

Recent reduction in the frequency of frost accounts for most of the increased growth of a high elevation spruce forest in northwestern China

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Abstract

Key message Using process-based models in combination with dendrochronological measurements provides a way to explain recent increased tree growth in northwestern China.

Abstract Dendrochronological studies of tree rings in a 250-year-old Qinghai spruce (*Picea crassifolia*) forest in the Qilian Mountains of northwestern China indicate a 60 % sustained increase in tree-ring growth between 1980 and 2009 compared with any time since 1785. Over the same period, the maximum, minimum, and average temperatures all increased by nearly 2 °C during the growing season (May through September), the frequency of frost decreased 18 days, precipitation remained unchanged, while atmospheric concentrations of CO₂ increased by 48 ppm. To explain how the changes in climatic variables might cause the increase in tree growth, we parameterized a process-based growth model (3-PG, physiological processes predicting growth) with values from the literature and performed a series of sensitivity tests. The results of our analysis indicated that a reduction in frost frequency during the growing season, which allows stomata to remain open, enhanced gross photosynthesis by 42 %. Up to a 20 % increase in P_G could be attributed to rising atmospheric CO₂ between 1980 and 2009, with half of this

attributed to increased light interception from a simulated 0.4 increase in canopy leaf area index. The increase in average and maximum temperatures had little direct effect on gross photosynthesis with the optimum temperature set between 9 and 10 °C. Indirectly, the increase in monthly average minimum temperature during the growing season, although small, crossed a threshold that reduced the impact of frost. Our analyses show the value of combining dendrochronological measurements with a process-based model to gain a more holistic understanding of how environmental factors interact to affect tree growth.

Keywords Process-based model · 3-PG · Qinghai spruce · Tree-ring analysis · Frost · Atmospheric CO₂

Introduction

Forests at high elevations, where only a few species are adapted to such a harsh environment, are particularly susceptible to climate change. In such places, gradual changes in climate may cross thresholds that cause rapid changes in tree growth, as well as increased susceptibility to attack from insects and pathogens (Raffa et al. 2008; Bentz et al. 2010; Yan and Niu 2008; Ayres and Lombardero 2000; Sturrock et al. 2011).

Dendroclimatic studies have contributed much to the interpretation of past climatic conditions through statistical correlations between ring widths and annual and seasonal patterns in precipitation and temperature. For example, Salzer et al. (2009) report that high elevation Great Basin bristlecone pine (*Pinus longaeva*) at three sites in western North America showed ring growth in the second half of the 20th century that was greater than during any other 50-year period in the last 3700 years. A similar

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unprecedented increase in growth over a 425-year chronology was reported in *Juniperus przewalskii* from the Xiqing Mountains in northeast Tibet in association with an increase in minimum winter temperature of 2.5 °C (Gou et al. 2007). In an analysis of 225-year-old Qinghai spruce (*Picea crassifolia*) growing at 3200 m elevation in the eastern Qilian Mountains of northwestern China, Gao et al. (2015) reconstructed a warming trend during July that began around 1900 and has continued, with eight of the ten warmest Julys recorded during the period 1990–2009. There was no indication that variation in precipitation had any effect on growth over the last 53 years.

Atmospheric concentrations of CO₂ now exceed 400 ppm, and minimum temperatures are increasing asymmetrically compared with the maximum (Walther et al. 2002). As a consequence of these rapid asymmetrical changes, statistical correlations of growth with basic weather data are becoming less reliable (Briffa et al. 1998; Gao et al. 2013) and much more variable (Zhang and Wilmking 2010). As an alternative to conventional dendrochronological analysis, process-based modeling may offer a more holistic interpretation (Evans et al. 2006).

Process-based models offer an alternative means of evaluating growth responses because, unlike statistical models, they include functions that define thresholds to constrain photosynthesis, transpiration, and growth and do not require site-by-site tuning (Evans et al. 2006). Li et al. (2014) applied a process-based model to predict the growth of individual *Pinus koraiensis* trees in one stand located in the Changbai Mountains in northeastern China.

