Radiocarbon bomb spike reveals biological effects of Antarctic climate change

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Abstract

The Antarctic has experienced major changes in temperature, wind speed and stratospheric ozone levels during the last 50 years. However until recently continental Antarctica appeared to be little impacted by climate warming, thus biological changes were predicted to be relatively slow. Detecting the biological effects of Antarctic climate change has been hindered by the paucity of long-term data sets, particularly for organisms that have been exposed to these changes throughout their lives. We show that radiocarbon signals are preserved along shoots of the dominant Antarctic moss flora and use these to determine accurate growth rates over a period of several decades, allowing us to explore the influence of environmental variables on growth and providing a dramatic demonstration of the effects of climate change. We have generated detailed 50-year growth records for *Ceratodon purpureus* and three other Antarctic moss species using the 1960s radiocarbon bomb spike. Our growth rate and stable carbon isotope ($\delta^{13}C$) data show that *C. purpureus'* growth rates are correlated with key climatic variables, and furthermore that the observed effects of climate variation on growth are mediated through changes in water availability. Our results indicate the timing and balance between warming, high wind speeds and elevated UV fluxes may determine the fate of these mosses and the associated communities that form oases of Antarctic biodiversity.

Introduction

Polar regions, including the maritime and sub-Antarctic and the Arctic, have experienced some of the most rapid and severe climatic shifts over the last century with temperatures increasing by up to 0.5 ˚C per decade (Adams *et al.*, 2009, Anisimov *et al.*, 2007, Turner *et al.*, 2007). In contrast, whilst the Antarctic continent has experienced a pronounced decrease in springtime stratospheric ozone and increases in wind speed (McKenzie *et al.*, 2011, Perlwitz *et al.*, 2008, Son *et al.*, 2010, Turner *et al.*, 2005), until recently, there was little evidence that East Antarctica had experienced significant warming (Chen *et al.*, 2009, Steig *et al.*, 2009b). Biological changes in this region were thus predicted to be relatively slow and difficult to detect (Anisimov *et al.*, 2001). Research published since the last IPCC report (Chen *et al.*, 2009), however, points to mounting evidence of increasing temperatures around the Antarctic continent and highlights the need to assess how terrestrial Antarctic ecosystems are responding (Anisimov *et al.*, 2007). Recent climate-induced changes to terrestrial vegetation and limnetic systems have already been reported in the maritime Antarctic, the sub-Antarctic islands and the Arctic (Anisimov *et al.*, 2007, Day *et al.*, 2009, Day *et al.*, 2008, Forbes *et al.*, 2010, Fowbert & Lewis Smith, 1994, Grobe *et al.*, 1997, Hill & Henry, 2011, Hill *et al.*, 2011, Lantz *et al.*, 2009, Parnikoza *et al.*, 2009, Quayle *et al.*, 2002, Smol & Douglas, 2007, Wilson & Nilsson, 2009).

Oases supporting long-lived plant communities such as those in the Windmill islands of East Antarctica (Melick & Seppelt, 1997) offer a unique window to examine the effects of climate change in continental Antarctica. Antarctic mosses are ideally suited for such

studies since they are the dominant flora in coastal regions and sequester atmospheric carbon isotope signals along their shoots, allowing radiocarbon dating and growth rate analysis. As mosses are non-vascular plants that grow in an incremental fashion from the shoot tip, they retain a record of atmospheric carbon encountered over their photosynthetic lifespan along the length of their shoots. Above ground nuclear testing in the late 1950s and early 1960s resulted in a dramatic increase in atmospheric radiocarbon (^{14}C), known as the ^{14}C 'bomb spike' (Hua & Barbetti, 2004). Our hypothesis was that the atmospheric ^{14}C signal would be faithfully retained along Antarctic moss shoots (gametophytes) as evidenced by the presence of the ^{14}C bomb spike. Whilst methods for radiocarbon dating peat beds are well established, here we sought to trace the ^{14}C signal along intact, living moss shoots, preserved due to the extreme cold in Antarctica. Validation of this method would open up the possibility of tracking changes in moss growth rates over past decades and even centuries and for moss growth rates to be determined in remote and so far unstudied locations. Attempts to measure growth using traditional methods are limited to areas with frequent access and rely on markers being undisturbed by frost heaving and visiting birds (Selkirk & Skotnicki, 2007). A reliable long-term record is required if we are to attribute changes in growth rate to environmental factors.

Measurement of the δ^{13}C signal along the shoot can be used to indicate past changes in water availability. As mosses dehydrate, resistance to CO_2 uptake due to water surrounding the shoot is reduced, increasing the degree to which RuBisCO discriminates against the heavier ^{13}C isotope, resulting in a more negative δ^{13}C (Rice, 2000, Rice &

Giles, 1994). Similarly, photosynthesis decreases as mosses dehydrate, reducing chloroplastic demand for CO_2, further increasing discrimination against ^{13}C and lowering $\delta^{13}C$ (Rice, 2000). A more negative $\delta^{13}C$ would thus be found in mosses growing in drier sites, or closer to the growing shoot tip if moss beds were experiencing a drying climate.

In this study we used a combination of radiocarbon and stable isotope analysis of long gametophytes to answer the questions: (i) Can the ^{14}C bomb spike be used to determine the age and growth rate of Antarctic moss shoots? (ii) Have changes in temperature, wind speed or ozone depth over the last 50 years influenced growth and the availability of water to the East Antarctic moss flora? Linking the growth of these plants to environmental variables provides a rare opportunity to test their sensitivity to current and predicted climate change.

Materials and Methods

Sample collection and AMS ^{14}C analysis

Moss turf 'cores' were collected from five sites in East Antarctica in January 2005 (Table 1; Fig. 1). Four sites were in the Windmill Islands region; two on Clark Peninsula (Antarctic Specially Protected Area (ASPA) 136) and two on Bailey Peninsula (ASPA 135 and Red Shed), each $\leq$ 5 km from Casey. The fifth site was at Grimmia Gorge in the Vestfold Hills. *Ceratodon purpureus* from Clark and ASPA 135 was collected from slopes that receive water from snowmelt for part of the summer growing season. The Red Shed site and the second Clark Peninsula site (Clark 2) were on the edge of large melt lakes and streams, respectively, and are wet throughout the season. Samples at Grimmia

Gorge were both growing in cracks in a rock wall above a melt stream, approximately 1 km from the nearest glacial tongue. Note that permanently wet sites e.g. Red Shed and Clark 2 (*Schistidium antarctici*) will be buffered by water and are likely to remain cold throughout the season whilst sites that dry out are likely to experience more varied temperatures.

