Stomatal evidence for a decline in atmospheric CO$_2$ concentration during the Younger Dryas stadial: a comparison with Antarctic ice core records

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ABSTRACT: A recent high-resolution record of Late-glacial CO$_2$ change from Dome Concordia in Antarctica reveals a trend of increasing CO$_2$ across the Younger Dryas stadial (GS-1). These results are in good agreement with previous Antarctic ice-core records. However, they contrast markedly with a proxy CO$_2$ record based on the stomatal approach to CO$_2$ reconstruction, which records a ca. 70 ppm mean CO$_2$ decline at the onset of GS-1. To address these apparent discrepancies we tested the validity of the stomatal-based CO$_2$ reconstructions from Kr˚akenes by obtaining further proxy CO$_2$ records based on a similar approach using fossil leaves from two independent lakes in Atlantic Canada. Our Late-glacial CO$_2$ reconstructions reveal an abrupt ca. 77 ppm decrease in atmospheric CO$_2$ at the onset of the Younger Dryas stadial, which lagged climatic cooling by ca. 130 yr. Furthermore, the trends recorded in the most accurate high-resolution ice-core record of CO$_2$, from Dome Concordia, can be reproduced from our stomatal-based CO$_2$ records, when time-averaged by the mean age distribution of air contained within Dome Concordia ice (200 to 550 yr). If correct, our results indicate an abrupt drawdown of atmospheric CO$_2$ within two centuries at the onset of GS-1, suggesting that some re-evaluation of the behaviour of atmospheric CO$_2$ sinks and sources during times of rapid climatic change, such as the Late-glacial, may be required.

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KEYWORDS: atmospheric carbon dioxide concentration; stomatal density; Younger Dryas; Atlantic Canada.

Introduction

Understanding how atmospheric CO$_2$ concentrations fluctuated during episodes of abrupt environmental changes, particularly those characterising the Late-glacial (ca. 14 000 to 10 000 yr BP), has important implications for our ability to predict future climatic responses and potential feedback to anthropogenic increases in CO$_2$. A recent high-resolution ice-core record from Dome Concordia in Antarctica demonstrates that the atmospheric CO$_2$ concentration increased by 76 ppm in four incremental steps between the Last Glacial Maximum (ca. 18 000 yr BP) and the early Holocene (ca. 11 000 yr BP) (Monnin et al., 2001). Moreover, a trend of gradually rising CO$_2$ from 237 ppm to 259 ppm was recorded by these authors across the Younger Dryas stadial (now referred to as Greenland Stadial 1 or GS-1, Björck et al., 1998), an event which marks an abrupt return to near-glacial conditions in the North Atlantic between 12 900 and 11 500 yr BP. These results are in good agreement with the general trends in atmospheric CO$_2$ recorded in existing Antarctic ice-cores from Byrd (Neftel et al., 1988) and Vostok (Barnola et al., 1987). However, they contrast markedly with the pattern of CO$_2$ change and absolute concentrations reconstructed over the same interval from changes in leaf macrofossil stomatal density (Beerling et al., 1995). This stomatal-based record from Kr˚akenes in Norway (Beerling et al., 1995) shows a significant and rapid decline in atmospheric CO$_2$ from median values of 273 to 210 ppm at the onset of GS-1. Clearly, as CO$_2$ records from three Antarctic ice-cores are in good agreement in terms of the general trend of CO$_2$ change over this important interval, further investigation of the trends derived using the stomatal approach to atmospheric CO$_2$ reconstructions is required.