We took advantage of the tree-ring analysis performed by Gao et al. (2015) on Qinghai spruce to apply a process-based model to assess environmental factors that might explain such a rapid increase in growth between 1980 and 2009 compared with the period 1957–1979. We found sufficient information in the literature to parameterize such a model for *P. crassifolia*, along with methods to derive estimates of incident solar radiation, evaporative demand, and the frequency of frost from conventional weather records (Running et al. 1987).

In this paper, we use a process-based growth model, 3-PG, (physiological principles predicting growth) model developed by Landsberg and Waring (1997) to assess the relative importance of different environmental factors alone, and in concert, that might account for a recent sustained increase in tree-ring growth between 1980 and 2009. We ran simulations with 3-PG model to assess the relative importance of three factors on tree growth: (1) a 48 ppm rise in the concentration of atmospheric CO₂, (2) a nearly 2 °C increase in mean, maximum, and minimum temperatures for each month from May to September, and (3) a decrease of 18 days in the frequency of frost during the 5-month growing season.

Materials and methods

Study site

The Qilian Mountains are located on the northeastern margin of Qinghai-Tibet Plateau in northwestern China. Climatic conditions are typical of a continental highland with cold winters, a cool growing season, and sparse precipitation, most of which occurs in the summer. The study site (37.9°N, 101.4°E at an elevation of 3190–3210 m a.s.l.) is located in the Shiyang River Basin in the eastern Qilian Mountains (Fig. 1).

Qinghai spruce (*P. crassifolia*) is the dominant conifer in the Qilian Mountains. The spruce grows very slowly (12 m height at 100 years, Liu 1988), on north-facing or otherwise shaded slopes (Gao et al. 2015). The forests are generally open with a projected leaf area index (*L*) $\leq 3.0 \text{ m}^2 \text{ m}^{-2}$ (Tian et al. 2011). The soils at the study site are relatively deep (Gao et al. 2015) and classified as alpine forest gray-brown and subalpine shrub meadow types with a clay-loam texture (Nie et al. 2009).

Climatic data

Temperature and precipitation data from meteorological stations at Menyuan (elevation 2850 m) and Qilian (elevation 2787 m) were combined and averaged at monthly intervals according to procedures described by Jones and Hulme (1996) into one series over the period 1957–2009. To make the temperature data representative for the study site (65–100 km distance from the meteorological stations), we decreased the previously derived temperature values by 0.6 °C per 100 m gain in elevation. We averaged

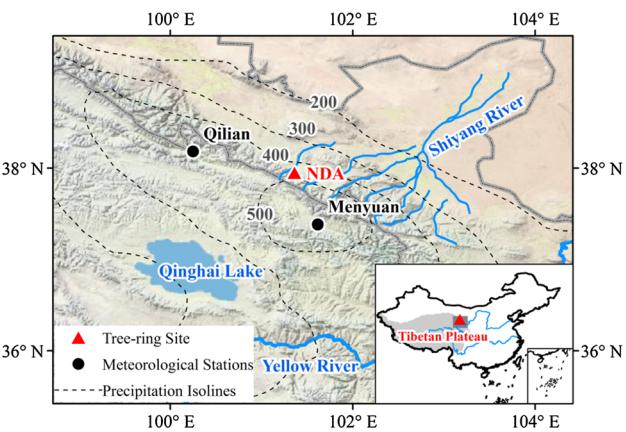


Fig. 1 Map showing the locations of the tree-ring sampling site (NDA, red triangle at 3200 m) and the two nearest meteorological stations (black dots Qilian at 2790 m and Menyuan at 2851 m elevation). The dash lines indicate mean annual precipitation (100 mm year⁻¹) contours provided from the Tropical Rainfall Measuring Mission (TRMM) satellite for the period AD1998–2012 (Huffman et al. 2007). Map adapted from Gao et al. (2015)

the precipitation data from both stations, although it is likely that values at the study site were slightly higher than recorded at either station (Gao et al. 2015).