A sample of 10-20 adjacent shoots were separated from each core as an intact unit, weighed and cut into 3 mm sections, yielding 14-19 sections per core. It was not feasible to analyse every shoot section due to financial constraints, therefore a number of shoot sections with approximately equal spacing along each shoot core were selected for preliminary ^{14}C analysis to estimate the position of maximum ^{14}C; analysis of additional sections was used to confirm the position of the ^{14}C peak and trace the bomb spike through the shoots at a higher resolution. Due to the tightly packed nature of Antarctic moss turfs (500-900 shoots cm^{-2}, (Wasley *et al.*, 2006)) the growing tips of the adjacent 10-20 shoots were within approximately 0.5 mm of each other, thus we assumed sections from shoots within a core section have similar ages. A total of 69 core sections were analysed for ^{14}C activity (7-18 sections per core). Sections were pre-treated with 2M HCl at 60 ºC for two hours to remove carbonate contamination, converted to graphite and analysed for ^{14}C at the STAR accelerator mass spectrometry (AMS) Facility at ANSTO (Fink *et al.*, 2004, Hua *et al.*, 2001). The typical carbon mass of each section was 0.2-0.5 mg. A subsample of the graphite was analysed for δ^{13}C using a continuous-flow Micromass Elemental Analyzer/Isotope Ratio Mass Spectrometer (EA/IRMS, IsoPrime, Manchester, U.K.) to correct the final ^{14}C value for isotopic fractionation. All ^{14}C data are

reported in percent modern carbon (pMC, Table S1, Stuiver & Polach, 1977). Where no measured $\delta^{13}C$ value was available, pMC was calculated using an assumed $\delta^{13}C$ value of -25‰.

Correction of moss shoot $\delta^{13}C$ for temporal changes in atmospheric $\delta^{13}C$

Shoot $\delta^{13}C$ is influenced by $\delta^{13}C$ of atmospheric CO_2 which has decreased since the 1700s due to emission of ^{13}C-depleted CO_2 from fossil fuels (Francey *et al.*, 1999, Friedli *et al.*, 1986). $\delta^{13}C$ records of atmospheric CO_2 for the period 1953-2001 obtained from firn and ice core samples from Law Dome (Francey *et al.*, 1999), combined with direct atmospheric CO_2 measurements from Mawson (Allison *et al.*, 2003) showed a strong negative linear trend over this period (r=-0.99). We used the equation of a linear regression through the data (P<0.0001) to estimate atmospheric $\delta^{13}C$ for each year. To isolate changes in plant $\delta^{13}C$ due to water availability, shoot section $\delta^{13}C$ was corrected for the atmospheric $\delta^{13}C$ corresponding to the calibrated ^{14}C age for that section, including a multiplication factor of 1.1 to correct for fractionation during C3 photosynthesis (Arens *et al.*, 2000).

Calibration of ^{14}C ages

The maximum ^{14}C concentrations measured in each core (144.5-151.5 pMC; see Fig. 2) were substantially lower than the maximum value of annual atmospheric bomb ^{14}C in the Southern Hemisphere (SH, 163.9 ± 0.4 pMC in 1966, Hua & Barbetti, 2004). As each 3 mm section of the shoot core represents more than a year of growth and contains part of 10-20 shoots with slightly different ages, the ^{14}C content of each section has been

assimilated over a period of more than a year. This integration, related to the growth rate of each core, causes the bomb ^{14}C maxima in shoot cores to become lower, flatter and occur later compared to the annual atmospheric bomb curve. We assumed that this integration of atmospheric ^{14}C in the moss shoots could be expressed as a Gaussian curve with a shoot-specific time width τ (sigma value) as per Goslar *et al.* (2005). We then calculated the degree of integration required to obtain the bomb ^{14}C maxima observed in each core by varying τ, using our reconstructed annual atmospheric ^{14}C for the SH for the period 1920-2005. Annual atmospheric ^{14}C was reconstructed using (1) ^{14}C data in annual tree rings from the Washington State, USA for the pre-bomb period (1920-1954, Stuiver *et al.*, 1998). Note that no such data are available for the SH. Moreover, there is negligible difference between decadal SH tree ring ^{14}C and that from the Northern Hemisphere for the above period, with a weighted average difference of 0.7 ± 0.9 ‰ (McCormac *et al.*, 2004, Reimer *et al.*, 2004a); (2) Updated annual atmospheric ^{14}C data for the SH for 1955-2002 of Hua and Barbetti (2004) averaged over November-February, when the majority of photosynthesis occurs in mosses from the Windmill Islands (Melick & Seppelt, 1997); and (3) beyond 2002, the data were obtained by extrapolation of the above SH bomb data using an exponential function as per Goslar *et al.* (2005). We finally reconstructed a SH calibration curve for each core corresponding to its τ-value of integration. These calibration curves were used in conjunction with the CaliBomb program (Reimer *et al.*, 2004b) to determine the calibrated age of core sections. As bomb ^{14}C delivers two possible calendar ages, likely calibrated age ranges for each moss core section were selected on the basis of their position relative to the maximum ^{14}C activity in the core. The calibrated age of core sections with 2σ uncertainty together with our

reconstructed annual atmospheric ^{14}C curves for the SH for different τ values are shown in Fig. S1.

Growth rate calculation

Growth rates were determined by plotting the calibrated ^{14}C age of core sections against the distance from the growing tip of the shoot core. Sections with ^{14}C calibrated ages older than 1955 (pre-bomb period) were not used for growth rate calculations. To obtain estimates of changes in growth rate over time, growth rates were estimated for the year corresponding to the mean calibrated ^{14}C age of each shoot core section from the gradient of a cubic spline (λ-value=10) fitted to the data (Quinn & Keough, 2002), weighted according to the error associated with each age estimate. The mean and standard error of growth rate over the length of each core was estimated from the slope of a weighted linear regression through the plotted points. The number of growth rate estimates for each core was equal to the number of calibrated ^{14}C ages, yielding 6-14 growth rate estimates between 1955 and 2003 (calibrated ^{14}C year AD for the oldest and youngest reliably dated core sections, respectively) for each core.

