The comments by Birks *et al.* misrepresent our interpretation of stomatal index (SI) changes in *Betula* leaves in terms of changes in atmospheric CO₂ concentration (1, 2). A principal argument seems to be based on the observation that SI values for *B. pubescens* leaves collected in Norway and Finland do not match the historical relation between mean SI and CO₂ as reconstructed in the Netherlands.

In order to determine the rate of historical responsiveness to atmospheric levels of CO₂, it is essential to use high-resolution SI data that (i) have not been significantly affected by influences of environmental conditions other than CO₂ values, and (ii) that can be

calibrated against the (1958–present) Mauna Loa record of increases of atmospheric CO₂ levels. Because of generally low temporal resolution and insufficient environmental information, herbarium data are not necessarily reliable. For our calibration, we therefore relied primarily on the near-annual record of leaves in currently accumulating peat that can be linked to individual trees or populations (2). Through consistent harvest of modern leaves, calibration is annually updated.

The herbarium-based SI data from Norway and Finland have a low temporal resolution. The period of Mauna Loa monitoring is under-represented. More importantly, the effect of latitude on SI values may not have been taken into consideration. A systematic study of modern *Betula* leaves along a north-south transect from northern Scandinavia to the Netherlands has confirmed the dependence of SI values on progressively changing photoperiods (3). Mean differences in SI values can reach 3%. In CO₂ estimates, such differences would constitute a 50 ppmv discrepancy. The most sensitive geographic ranges are latitudes between 55 and 70N. Consequently, in contrast to the latitudinally restricted data from the Netherlands, herbarium data combining random localities in Scandinavia could well have been influenced by the relation between SI and photoperiod. In any event, it is obvious that response curves have to be separately established for latitudinally contrasting regions. Our ongoing studies in Finland corroborate the applicability of *Betula* leaves from high-latitude peat deposits in correlating SI data with increasing CO₂ levels. In contrast to the suggestion of Birks *et al.*, stomatal frequency analysis of genetically controlled material (*B. pubescens*, *B. pendula*, *B. nana*, and related hybrids) indicates that mean SI patterns are hardly influenced by genotypic variability (4).

The comment on statistics makes a point that may be technically justified, but does not invalidate any of the conclusions of our report. In our reconstruction of CO₂ concentrations, we experimented with both classical and inverse regression analysis. As can be expected, there is no conflict between the two techniques when mean SI values for fossil leaves correspond to modern values that have been calibrated against the Mauna Loa record. Only the CO₂ estimates for our earliest data points had to be used on extrapolation, under the assumption (not yet validated by controlled-environment experiments) that the high SI values still reflect the linear part of a sigmoid stomatal frequency response to changes in atmospheric CO₂ levels. Within comparable uncertainty limits, the two techniques result in a 15 to 20 ppmv difference in the estimated CO₂ concentration. In order to facilitate comparisons with the Antarctic

ice core measurements, we have preferred the lower estimates (260 ppmv) derived from classical regression analysis.

Both Birks *et al.* and Indermühle *et al.* note that our results conflict with previous estimates of atmospheric CO₂ levels based on stomatal frequency data for *Salix herbacea* (5). However, apart from the fact that the applied training set includes field and herbarium material from altitudinally and latitudinally contrasting growth areas in Scandinavia, the United Kingdom, and Austria, stomatal frequency analysis of *S. herbacea* was restricted to SD measurements. It should be noted that SI values constitute a much more sensitive proxy for detecting changes in atmospheric CO₂ levels (6). SI values express stomatal frequency changes independently of variation in epidermal cell size, and are therefore less influenced by environmental factors other than CO₂ levels.

We realize that our results cannot be reconciled with the ice-core records from Antarctica. Although the time-correlation is not necessarily correct, the figure composed by Indermühle *et al.* (figure 1) illustrates that some of the Taylor Dome data points would correspond to our Preboreal record. We have no explanation for the discrepancy. The early Holocene CO₂ trend has also been detected in a record of *Betula* leaves from Denmark where, in addition to the Preboreal Oscillation, younger cooling events at 7.2, 3.4, and 2.5 kyr also correlate with lowered CO₂ concentrations (7). We believe that these preliminary results, in combination with the consistent replication of the familiar CO₂ increase after the Industrial Revolution, provide ever-increasing evidence for the integrity of leaf-based CO₂ quantification.

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