To drive a process-based growth model, we derived incident solar radiation (ϕ_{par}), mean daytime vapor pressure deficit (D), and the frequency of frost (F) per month. The mean daily incident solar radiation (~50 % of which is photosynthetically active) was estimated from the difference between daily averaged maximum and minimum temperatures each month and knowledge of the latitude, elevation, slope, and aspect of the study site (Coops et al. 2000). The mean daytime vapor deficit (D) for each month was estimated by assuming that the minimum temperature corresponds to the dewpoint temperature in most forested areas (Kimbrell et al. 1997) and that D was 2/3 of the maximum value; the minimum temperature (T_{\min}) served as a basis for predicting the frequency of frost (<−2 °C) each month (Eqs. 1a, 1b) (Waring and McDowell 2002).

$$\text{Days of frost per month } (F) = -2.0(T_{\min}) + 11.6 \quad (1a)$$

$$\text{If } T_{\min} \leq -9^{\circ}\text{C}, F = 30; \text{ if } T_{\min} \geq 6.0^{\circ}\text{C}, F = 0 \quad (1b)$$

Tree-ring data

Tree-ring growth data were acquired from dual increment cores extracted from 27 spruce trees at the study site. There were no missing rings for these series and reasonable inter-series correlations ($r = 0.65$). All ring-width series, measured with a precision of 0.001 mm, were included to develop the final chronology. The conventional straight lines or negative exponential curves were used to remove the age-related growth trend. The “signal-free” version of program ARSTAN served to calculate the standard tree-ring chronology (Melvin and Briffa 2008; Cook et al. 2013). Additional details on the preparation and analysis of increment cores are presented in Gao et al. (2015).

3-PG model

There are a number of physiologically based process growth models to choose among (Mäkelä et al. 2000; Constable and Friend 2000). The 3-PG model differs from others primarily in a number of simplifying assumptions that: (1) monthly mean climatic data are adequate to capture major trends in forest growth; (2) autotrophic respiration (R_a) and net primary production (P_N) are approximately equal fractions of gross photosynthesis (P_G) (Campioli et al. 2015); and (3) the proportion of P_N allocated to roots increases from 25 to 80 % as nutrients (particularly nitrogen) become progressively less available.

Beer’s Law is among a number of biophysical principles embedded in the model. This law allows the model to estimate the fraction of visible radiation absorbed by the canopy as an exponential function (Eq. 2) of increasing L (Campbell and Norman 1998).

$$\phi_{\text{apar}} = 1 - \exp(-kL) \quad (2)$$

where ϕ_{apar} is absorbed photosynthetically active radiation ($\text{MJ m}^{-2} \text{month}^{-1}$), k is the extinction coefficient (~0.5 for conifers), and L is the (projected) leaf area index.

Gross photosynthesis, canopy evaporation and transpiration, growth allocation and litter production are also predicted at monthly intervals (Δt) as functions of L and ϕ_{apar} . The model reduces potential photosynthesis and transpiration by imposing restrictions on stomatal conductance through modifiers (f), taking values between 0 = complete restriction and 1.0 = no restriction. These modifiers combine (in Eq. 3) to account for the effects of frost, non-optimal temperatures, constraints imposed by the vapor pressure deficits, limitations in the availability of soil water and nutrients, and the effect of variation in atmospheric concentrations of carbon dioxide (CO_2).

$$P_G = P_{\text{Eff}} \phi_{\text{apar}} f(T) f(F) f(D) f(\theta_s) f(N) f(\text{CO}_2) \quad (3)$$