Correlation of environmental variables with growth rate and corrected $\delta^{13}C$

The influence of site, temperature, wind speed and stratospheric ozone depth (as a proxy for UV-B radiation) on growth rate and δ^{13}C of *C. purpureus* were explored using Analysis of Covariance (ANCOVA). Mean monthly temperature and the number of days where temperatures exceeded 0 ˚C for Casey Station for 1969-2005 and nearby Wilkes Station (2.4 km) for 1960-1968 were obtained from www.antarctica.ac.uk/met/gjma.

Mean monthly wind speed data were obtained from www.antarctica.ac.uk/met/READER/data.html. Long-term (>40 years) stratospheric ozone depth records are not available for Casey Station, thus the monthly stratospheric ozone depth record for Amundsen-Scott (90ºS, 0ºE, 1962-2005, www.woudc.org) was used as a proxy. The Amundsen-Scott record provided the best correlation of both October (r=0.96, P<0.0001) and summer ozone depth (December-February, r=0.93, P<0.0001) with the satellite ozone record for the latitudinal band including Casey (1979 to present, obtained from toms.gsfc.nasa.gov/ozone/ozoneother.html) of the available long-term ozone records for Antarctic stations (Amundsen-Scott, Faraday, Hallett, Syowa). Data for environmental factors were paired to growth rate and $\delta^{13}C$ values for the appropriate summer season. The five-year running mean for each environmental variable provided better correlations than environmental data for individual years as (1) each 3 mm shoot 'core' section represents on average 3-5 years of growth (see Table 1) and (2) growth rates were estimated from the gradient of a spline, effectively averaging the growth rate over several years. Five year means of data averaged over December-February provided the best correlations of growth rate with temperature and wind speed, with five year means of ozone depth averaged over November-January providing the best correlations with growth rate. Data were transformed where necessary to fulfil the assumptions of normality and homoscedacity. All analyses were performed using JMP version 5.1 & 7.0 (SAS Inc., Cary, NC, USA).

Results

We used accelerator mass spectrometry (AMS) ^{14}C analysis to identify the mid-1960s bomb spike in six shoot cores of four moss species collected from the Windmill Islands and Vestfold Hills, East Antarctica in January 2005. Calibrated ^{14}C ages of sections at the base of five of the six cores predated the 1966 SH peak in atmospheric bomb [14]C (Fig. 1, Hua & Barbetti, 2004). As the material analysed comprised intact shoots with healthy growing tips when collected, our results indicate that moss shoots from these colonies are more than 40 years old.

Calibrated ^{14}C ages revealed similar very slow average growth rates for all species (0.6 to 1.3 mm yr^{-1}, Table 1), however we detected considerable variation in growth rates over time for all four moss species as well as at the various locations (Fig. 3). Growth rates in the 1990s and early 2000s were lower than in 1980 for all four cores obtained from the Windmill Islands (three *Ceratodon purpureus* and one *Schistidium antarctici*) whilst the two cores from the Vestfold Hills region showed higher growth in the most recent decades. In sites where two different species were measured the timing and direction of changes in growth rates in each species were typically comparable (lower panels in Fig. 3).

For the three *Ceratodon purpureus* shoot cores (the species for which the most ^{14}C data were available, Fig. 2 & Table S1) from the Windmill Islands, growth rates were much more variable for the *C. purpureus* cores from ASPA 135 and Clark Peninsula than the core collected from the Red Shed site (Fig. 3). We speculate differences in the variability of growth rates between cores are likely to reflect differences in microclimate between

sampling sites, with the least variation observed at the wettest site (Red Shed). At both ASPA 135 and Clark growth rates were much higher in past decades, particularly the 1970s and late 1950s (for ASPA 135) and the early 1980s (for Clark). By the mid-1990s, growth had decreased more than 7 fold compared to the late 1950s rate at ASPA 135 and almost 3 fold relative to the early 1980s at the Clark site.

Moss growth rates were strongly inversely related to wind speed and positively related to both temperature and ozone depth over the summer season for the period for which both growth rate and climate data were available (1960-2002). Most strikingly growth rates were significantly negatively correlated with wind speed during the summer growing season (December-February, r^2=0.78, P=0.0004, Fig. 4a, Table 2), with the strongest correlation at the Clark Peninsula site (wind by site interaction, P=0.0035). Growth rates were positively correlated with both melt days (days above 0 ℃) and summer temperature (r^2=0.69, P=0.003, Fig. 4b and r^2=0.61, P=0.002, Fig. 4c, respectively). Growth rates were positively correlated with ozone depth at two of the three sites (ASPA 135 and Red Shed, r^2=0.61, P=0.01, Fig. 4d).

Our results point to a profound influence of recent climate change on the Antarctic flora, with stable carbon isotope (δ^{13}C) profiles indicating the observed effects of temperature and wind speed are most likely due to the impact of these climate variables on water availability. For all *C. purpureus* shoots δ^{13}C was negatively correlated with summer wind speed (r^2=0.66, P=0.043, Fig. 4e, Table 3) and positively correlated with both

temperature (days above 0°C - r^2=0.80, P=0.0032, Fig. 4f; Dec-Feb temperature - r^2=0.79, P=0.0014, Fig. 4g) and ozone depth (r^2=0.68, P=0.042, Fig. 4h).

δ^{13}C of *C. purpureus* shoot core sections differed significantly between sites, with lower values for ASPA 135 compared to the other sites, indicative of a drier microhabitat (P=0.0014, $F_{2,25}$=8.93). Shoot δ^{13}C, at two of the three *C. purpureus* sites, became substantially more negative between the 1950s and the present day (ASPA 135 r^2=0.42, P=0.042, $F_{1,8}$=5.87, Red Shed r^2=0.38, P=0.078, $F_{1,7}$=4.24, Fig. 5), indicative of a drying trend. Furthermore, growth rates were positively correlated with δ^{13}C at the two drier sites (r^2=0.63, site by δ^{13}C interaction P=0.0071, Fig. 6, Table 2), suggesting growth of *C. purpureus* in the Windmill Islands region is water-limited, except perhaps where moss beds are adjacent to lakes as at the Red Shed site.

Discussion

The ^{14}C bomb spike method has extended the period over which the growth rates of Antarctic mosses have been measured from a maximum of one or two decades (Selkirk & Skotnicki, 2007) to almost half a century and revealed the potentially extreme longevity of these plants. Our results confirm that the ^{14}C bomb spike can be used to estimate the age of colonies and detect changes in growth rates over several decades. By generating detailed growth rate data, we have demonstrated that growth of Antarctic *C. purpureus* is closely coupled with environmental variables. Most importantly our data show that even the biota of continental Antarctica has displayed striking responses to recent climate change and suggest that the causative explanation is variation in water availability.