The stomatal approach to estimating palaeo-CO$_2$ levels relies on a well-established inverse relationship between
atmospheric CO₂ concentration and stomatal frequency of terrestrial leaves of many C3 species (Woodward, 1987). Stomatal frequency of some species, however, particularly grasses and C4 plants, are insensitive to changes in CO₂ concentration (Raven and Ramsdien, 1989; Praet and Jiang, 1995). For those species that are CO₂ sensitive, an inverse relationship between CO₂ concentration and stomatal frequency has been demonstrated on time-scales of weeks (Woodward and Bazzaz, 1988), years (Beerling et al., 1998), centuries (Woodward, 1987; Beerling and Chaloner, 1993; Wagner et al., 1996, 1999) and millennia (McElwain et al., 1995; Rundgren and Beerling, 1999). Furthermore, a genetic basis for the response is provided by the recent identification of a CO₂ sensitive gene in Arabidopsis thalia that is involved in the control of stomatal development from epidermal cell initials (Gray et al., 2000). The robustness of this proxy-CO₂ method is further supported by a high-resolution stomatal-based CO₂ reconstruction spanning the Holocene (Rundgren and Beerling, 1999), which demonstrates almost identical trends in atmospheric CO₂ change through the Holocene as those measured from Taylor Dome (Indermühle et al., 1999). The striking similarity in the general trends of CO₂ change spanning the Holocene reconstructed from stomatal-based and ice-core methods highlights the need to investigate further their apparent differences during the Late-glacial period.

Here we present two new Late-glacial stomatal-based CO₂ records from different lake sites in Atlantic Canada and critically compare them with existing ice-core and stomatal-based records to address these apparent discrepancies between proxy and ice-core CO₂ records. The accuracy of Late-glacial CO₂ records from Byrd in Antarctica (Neftel et al., 1988) have been questioned recently, however, owing to a large scatter of data during GS-1 (of up to 30 ppm) (see fig. 2 in Blunier et al., 1997) and in the early Holocene (of >30 ppm) (Indermühle et al., 1999; Marchal et al., 1999). Because these effects may reflect contamination within the ice, we have confined comparison of our data to CO₂ records from Dome Concordia, which are currently considered the most accurate high-resolution reconstructions available for the Late-glacial (Monnin et al., 2001). Similarly, although CO₂ reconstructions from Vostok and Taylor Dome are also considered accurate and reliable, only six measurements are available between 16000 and 10000 yr BP in the case of the former (Barnola et al., 1987) with no records available across GS-1 in the case of the latter (Indermühle et al., 1999).

High-resolution (ca. 20 to 37 calendar yr) proxy-CO₂ records were determined from stomatal frequencies of subfossil leaves of Dryas integrifolia, Picea mariana, P. glauca and Larix laricina obtained from sediment cores from Splan Pond and Pine Ridge Pond. The proxy-CO₂ record from Pine Ridge Pond was compared with a chironomid-derived terrestrial temperature record (Walker et al., 1992; Levesque et al., 1994) from the same core in order to investigate the phase relationship between CO₂ and temperature change on a centennial time-scale during GS-1. This was undertaken because, despite important advances in synchronisation of Arctic and Antarctic CO₂ temperature records using atmospheric methane (Blunier et al., 1997; Blunier and Brook, 2001) and molecular O₂ (Sowers and Bender, 1995), the error associated with the gas age and ice age difference in Dome Concordia (±200 to ±550 yr; Monnin et al., 2001) makes it difficult to assess the phase relationships between temperature and CO₂ on centennial time-scales. This critically hampers our understanding of the cause and effect underpinning rapid climatic fluctuations.

**Locality information**

Pine Ridge Pond (45°34’N, 67°06’W) and Splan Pond (45°15’20”N, 67°19’50”W) are located in New Brunswick, Atlantic Canada (Fig. 1). Pine Ridge Pond is 100 m in diameter and situated within the Saint Croix Highlands at an elevation of 90 m, within the Appalachian physiographic region (Levesque et al., 1994); Splan Pond is ca. 4 ha in area, 106 m in elevation, and is located 7.2 km north-west of St Stephen, New Brunswick (Mayle and Cwynar, 1995). Both sites have AMS 14C-based chronologies (Mayle et al., 1993).