where P_G is gross photosynthesis ($\text{gC m}^{-2} \text{month}^{-1}$), P_{Eff} is photosynthetic light-use efficiency expressed as gC MJ^{-1} , ϕ_{apar} is the photosynthetically active radiation absorbed by the canopy, T represents any limitation imposed by deviation from optimum temperature (T_{opt}), F is derived from the proportion of days <−2 °C per month, D is the constraint imposed by the daytime vapor pressure deficits in kPa, θ_s represents the extent that soil water deficits in the rooting zone restrict canopy stomatal conductance (G_c), N represents nutritional restrictions, and CO_2 denotes the influence that variation in atmospheric carbon dioxide (ppm) has on P_{Eff} . We used Eq. (4a) to assess the effect of variation in atmospheric concentrations of CO_2 based on data acquired at FACE studies (Ainsworth and Rogers 2007). Almeida et al. (2009) developed a related formula to predict the response of G_c with maximum canopy conductance (G_{\max}) substituted for P_{Eff} in Eq. (4b). The function $f(\text{CO}_2)$ is calculated in reference to atmospheric concentrations of 350 ppm and may be above or below unity. A similar response to rising concentrations of atmospheric CO_2 affects water-use efficiency by reducing G_{\max} (Eq. 4b). The equations predict that raising atmospheric CO_2 levels by 72 ppm from 315 ppm in 1957 to 387 ppm in 2009 should result in a 5.3 % increase in P_{Eff} and a 9.5 % increase in G_c .

$$\begin{aligned} f(\text{CO}_2) \text{ as it modifies } P_{\text{Eff}} \text{ in Eq.3} \\ = 0.2553 \ln(\text{CO}_2) - 0.4981 \end{aligned} \quad (4a)$$

$$\begin{aligned} f(\text{CO}_2) \text{ as it modifies } G_{\max} \text{ when solving for } G_c \\ = -0.464 \ln(\text{CO}_2) + 3.7343 \end{aligned} \quad (4b)$$

The 3-PG model is programmed to reduce transpiration (and photosynthesis) to zero based on the number of frost days. This subfreezing threshold is sufficient to cause complete stomata closure for at least 24 h (Hadley 2000) and at times much longer (Lamontagne et al. 1998). The soil water modifier is determined from the ratio of the amount of water available in the root zone of the trees (θ_s) to the maximum value (θ_{\max}). θ_{\max} is the water holding capacity of the soil, which is the difference between the water content in the root zone at field capacity and at the wilting point. For any given month, the available soil water (θ_s) is calculated from:

$$\theta_s(t + \Delta t) = \theta_s(t) + (P - E - T_{\text{rans}}) \quad (5)$$

where $\theta_s(t)$ is the value at the beginning of the month, Δt represents the change, P , E and T_{rans} denote the monthly values of precipitation, evaporation and transpiration, respectively. The model includes a term to account for rainfall interception by the forest canopy; this water is assumed to be lost by evaporation, giving E . Transpiration is calculated from the Penman–Monteith equation (Monteith and Unsworth 1990), which incorporates a canopy conductance term derived from stomatal conductance and L . If the value of θ_s on the left-hand side of Eq. (5) exceeds θ_{\max} , i.e., the whole root zone is at field capacity, the excess is assumed to be lost as runoff or drainage.

At monthly time steps, the model is unable to compute a snow water balance accurately, although one may assume that precipitation in months with average temperatures well below freezing is largely in the form of snow. At annual time steps, the model sums monthly changes in tree number, mean diameter, stand basal area, above-ground volume and biomass and updates L . Without knowledge of stand characteristics, we assumed low stocking of 200 trees ha^{-1} to prevent changes in number associated with self-thinning (Drew and Flewelling 1977), and kept maximum values of $L < 3.0 \text{ m}^2 \text{ m}^{-2}$ and monthly transpiration $< 60 \text{ mm}$ based on observations by Tian et al. (2011). Normally, as trees grow in height, hydraulic limitations are imposed on stomata that reduce the maximum rates of photosynthesis and transpiration (Brodrribb and Field 2000; Warren and Adams 2000; Koch et al. 2004).