Indeed we argue that water availability is a key determinant of the future trajectory of Antarctic ecosystems.

Our data suggest two opposing trends are strongly influencing Antarctic moss growth rates, with high summer wind speeds reducing water availability to shoot cores whereas high summer temperatures increase water availability. Although we found that high summer temperatures are positively correlated with growth, the most important impact of increased temperature appears to be increased melt and an increased length of growing season (c.f. Fig 4b & c). In contrast, the negative effect of increased wind speed is explained by the drying effect of wind, increasing evaporation and desiccating plants until metabolism ceases. Although UV-B radiation can potentially influence growth rates through UV-induced damage or metabolic costs associated with UV protection (see below), the positive association between $\delta^{13}C$ and ozone depth (used as a proxy for UV-B radiation) was unexpected since UV-B had no effect on $\delta^{13}C$ of two *Sphagnum* moss species (Niemi *et al.*, 2002). The observed association between ozone depth and $\delta^{13}C$ is presumably due to correlations between springtime ozone depletion and the Southern Annular Mode, with large ozone depletion events associated with stronger circumpolar flow and increased summer wind speeds at coastal Antarctic sites (Perlwitz *et al.*, 2008, Roscoe & Haigh, 2007, Son *et al.*, 2010, Thompson & Solomon, 2002).

The opportunity provided by the ^{14}C bomb spike clearly shows that the Antarctic flora is extremely slow growing, highly sensitive to the limited climatic change that has occurred in the region over the last 50 years, and provides insight into the effects of climatic

change predicted for this century. Our results provide clear evidence of reduced water availability at Red Shed and ASPA 135, two sites with high biodiversity in East Antarctica. Although there is no clear evidence of warming from station meteorological records in the region, recent studies of ice-sheet mass balance have shown accelerated ice loss since 2006 from the East Antarctic sheet in the vicinity of Casey Station (Chen *et al.*, 2009) and infrared satellite data suggest that, contrary to previous reports, East Antarctica has warmed by 0.1 ˚C per decade since 1957 (Steig *et al.*, 2009a, Steig *et al.*, 2009b). Increasing temperature and precipitation in polar regions due to climate change (Christensen *et al.*, 2007) were predicted to result in increased growth rates through increases in water availability and length of the growing season (Robinson *et al.*, 2003). However, our results show that moss growth rates have declined in the Windmill Islands since 1980. The environmental factor most likely responsible for this change is increasing wind speeds. Surface wind speeds have significantly increased over the world's oceans over the past two decades (Young *et al.*, 2011) and around the Antarctic continent as a result of ozone depletion and increasing greenhouse gases (Perlwitz *et al.*, 2008, Son *et al.*, 2010). Increased wind speeds have been observed in both the Windmill Islands (Fig. 7) and Vestfold Hills over the last 50 years, leading to a negative impact on water availability and growth (Hodgson *et al.*, 2006, Turner *et al.*, 2005). The influence of changing wind patterns is rarely considered in studies of the biological effects of climate change despite its potential influence on important ecological drivers such as water balance, pollination, nutrient transfer and dispersal. Our results suggest that changes in wind speed can have a significant impact on water-limited ecosystems.

Climate-induced increases in stratosphere to troposphere ozone flux suggest the UV index over Antarctica will remain higher than pre-ozone depletion this century, despite recovery of the Antarctic ozone hole to pre-1970s levels (Hegglin & Shepherd, 2009). Positive correlations of growth rates with ozone depth at two of our sites indicate ozone depletion, and the associated increases in UV-B radiation, may have reduced growth of Antarctic *C. purpureus* either through UV-induced damage or metabolic costs associated with UV protection, such as the synthesis of UV-screening compounds or repair of DNA damage (Clarke & Robinson, 2008, Newsham & Robinson, 2009, Snell *et al.*, 2009, Turnbull & Robinson, 2009){Dunn, 2006 #245}. The timing and balance between the positive influence of warming and the negative influence of high wind speeds and UV fluxes may determine the fate of these oases of Antarctic biodiversity.

This study clearly shows that modern radiocarbon analysis can be used to determine accurate growth rates for extant Antarctic mosses, enabling correlation of growth to environmental parameters for the first time and allowing impacts of climate change to be assessed in a key component of terrestrial Antarctic ecosystems. Combining accurate dating with stable isotope analysis can yield important insights into changes in water availability at the local scale. For cold remote locations like Antarctica, where climate records are limited and of relatively short duration, this ability of mosses to act as a microclimate proxy has the potential to increase our knowledge of fine-scale climate change. These techniques ought to be broadly applicable in many other regions where perennial moss beds exist and form a dominant component of the vegetation, including alpine, Arctic, maritime and sub-antarctic regions (e.g. Woodin *et al.*, 2009).

In conclusion, we have shown that radiocarbon and $\delta^{13}C$ profiles demonstrate changes in growth rate and water availability in Antarctic moss tissue over multiple decades. By linking growth of Antarctic mosses to environmental records, we demonstrate that unexpectedly these plants have responded to recent climatic change within the East Antarctic region. Moss communities represent some of the most complex terrestrial ecosystems in continental Antarctica. Our research provides a better understanding of how these ecosystems will respond to future climate change.

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SUPPORTING INFORMATION

The following Supporting Information is available for this article:

Table S1. Radiocarbon content, calibrated ^{14}C age and measured δ^{13}C of moss shoot core sections.

Figure S1. Radiocarbon calibration bomb curves with different τ-values showing calibrated ages of 3 mm moss sections. The bomb curve with $\tau = 0$ yr is our reconstructed annual atmospheric ^{14}C for the SH. Vertical and horizontal error bars are 1 and 2σ, respectively.

Additional Supporting Information may be found in the online version of this article.

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Figure Legends

Figure 1. Location of the Windmill Islands and Vestfold Hills East Antarctica (a) and details of sampling sites within the Windmill islands (b) and the Vestfold Hills (c).