**Methods**

**Calculation of stomatal frequency**

Stomatal frequency of Angiosperm leaves is conventionally expressed in terms of stomatal density (SD), the number of stomata per mm² leaf area, and stomatal index (SI), the proportion of stomata expressed as a percentage of epidermal cells. The arrangement of stomata into rows or bands parallel to the long axis in our three conifer species (P. mariana, P. glauca and L. laricina) prevented assessment of stomatal frequency based on area (i.e. SD and SI). Instead, stomatal frequency was calculated from the sum of the mean abaxial and adaxial number of stomata per 1 mm row length (SNL, stomatal number per length) in the case of L. laricina. In the case of P. mariana and P. glauca the abaxial surface SNL was calculated and multiplied by the mean number of stomatal rows per leaf (SDL, stomatal density per length). Stomatal frequency in D. integrifolia was measured conventionally by calculating the stomatal density on the abaxial leaf surface (see McElwain et al. (1995) and Poole and Kürschner (1999) for details on methods). Stomata were observed and counted using a Leica epifluorescence microscope (×400 magnification) within a 0.189 mm² gridtulc. The stomata of all three conifer species were counted using a Leica epifluorescence microscope (×200 magnification) along the length of a calibrated 0.8 mm scale bar.

![Figure 1 Site map showing the locations of Pine Ridge Pond, Splan Pond and Mayflower Lake in Atlantic Canada](image-url)
Sources of historical leaf material

Leaf material was obtained from herbarium sheets from the Royal Botanical Gardens Kew of *L. laricina* (collected between 1822 and 1964), *P. mariana* (1875–1999), *P. glauca* (1851–1992) and *D. integrifolia* (1766–1988). In the case of *Picea*, both *P. mariana* and *P. glauca* were incorporated into a single training set as both species showed similar SDL response rates to CO$_2$. Herbarium material for all four species represented in the lake sediment cores was chosen from a wide range of localities in northern USA and Canada, within the individual species natural climatic ranges and tolerances, so as to minimise the potential effects of other biological and environmental factors on stomatal density. Herbarium leaves of cultivated trees from Scotland, North America and England were also included in the calibration data sets as no significant differences in stomatal frequencies were observed between cultivated and naturally growing trees collected in the same year and which had therefore grown in the same CO$_2$ concentration. Leaf material from herbarium sheets collected from high elevations was not included in the calibration data sets in order to avoid the effects of decreased CO$_2$ partial pressure with increasing elevation on stomatal frequency.

Calibration of historical data sets

Species- and genus-specific responses of stomatal frequency (i.e. SD, SNL and SDL) to atmospheric CO$_2$ concentration were determined by calibrating historical stomatal frequency data obtained from herbarium sheets from the Royal Botanical Gardens Kew against the historically recorded CO$_2$ concentrations at the time of growth (Neftel et al., 1988; Keeling and Whorf, 2000). Mean stomatal frequency (SD, SNL and SDL) of two to ten observations per leaf was regressed against CO$_2$ concentration in which the leaf developed. In cases where more than one leaf was available for the same CO$_2$ concentration a mean stomatal frequency from three to six leaves was obtained, each with two to ten observations per leaf (i.e. *Dryas* and *Picea*). A total of 79 *D. integrifolia* leaves, 62 *Picea* and 30 *Larix* needles were utilised for the calibration data sets. Inherent variability within stomatal density caused by factors such as light intensity, temperature and water availability, although minimal compared with the effect of CO$_2$ concentration, are all accounted for within the 90% confidence limits of the regression equations (Fig. 2).

Calculating CO$_2$ concentration from stomatal frequency

Changes in atmospheric CO$_2$ concentration ($\hat{x}$) during GS-1 were determined from stomatal frequencies ($y'$ = SD, SDL or SNL) of subfossil leaves of *Dryas integrifolia*, *Picea mariana*, *P. glauca* and *Larix laricina* preserved in Pine Ridge Pond and Splan Pond (Tables 1 and 2). Intrinsic variation in stomatal frequency within and among leaves/needles was calculated from means of three leaves/needles per tree/shrub and five to ten areas per leaf. A total of 119 and 130 leaves were investigated from Pine Ridge Pond and Splan Pond respectively. Subfossil stomatal frequency records were calibrated against taxon-specific historic training sets (Fig. 2) using inverse regression analysis (Draper and Smith, 1981) according to $\hat{x} = \frac{335.4 - y'(SDL)}{0.795}$ for *Picea* spp., $\hat{x} = \frac{0.252}{55990885.4}$ for *Larix laricina* and $\hat{x} = \frac{y' - \overline{y}}{b(1 - g)} \pm \frac{ts}{b(1 - g)} \frac{\sqrt{(1 - g)^2 + (1 - g)^2} + (y' - \overline{y})^2}{b^2SS_x}$ for *Dryas integrifolia*. Where two species occurred together at the same depth, a mean predicted CO$_2$ concentration was obtained. Confidence limits for the predicted CO$_2$ concentration were calculated by applying the following formula (adapted by P. Mitchell from Draper and Smith (1981)) for inverse confidence limits