Model parameterization

We eliminated the self-thinning and age effect from our simulations by selecting a low stocking level (200 trees ha^{-1}) and by setting the maximum age at

1000 years to inactivate these subroutines (Table 1). Most of the other parameter values reported in Table 1 were derived from measurements made on *P. crassifolia*. Zhao et al. (2008) was particularly valuable in documenting that the concentration of nitrogen in spruce needles was extremely low (0.7–0.8 % of dry mass). With such a low value, soil fertility is unlikely to have changed over the period of study, and can be assumed to remain low (fertility ranking = 0.1), with light-use efficiency also low (0.03 mol C/mol photon, equivalent to 1.65 gC/MJ absorbed PAR). We were unable to fine measurements of the photosynthetic temperature optimum (T_{opt}), maximum (T_{\max}) and minimum (T_{\min}) for *P. crassifolia*, and substituted values reported for *P. abies* in the Austrian Alps (Tranquillini 2012) and for *P. mariana*, a spruce native to the boreal forests of Canada (Lamhammedi and Bernier 1994). The equations to describe the normalized (0–1) functional relationship between P_G and monthly temperature values are:

$$\begin{aligned} f(T) = & \text{If } (T_{\text{av}} \leq T_{\min}) \text{ or } (T_{\text{av}} \geq T_{\max}), \text{ then } f(T) = 0 \\ \text{Else } f(T) = & ((T_{\text{av}} - T_{\min}) / (T_{\text{opt}} - T_{\min})) \\ & \times ((T_{\max} - T_{\text{av}}) / (T_{\max} - T_{\text{opt}}))^{(T_{\max} - T_{\text{opt}}) / (T_{\text{opt}} - T_{\min})} \end{aligned} \quad (6)$$

Averaged monthly climatic data at the study site

A summary of mean monthly climatic conditions for the period 1957–2009 appears in Table 2. At the study site, the annual mean temperature averaged $-0.35 \text{ }^{\circ}\text{C}$ for the same period, while the average maximum temperature in July was $17.9 \text{ }^{\circ}\text{C}$ and the average minimum temperature in January was $-23.2 \text{ }^{\circ}\text{C}$. Total annual precipitation, averaged from the two weather stations, was 465 mm. Less than 10 % of annual precipitation falls between November and March when mean temperatures are $<-4.5 \text{ }^{\circ}\text{C}$; this small amount probably is lost through sublimation; 86 % fell in the growing season. During the growing season, temperatures averaged 8.5 and 72 % of the annual incident radiation (4622 MJ m^{-2}) was available to be absorbed by the canopy. The warmest years of the record was 2009, with annual mean temperatures of $1.05 \text{ }^{\circ}\text{C}$; the coldest years were 1962 ($-1.48 \text{ }^{\circ}\text{C}$) and 1983 ($-1.43 \text{ }^{\circ}\text{C}$). 1962 was the driest year, with an annual precipitation of 360 mm, while 1989 was the wettest year (604 mm). Atmospheric concentrations of CO_2 over the period rose 72 ppm, from 315 to 387 ppm (<http://www.esrl.noaa.gov/gmd/ccgg/trends/>).

Statistical comparisons of trends and model sensitivity analyses

Trends in the climatic driving variables, including CO_2 , were quantified using linear regression analyses to contrast

Table 1 3-PG model parameters for *Picea crassifolia* used in this study

Variables	Symbols	Units	Functions and parameter values	References
Photosynthetic efficiency	P_{Eff}	mol C mol^{-1} photon	0.03	Schulze et al. (1994)
Temperature constraints	T_{opt} , T_{min} , T_{max}	°C	$T_{\text{min}} = -2$ °C, $T_{\text{opt}} = (9$ °C 10 °C, $T_{\text{max}} = (30$ °C) 40 °C	Tranquillini (2012), Lamhamedi and Bernier (1994)
Stocking density	—	trees ha^{-1}	200	Set to prevent self-thinning
Leaf Area Index	L	$\text{m}^2 \text{ m}^{-2}$	≤ 3.0	Tian et al. (2011)
Max. Avail. soil water storage	θ_{max}	mm	200 and (50–300)	Range analyzed
Tree height at 100 years	—	m	12.1	Liu (1988)
Soil texture	—	—	Clay loam	Nie et al. (2009)
Soil fertility ranking	N_s	—	0.10	Appropriate for 0.7–0.8 % of foliar nitrogen (Zhao et al. 2008)
Allometric Eq. for stem mass	—	kg	0.0685 (dia, cm) ^{2.3617}	He et al. (2013)
Foliage: stem partitioning ratio	—	—	1.0	This study to maintain stable L at age >25 years
Foliage turnover	—	—	0.0167 month ⁻¹ , 0.20 year ⁻¹	Luo et al. (2002)
Max. age	—	years	1000	Set to eliminate age effect
Max. fraction allocated to roots as function of soil fertility	—	—	0.80	Landsberg and Waring (1997)
Min. fraction allocated to roots	—	—	0.25	Landsberg and Waring (1997)
Wood density	—	kg/m^3	390	Brown et al. (1949)