Figure 2. Dating of Antarctic mosses using bomb ^{14}C. a, Annual SH atmospheric ^{14}C for 1945-2002. This ^{14}C record comprises SH atmospheric ^{14}C for 1955-2002 (Hua & Barbetti, 2004) supplemented with ^{14}C data from annual tree rings from Washington State, USA for 1945-1954 (Stuiver *et al.*, 1998) because annual ^{14}C tree-ring data for the SH are not available for the pre-bomb period. **b,** ^{14}C content of shoot sections from four moss species collected from the Vestfold Hills and Windmill Islands, East Antarctica (n=7-18). Note that one sample (section) of *B. recurvirostre*, Grimmia Gorge was lost during target preparation for AMS analysis. **c,** Dated *C. purpureus* shoot from ASPA 135, showing approximate ^{14}C calibrated dates for the growth period of shoot sections. All ^{14}C values are shown in percent modern carbon (pMC, Friedli *et al.*, 1986). Y-axis error bars are 1σ, X-axis error bars in (b) represent the length of shoot sections.

Figure 3. Changes in growth rate of mosses from the Windmill Islands and Vestfold Hills over time. Growth rates were estimated from the gradient of a spline fitted to plots of the calibrated ^{14}C age of shoot core sections against their distance from the growing tip. Clark – *C. purpureus* (open squares), *S. antarctici* (closed squares); Grimmia Gorge – *B. recurvirostre* (open triangles), *B. pseudotriquetrum* (closed triangles). Note that Clark samples are from separate sites on Clark Peninsula (see Table 1, Figure 1). X-axis error

bars represent calibrated ^{14}C age range at 2σ, Y-axis error bars represent the maximum difference between growth rate estimates from the spline curve using upper and lower limits of the calibrated ^{14}C age range compared to the mean ^{14}C age.

Figure 4. Correlations between critical climatic variables and growth rates (top panel) and corrected δ^{13}C (bottom panel) of Antarctic mosses. *Ceratodon purpureus* cores are from three sites in the Windmill Islands, East Antarctica (colours green, red and blue represent ASPA 135, Red Shed and Clark, respectively). Model r^2 values from Analysis of Covariance of the combined (3) data sets are shown for each variable. The Clark Peninsula core could not be included in the ozone growth rate model, due to a non-linear association of growth rate and ozone depth at this site. Corrected δ^{13}C is shoot δ^{13}C after correcting for decreasing atmospheric δ^{13}C over time due to the combustion of fossil fuels (see Materials and Methods for more information). See legend of Fig. 3 for description of growth rate error bars (a-d). Error bars for corrected δ^{13}C are 1σ (e-h).

Figure 5. Change in corrected δ^{13}C over time for *Ceratodon purpureus* cores from Windmill Islands, East Antarctica (colours green, red and blue represent ASPA 135, Red Shed and Clark, respectively). See legend of Fig. 3 and Fig. 4 for definition of corrected δ^{13}C and its error bars.

Figure 6. Correlation between corrected δ^{13}C and growth rates of *C. purpureus* cores from three sites in the Windmill Islands, East Antarctica (colours green, red and blue represent ASPA 135, Red Shed and Clark, respectively). The model r^2 value from

Analysis of Covariance of the combined (3) data set is shown. See legend of Fig. 4 for definition of corrected $\delta^{13}C$ and error bars.

Figure 7. Change in mean summer wind speed (December-February) over time for Casey Station. Mean daily wind speed in km h^{-1} = -183.7422 + 0.102172*Year (r^2=0.17, P=0.0069). Data from Windmill Islands Bureau Of Meteorology sites (Wilkes base 1960-1968, Casey "Tunnel" 1969-1989 and Casey Station 1990-2009).

Tables

Table 1. Location, mean corrected $\delta^{13}C$, growth rates ($\pm 1\sigma$) and changes in growth rate over time for four moss species from East Antarctica.

Species	Site	Latitude and longitude	Average growth rate (mm yr^{-1})	Variation in growth rate (mm yr^{-1})	$\delta^{13}C$ (‰)
Bryoerythrophyllum recurvirostre	Grimmia Gorge, Vestfold Hills	68º36' S, 78º30' E	0.94 ± 0.06	0.48 - 2.37	-25.6 ± 0.2
Bryum pseudotriquetrum	Grimmia Gorge, Vestfold Hills	68º36' S, 78º30' E	1.33 ± 0.09	0.97 - 2.61	-26.4 ± 0.2
Ceratodon purpureus	ASPA 135, Windmill Islands	66º16' S, 110º32' E	0.75 ± 0.08	0.23 - 3.47	-27.3 ± 0.2
Ceratodon purpureus	Red Shed Windmill Islands	66º16' S, 110º31' E	0.63 ± 0.02	0.45 - 0.71	-26.0 ± 0.1
Ceratodon purpureus	Clark Peninsula 1, Windmill Islands	66º15' S, 110º34' E	0.82 ± 0.09	0.22 - 1.69	-26.4 ± 0.2
Schistidium antarctici	Clark Peninsula 2, Windmill Islands	66º15' S, 110º35' E	0.60 ± 0.06	0.45 - 1.16	-22.3 ± 0.6

Table 2. ANCOVA results examining influence of environmental variables and corrected $\delta^{13}C$ on growth rate of *C. purpureus* cores from the Windmill Islands.

	d.f.	*F*	*P*
Model $r^2 = 0.78$			
Wind (Dec-Feb)	1	20.10	0.0004
Site	2	4.84	0.023
Wind*site	2	8.24	0.0035
Model $r^2 = 0.69^+$			
Days above 0 ºC	1	12.61	0.0029
Site	2	7.36	0.0059
Days above 0 ºC*site	2	3.22	0.069
Model $r^2 = 0.61^+$			
Mean temperature (Dec-Feb)	1	12.69	0.0022
Site	2	4.01	0.036
Mean temperature*site	2	4.45	0.027
Model $r^2 = 0.61^*$			
Ozone depth (Nov-Jan)	1	9.17	0.013
Site	1	3.24	0.10
Ozone depth*site	2	3.34	0.097
Model $r^2 = 0.63^+$			
Corrected $\delta^{13}C$	1	19.12	0.0002
Site	2	15.12	<0.0001
$\delta^{13}C$*site	2	6.33	0.0071

[*]only Red Shed and ASPA 135 sites
[+]excluding 1 outlier
d.f. degree of freedom