$$\hat{x} = \frac{y' - \overline{y}}{b(1 - g)} \pm \frac{ts}{b(1 - g)} \frac{\sqrt{(1 - g)^2 + (1 - g)^2} + (y' - \overline{y})^2}{b^2SS_x}$$

where $\hat{x}$ and $\overline{y}$ are the mean CO$_2$ concentration and stomatal frequency respectively of the taxon-specific historical data set (Fig. 2), $y'$ (SD, SDL or SNL) is the subfossil stomatal frequency, $t$ is Student’s $t$ for $(n - 2)$, $b$ is the slope, $SS_x$ is the sum-of-squares of $x$, $g = \frac{t^2}{SS_x}$, $s^2$ is the residual mean square, $m$ is the total number of leaf samples per depth and $n$ is the
sum of observations on all leaves per depth. In the case of *D. integrifolia*, the slope \(b\) was calculated according to
\[
b = \frac{1}{\sqrt{\frac{55990885.4}{(SD + 123.9)^2}}}
\]

However, as no single species spans the entire Late-glacial period (Levesque *et al.*, 1994; Mayle and Cwynar, 1995), the resultant CO₂ reconstructions for both ponds (Fig. 3) are composites of several species CO₂ records; the Late-glacial interstadial (Greenland Interstadial-1, GI-1, Björck *et al.*, 1998), Younger Dryas (GS-1) and early Holocene records being predominantly derived from stomatal frequencies of Picea, *Dryas integrifolia* and *Larix laricina* respectively. This approach is justified by the observation that the training sets of each species respond in the same direction and by a similar rate to CO₂ concentration (Fig. 2), and where species-specific estimates overlap, both yield closely matching CO₂ values.

The phase relationship between CO₂ concentration and GS-1 temperature change was determined by comparison between maxima and minima in the Pine Ridge Pond atmospheric CO₂ curve with those from a previous independently derived chironomid (midge)-based water temperature reconstruction (Levesque *et al.*, 1994, 1997) from the same sediment core (Fig. 3).
The reconstructed CO2 record from Splan Pond mirrors that of both CO2 and temperature records over this time interval (ca. 3 cm) is significantly higher than the observed lag and temperature reconstructions and CO2 records were derived from separate cores. Consequently, the errors associated with correlation of these separate cores (ca. 3 cm) was too large (Tables 1 and 2).

## Discussion

Late-glacial CO2 records from both Pine Ridge Pond and Splan Pond show three distinctive features that contrast markedly with Antarctic CO2 records from Dome Concordia (Monnin et al., 2001). They indicate that: (i) CO2 concentrations were higher than typical interglacial levels (i.e. 280 ppm, Petit et al., 1999); and (ii) a rapid increase in CO2 from near-glacial
to higher than full interglacial levels occurred during the transition from GS-1 into the early Holocene. A trend of marked reduction from high GI-1 CO₂ concentration to near-glacial CO₂ levels during GS-1 is in good general agreement with a stomatal-based record from a site in Norway (Kråkenes) (Beerling et al., 1995), which shows a reduction in GI-1 CO₂ concentration from median values of 273 ppm to 210 ppm during GS-1. These records differ somewhat in the timing of CO₂ decline during the transition from GI-1 into GS-1; in Kråkenes, the CO₂ decline precedes the temperature fall into the Younger Dryas. The stomatal-based CO₂ reconstructions also differ somewhat in the general trend of CO₂ change throughout GS-1. A gradual increase in CO₂ is recorded throughout GS-1 in Kråkenes, whereas an abrupt increase in CO₂ is recorded in both Pine Ridge Pond and Splan Pond at the termination of GS-1. Some of these differences may be attributed to somewhat lower sampling resolution in the CO₂ record from Kråkenes, which has a mean sample resolution of ca. 88 calendar yr, with significant temporal gaps of >150 calendar yr. The differences in the timing of Late-glacial CO₂ change in relation to that of temperature between both stomatal-based CO₂ records highlight the need for further investigation of atmospheric CO₂ dynamics during this important interval. The importance of all three independent CO₂ records from Kråkenes (Beerling et al., 1995), Pine Ridge Pond and Splan Pond is clearly that they show a consistent pattern of atmospheric CO₂ decline during the transition from GI-1 to GS-1—a feature not yet detected in ice-core records.