Values in brackets used in sensitivity tests

Table 2 Climatic data at the study site averaged monthly for the period 1957–2009

Climatic variables	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Mean temperature (°C)	-14.0	-10.5	-4.5	1.4	5.6	8.7	10.9	10.2	6.5	0.8	-6.9	-12.5
Maximum temperature (°C)	-4.9	-1.4	3.7	9.2	13.0	16.0	17.9	17.5	13.4	8.3	1.5	-3.6
Minimum temperature (°C)	-23.2	-19.6	-12.8	-6.4	-1.8	1.5	3.9	3.0	-0.4	-6.7	-15.3	-21.4
Precipitation (mm)	1.5	2.8	11.2	23.5	55.3	77.3	101.8	96.2	71.0	20.6	3.4	1.0
Vapor pressure deficit (kPa)	0.21	0.26	0.35	0.49	0.60	0.70	0.77	0.77	0.59	0.45	0.31	0.22
Solar radiation (MJ m^2/day)	1.2	4.1	10.1	18.3	24.8	27.5	25.8	20.5	12.2	5.3	1.6	0.6
No. of rainy day (days)	2.7	3.8	8.0	9.6	14.5	17.4	19.9	18.4	15.9	8.1	2.7	1.5
No. of frost day (days)	30	30	30	24.4	15.2	8.6	3.9	5.6	12.3	24.9	30	30

the two periods (1957–1979 and 1980–2009). After calibrating the model with averaged monthly climatic data (Table 2) and CO₂ atmospheric concentrations set at 345 ppm for the period 1957–2009, we conducted a series of sensitivity analyses with 3-PG to assess the relative importance of changing selected model parameter upon P_G . The linear regression equations derived to describe trends in climatic variables between 1980 and 2009 served to set environmental limits for the sensitivity analyses. In addition, we evaluated the extent that changes in the parameters (θ_{max} , T_{opt}) might affect results. Our primary interests were to evaluate the relative effects of nearly a 2 °C rise in T_{max} , T_{min} and T_{av} during the growing season between 1980 and

2009, a reduction of 18 days in frost, and a 48 ppm increase in atmospheric concentrations of CO₂.

Results

Model calibration

The allometric relationships for *P. crassifolia*, which assume 20 % leaf turnover annually, and no shift in the ratio of foliage to wood production with age (Table 1), produced nearly stable values of P_G and L using averaged climatic data after 50 years (Fig. 2), with CO₂ set at

345 ppm, soil fertility at 0.1 of maximum, and θ_{\max} at 200 mm (Fig. 2). The period to stand closure is nearly identical to that reported for an *Abies mariesii* forest

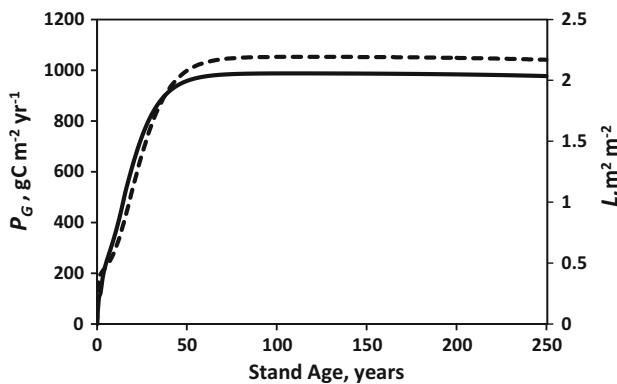


Fig. 2 3-PG model calibration run simulating gross photosynthesis (P_G) and leaf area index (L), both of which plateau after the Qinghai spruce stand exceeds 50 years in age using mean monthly climatic data and an average atmospheric concentration of CO₂ of 345 ppm for the period 1957–2009 (Table 2)