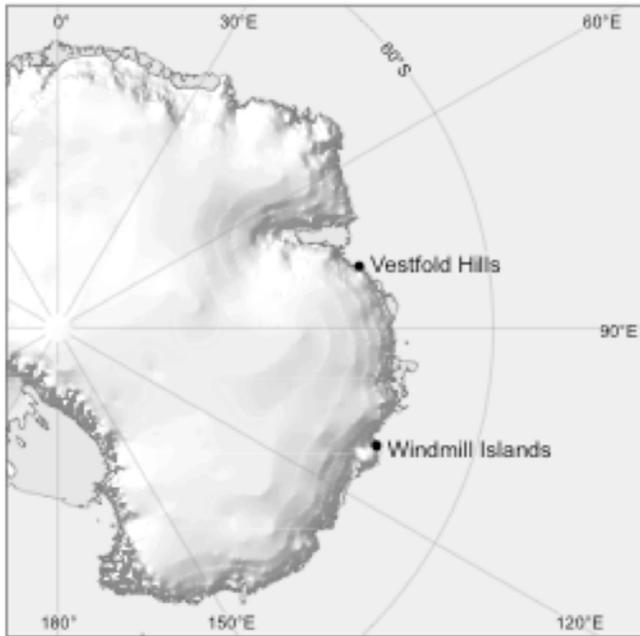**Table 3.** ANCOVA results examining influence of environmental variables on corrected

δ^{13}C of *C. purpureus* cores from the Windmill Islands.

	d.f.	*F*	*P*
Model $r^2 = 0.66$			
Wind (Dec-Feb)	1	4.85	0.043
Site	2	10.58	0.0012
Wind*site	2	0.36	0.70
Model $r^2 = 0.80$			
Days above 0 ºC	1	12.30	0.0032
Site	2	22.97	<0.0001
Days above 0 ºC*site	2	1.11	0.36
Model $r^2 = 0.79$			
Mean temperature (Dec-Feb)[+]	1	14.57	0.0014
Site	2	22.66	<0.0001
Mean temp*site	2	2.30	0.13
Model $r^2 = 0.68$			
Ozone depth (Nov-Jan)	1	4.89	0.042
Site	2	14.11	0.0003
Ozone depth*site	2	0.41	0.67

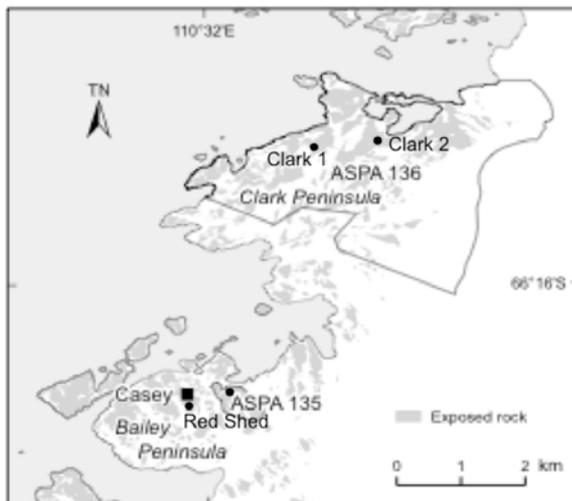[+]excludes 2 outliers
d.f. degree of freedom

a

0° 30°E 60°E
80°S
Vestfold Hills
90°E
Windmill Islands
180° 150°E 120°E

b

110°32'E
TN
Clark 1 • Clark 2
ASPA 136
Clark Peninsula
66°16'S
Casey ■ • ASPA 135
Bailey Red Shed
Peninsula

Exposed rock

0 1 2 km

c

Davis
68°35'S
Grimmia Gorge

Lake
Exposed rock

Sørsdal Glacier 78°10'E TN

0 2 4 km

a

pMC vs Year (AD)