As the Late-glacial interstadial (GI-1a) CO₂ reconstructions for both Splan and Pine Ridge ponds were based on small leaf sample sizes (n < 3), further investigation was carried out on nearby AMS 14C dated Mayflower Lake (Fig. 1) (Mayle and Cwynar, 1995), which contains abundant Picea macrofossils within GI-1a sediments. Stomatal analysis of 27 subfossil Picea leaves sampled over 6 cm in this lake revealed a GI-1a CO₂ concentration of 309 ± 6 ppm, confirming that GI-1a CO₂ concentrations were approximately 60 to 70 ppm higher than estimated from Antarctic ice-core reconstructions (Neftel et al., 1988; Monnin et al., 2001).

By the early Holocene, both ice-core measurements (Byrd, 269 ± 4 ppm (Neftel et al., 1988); Taylor Dome, 268 ppm (Indermühle et al., 1999); and Dome Concordia, 265 ppm (Monnin et al., 2001)) and stomatal-based CO₂ reconstructions (Splan Pond, 298 ± 2 ppm; Pine Ridge Pond, 286 ± 16 ppm; Kråkenes, Norway, 275 ± 20 ppm (Beerling et al., 1995); Borchert, Holland, 310 ± 26 ppm (Wagner et al., 1999)) are in good agreement in terms of the direction of CO₂ change. However, CO₂ estimates based on stomatal frequency changes appear systematically higher by a minimum of ca. 10 ppm (Beerling et al., 1995) to a maximum of ca. 40 ppm (Wagner et al., 1999) at this time. The interhemispheric difference in atmospheric CO₂ concentration (ca. 3 ppm) is too small to account for the significant offset between ice-core and stomatal-based records, suggesting that further investigation of the potential mitigating factors in both records are required to reconcile their differences. If ice-core records of Late-glacial CO₂ change are secure, then CO₂ reconstructions from stomatal frequency data appear to consistently underestimate CO₂ levels during the stadials and overestimate them during interstadials, regardless of different reproductive biologies (i.e. in gymnosperms and angiosperms) and functional types (i.e. arctic alpine shrubs and trees). The effect could, in part, be a result of the transfer functions utilised to predict CO₂ concentrations from past changes in stomatal frequency or the mitigating effects of as yet undetermined environmental variables other than CO₂ on stomatal frequency. The consistent discrepancies between ice-core and stomatal-based reconstructions of atmospheric CO₂ change therefore clearly merit further detailed investigation.

Both cold temperatures and/or increased water stress could potentially have reduced epidermal cell expansion in the leaves of Dryas integrifolia during GS-1, resulting in the observed high stomatal densities and predicted low CO₂ concentrations during this stadial (Tables 1 and 2). Calculation of stomatal indices would remove the effects of these factors on stomatal density. However, owing to the hirsute nature of Dryas integrifolia leaves, it was not possible to view the epidermal cell outlines unambiguously, so stomatal index could not be calculated. We note, however, that herbarium samples of D. integrifolia analysed for the historical training set were all derived from tundra type habitats with an arctic climate and would therefore have experienced similar temperature and water regimes during growth to those prevailing in New Brunswick during GS-1. Therefore, although reduced temperatures and precipitation may have exerted some effect on stomatal density, we believe the overriding control over the stomatal densities was CO₂ concentration during GS-1. This inference is supported by experimental observations indicating that CO₂ exerts a significantly greater effect on stomatal density and index than artificially manipulated fluctuations in temperature and humidity regimes (Beerling and Woodward, 1996; Kürschner et al., 1998).

According to Tschumi and Stauffer (2000) and Indermühle et al. (1999), a small amount of in situ CO₂ production, although considerably less likely than in Greenland ice-core records (Anklin et al., 1997), cannot be excluded as a possible source of error for all Antarctic ice cores or all climatic periods. Chemical impurities in ice, such as organic compounds and carbonates (indicated by Ca²⁺ levels), have been shown under certain conditions to result in in situ CO₂ production via oxidation and decarbonation reactions respectively (Smith et al., 1997; Tschumi and Stauffer, 2000). In situ CO₂ depletion reactions can also occur within ice (Smith et al., 1997), however, the chemistry associated with these reactions are currently not well understood. It has been suggested that the wide scatter of CO₂ estimates from closely spaced air bubbles in Byrd ice during the early Holocene (between 10 000 and 7000 yr BP) and during GS-1 may result from such in situ chemical reactions (Indermühle et al., 1999; Marchal et al., 1999). No evidence for such reactions has been recorded in Dome Concordia ice (Monnin et al., 2001), suggesting that chemical impurities cannot account for the discrepancies between stomatal-based and Dome Concordia ice CO₂ estimates spanning the Late-glacial.

Differences in temporal resolution may be implicated in the discrepancies between our stomatal-based CO₂ trends and Antarctic ice-core measurements. Owing to the length of time it takes for an air bubble to be enclosed within Dome Concordia ice (200 to 550 yr, Monnin et al., 2001), CO₂ measurements at each interval record a time-averaged sample of 200 to 550 yr. To test for this possibility, we have time-averaged our CO₂ records from both Splan Pond and Pine Ridge Pond by 550 yr, taken as the maximum estimated pre-Holocene age distribution of air in Dome Concordia (Fig. 4). We assume a constant sedimentation rate spanning the entire interval, where 1 cm is equivalent to 20 calendar yr (Splan) and 37 calendar yr (Pine Ridge) respectively based on the age–depth relationships (Mayle et al., 1993). A mean sample resolution was calculated for each locality to estimate the number of data points to be included in a running mean for each pond. In the case of Pine Ridge Pond, which possessed an average sampling resolution of 61 yr, a simple non-weighted average CO₂ concentration starting with the oldest was calculated from the next nine...
data points (= ca. 550 yr). The same exercise was repeated for Splan Pond, which possessed an average sampling resolution of 58 calendar yr. No interpolation was undertaken between individual data points. This analysis revealed a general rising trend in CO₂ concentration from ca. 245 ppm to ca. 300 ppm spanning GS-1 in Splan Pond, which mirror the trend of CO₂ increase from 230 to 275 ppm observed in Dome Concordia ice (Fig. 4).

In Pine Ridge Pond, however, although the marked CO₂ decline into GS-1 is removed by simple time averaging, the gradual trend of increase is not observed. If Dome Concordia ice is accurately recording a smoothed CO₂ signal during the Late-glacial, this suggests that the Splan Pond CO₂ record is more reliable in the latter half of GS-1 than that of Pine Ridge Pond, which shows greater amplitude fluctuations in CO₂. This gradual rising trend in CO₂ is lost in Splan Pond, however, when the time-average interval is reduced to less than 400 yr, at which point a significant reduction in atmospheric CO₂ during GS-1 re-emerges from the stomatal-based data. Consequently, based on this analysis, and our inference that a reduction in CO₂ concentration during GS-1 was the most plausible forcing factor for increased stomatal density of Dryas integrifolia leaves, we suggest that the stomatal records (which effectively capture a CO₂ signal from a single growth season) may represent a higher resolution record of CO₂ change over this interval than that recorded in Dome Concordia ice. The fact that atmospheric methane measurements from ice cores in general are much less susceptible to in situ reactions and can be undertaken on a smaller volume of ice than required for atmospheric CO₂ measurements helps explain why the methane records from Dome Concordia are apparently less smoothed than those of atmospheric CO₂ spanning GS-1.