b

C. purpureus, ASPA 135

C. purpureus, Red Shed

C. purpureus, Clark 1

S. antarctici, Clark 2

B. pseudotriquetrum, Grimmia Gorge

B. recurvirostre, Grimmia Gorge

pMC vs Distance from tip (mm)
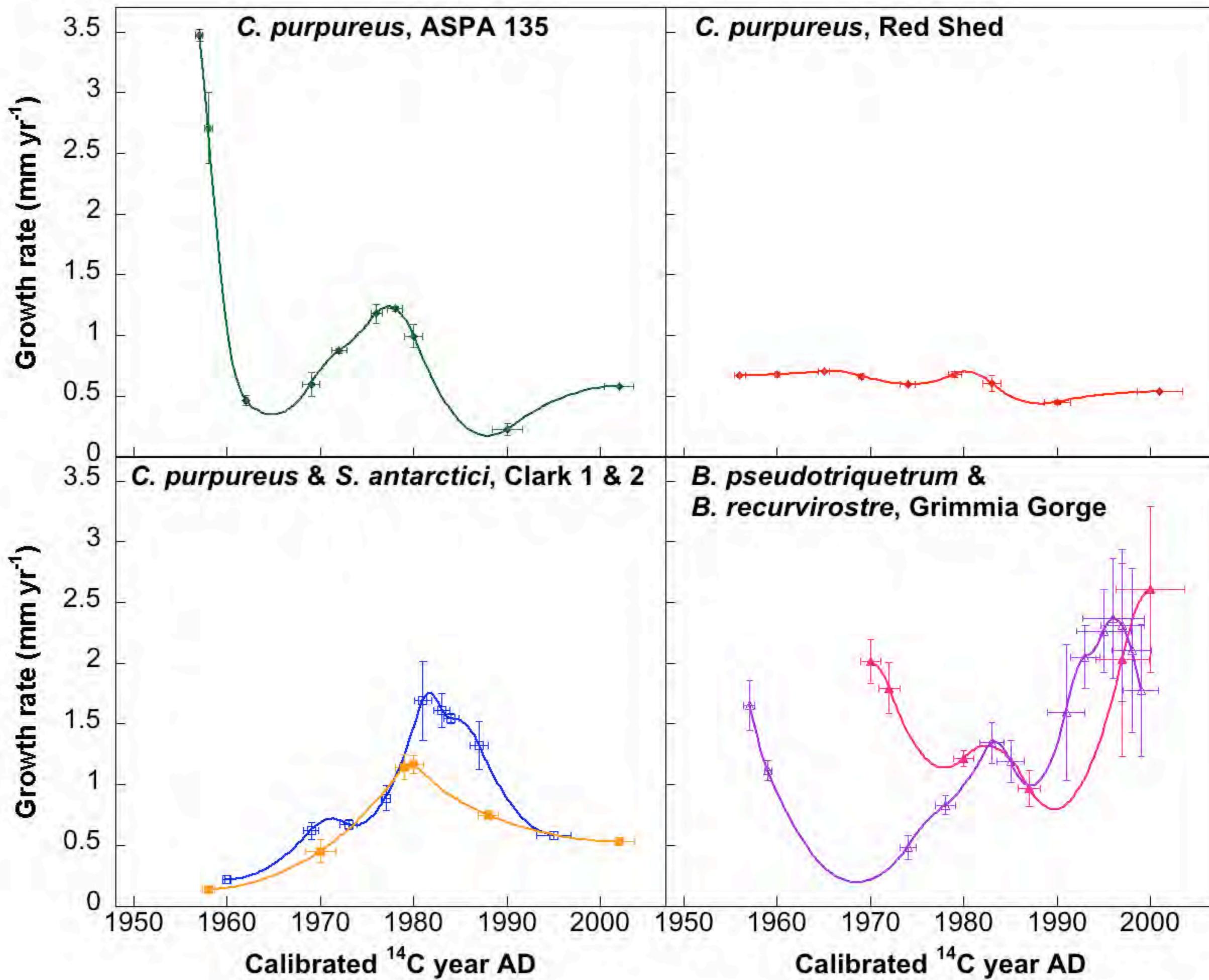
c

2002
1990
1978
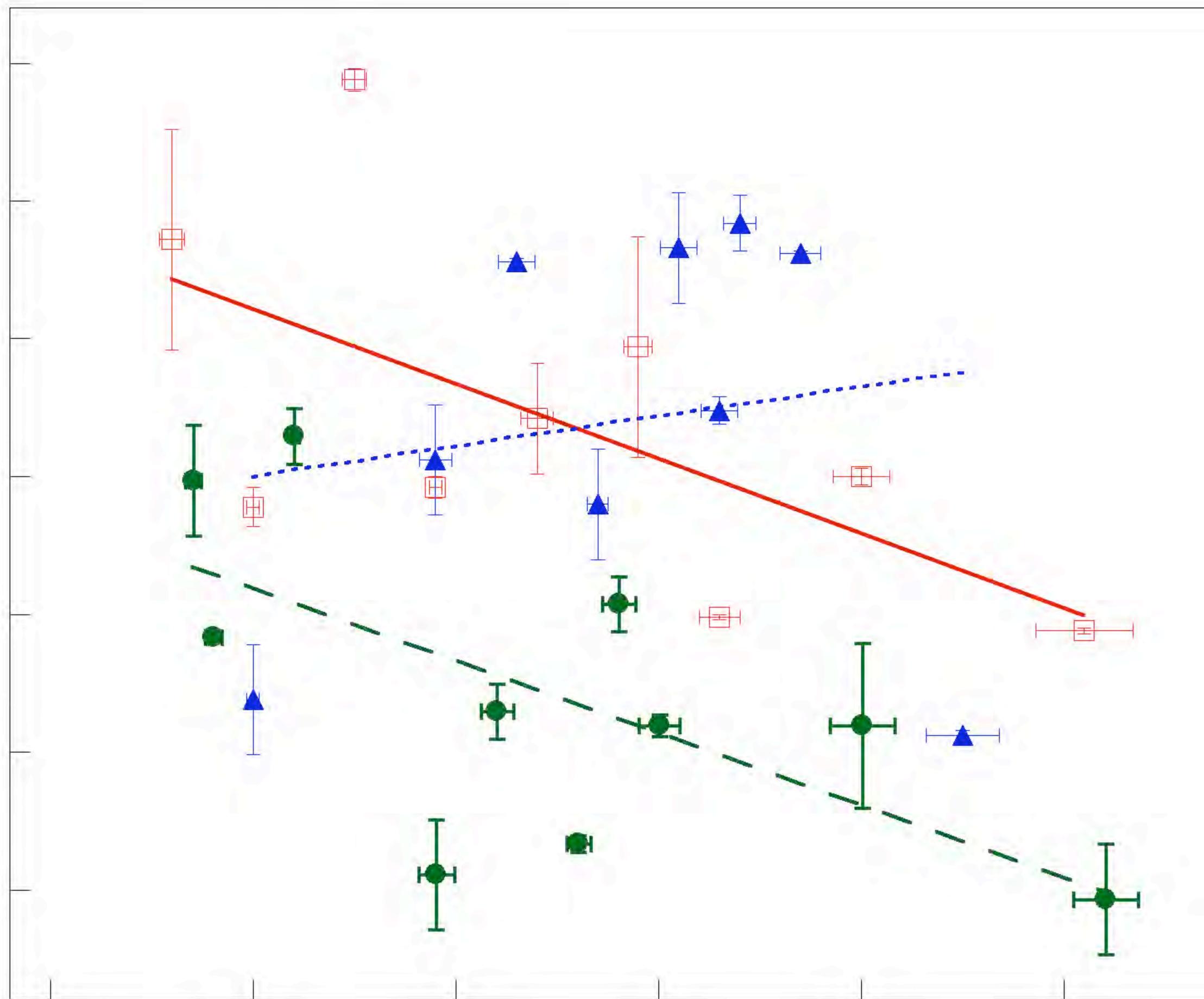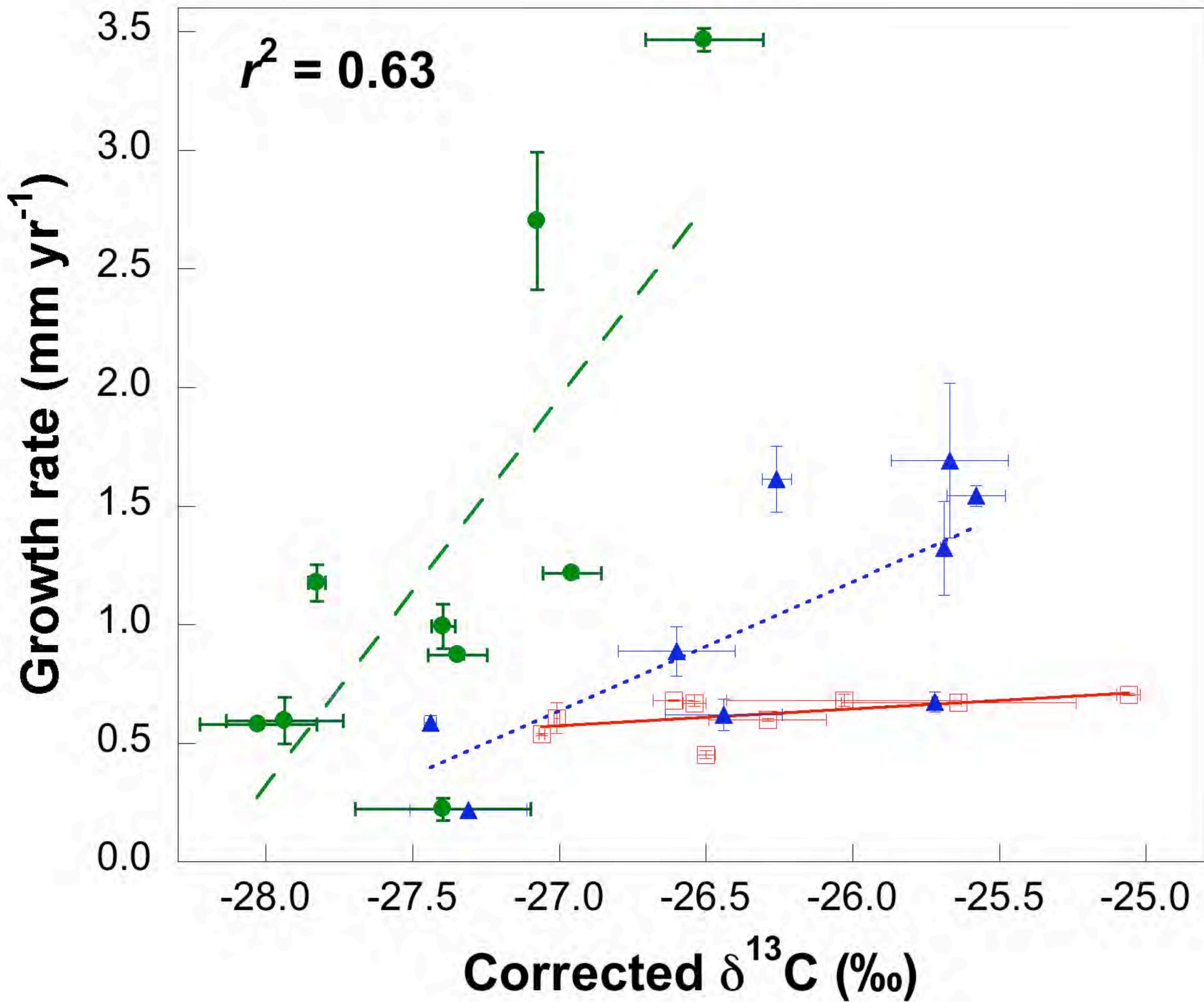1972
1962
1957