A reduction in atmospheric CO₂ concentration of the order of ca. 80 ppm within two centuries, as recorded here in both proxy CO₂ records, is consistent in both magnitude and rate of CO₂ decline with predictions from a three-dimensional simulation of the impact of Southern Ocean surface-nutrient depletion (owing to iron fertilisation) on atmospheric CO₂ (Sarmiento and Orr, 1991). This model predicts a 46 to 85 ppm oceanic drawdown of CO₂ within 100 yr under such a scenario. Similarly our results are consistent with the model predictions of Siegenthaler and Wenk (1984) for a rapid atmospheric CO₂ decline (within a century) in response to the effect of a reduction in thermohaline circulation (THC) on surface water chemical properties, such as that which occurred at the onset of GS-1 (Broecker et al., 1985). Other simulations of the impact of a reduction in thermohaline circulation on atmospheric CO₂ predict a small net increase in CO₂ (Marchal et al., 1998) qualitatively similar to that recorded in Dome Concordia spanning GS-1. It is interesting to note, however, that a sensitivity analysis of this model (Marchal et al., 1998) predicts a rapid and marked (ca. 60 ppm) CO₂ decline at the onset of GS-1, similar to that identified by all three stomatal-based CO₂ reconstructions (Pine Ridge, Splan and Kråkenes), when biological cycling (determined by the rates of production versus oxidation of organic matter and the rate of production versus dissolution of CaCO₃ in the oceans) is kept constant.

Our observation that atmospheric CO₂ decreased at the onset of GS-1, and that CO₂ change may have lagged rather than led GS-1 cooling, have important implications for our understanding of the role of atmospheric CO₂ in rapid climatic events. The temporal relationship between CO₂ and temperature demonstrated here on submillennial time-scales mirrors that observed over the longer term millennial time-scales of full-glacial–interglacial cycles (Barnola et al., 1987; Petit et al., 1999). The observed phase relationship in Pine Ridge suggests that CO₂ decline was not an initiator of GS-1 cooling but most probably played a significant role in amplifying initial Northern Hemisphere cooling by ca. 1°C globally. Furthermore, owing to the apparent synchronous increase of both temperature and CO₂ at the termination of GS-1, it cannot yet be ruled out that the abrupt ca. 90 ppm CO₂ rise (Fig. 3) may have initiated early Holocene climatic warming.

**Conclusions**

The stomatal records from two independent localities presented here confirm the observation by Beerling et al. (1995) that Late-glacial plant macrofossils apparently record a decline in atmospheric CO₂ concentrations at the onset of the Younger Dryas stadial. However, owing to the differences between all three terrestrial proxy CO₂ records and those of ice cores, further investigation of plant physiological responses are required to address why stomatal based CO₂ estimates appear to
systematically overestimate interglacial (i.e. early Holocene) and interstadial (i.e. GI-1) CO₂ concentrations compared with coeval ice-core measurements. An investigation of fluctuations in macrofossil leaf stomatal frequency from the Southern Hemisphere or tropical latitudes where temperature changes were not as severe should show identical trends to those reported here (Table 1 and 2) from Atlantic Canada, if CO₂ was, as we believe, the main controlling factor throughout the Late-glacial. It is possible that a number of the short-term fluctuations recorded using the stomatal methods cannot be detected in ice cores, such as Dome Concordia, with low ice accumulation rates. According to Neftel et al. (1988), CO₂ fluctuation with a duration of less than twice the bubble enclosure time (equivalent to approximately 134 calendar yr in the case of Byrd ice and up to 550 calendar yr in Dome Concordia) cannot be detected in the ice or reconstructed by deconvolution. The rapid atmospheric CO₂ reduction recorded from stomatal density changes in macrofossil leaves at the onset of GS-1 (within 120 to 185 yr) may therefore have escaped detection in Antarctic-ice records. If our high-resolution records of leaf stomatal fluctuations accurately record changes in atmospheric CO₂, our results indicate that Late-glacial CO₂ change paralleled those of atmospheric CH₄ throughout the Late-glacial interval. Our findings suggest that some re-evaluation of the behaviour of atmospheric CO₂ sinks and sources during times of rapid climatic change, such as the Late-glacial, may therefore be required.

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