10 mm

Wind speed — Days above 0 ºC — Temperature — Ozone depth
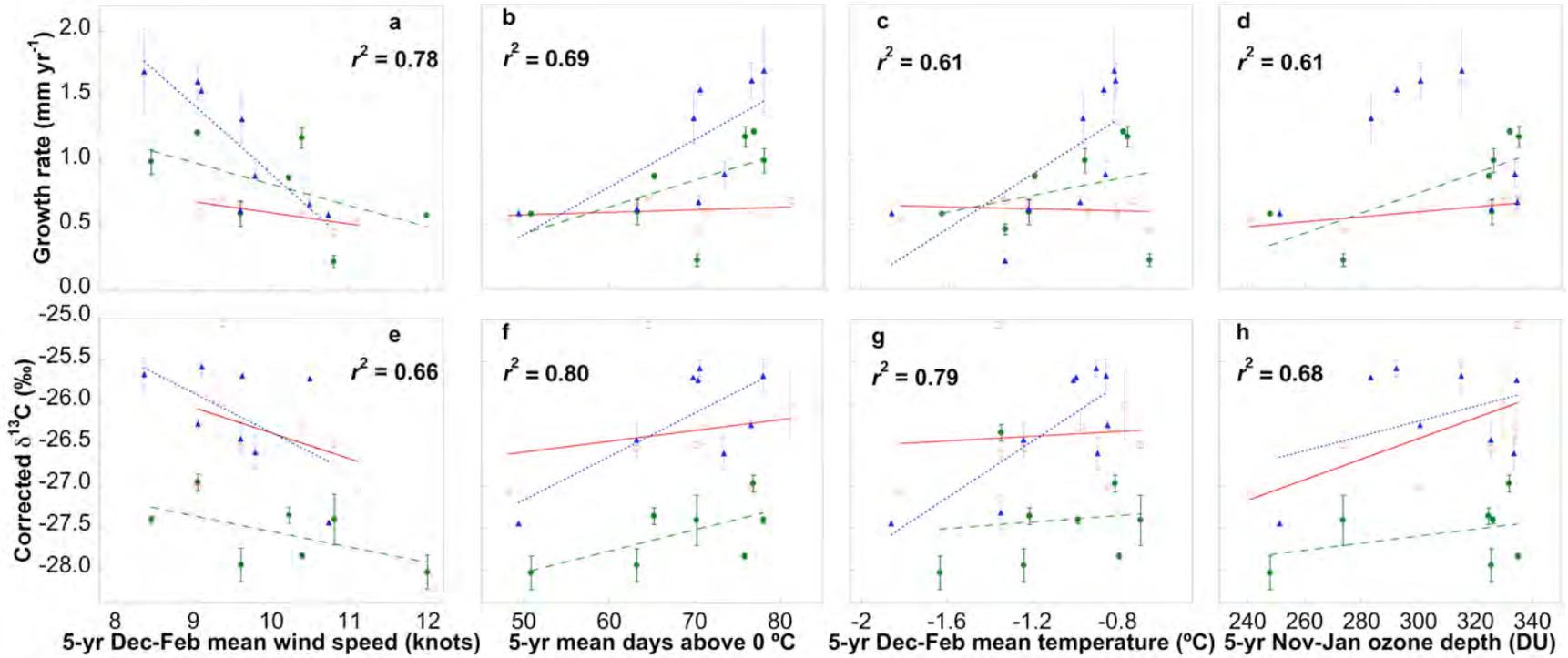
a — $r^2 = 0.78$

b — $r^2 = 0.69$

c — $r^2 = 0.61$

d — $r^2 = 0.61$

e — $r^2 = 0.66$

f — $r^2 = 0.80$

g — $r^2 = 0.79$

h — $r^2 = 0.68$

Growth rate (mm yr^{-1})

Corrected δ^{13}C (‰)

5-yr Dec-Feb mean wind speed (knots)

5-yr mean days above 0 ºC

5-yr Dec-Feb mean temperature (ºC)

5-yr Nov-Jan ozone depth (DU)