Fig. 3 Growth-ring chronology for 27 Qinghai spruce trees since 1785. The sustained, nearly linear rate of increase between 1980 and 2009 exceeds that recorded over most of the period of 225-year record. Graph derived from Gao et al. (2015)

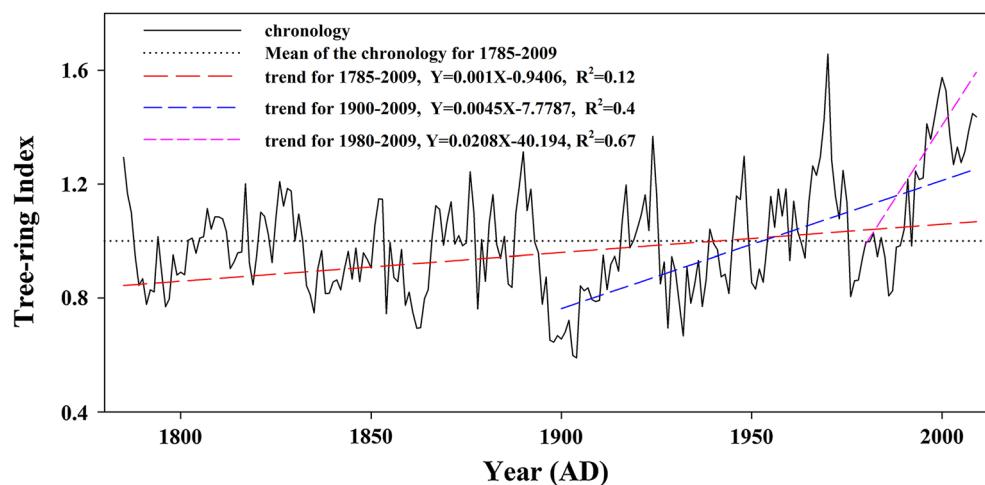


Table 3 Comparison of averages for 1957–1979 and 1980–2009 periods, with linear regression equations (x = calendar year) to predict corresponding values during the 5-month growing season (GS) in 1980 and 2009

Dependent variable	Average 1957–1979	Average 1980–2009	Equations 1980–2009	r^2	Predicted 1980	Predicted 2009	Change
Tree-Ring Index	1.125	1.203	$0.0208x - 40.194$	0.67	0.99	1.59	0.60
Frost days	50	42	$-0.6071x + 1253$	0.53	50.9	33.3	-17.6
CO ₂ , ppm (annual av.)	324	361	$1.6543x - 2938.1$	0.99	337	385	48.0
Av. mean GS Temp.	7.33	7.92	$0.0596x - 110.93$	0.62	7.08	8.81	1.73
Av. max GS Temp.	15.3	15.77	$0.0602x - 104.32$	0.56	14.88	16.62	1.75
Av. Min GS Temp.	0.8	1.6	$0.0628x - 123.65$	0.53	0.69	2.52	1.82
Av. GS D, kPa	0.68	0.69	$0.0024x - 4.087$	0.32	0.64	0.71	0.07

growing near timberline in Japan (Tadaki et al. 1977). The maximum equilibrium L at slightly $>2.0 \text{ m}^2 \text{ m}^{-2}$ is reasonable (Tian et al. 2011), although it, along with P_G , would normally be expected to decrease with increasing stand age (Waring and McDowell 2002). For the purpose of comparing age-detrended tree-ring analyses, we consider the model calibration to be suitable.

Trends in growth and climatic variation

From the full tree-ring analysis published by Gao et al. (2015) for the period 1785–2009, we derived the average growth index, along with linear trends since 1785, 1900 and 1980 (Fig. 3). Over the most recent 30-year period, the tree-ring index increased by 60 % compared to the equivalent period immediately preceding (Table 3).

The linear regression analyses between the tree-ring indices and climatic variables that we performed to determine if trends differed significantly between the two periods are presented in Table 3 and Fig. 4. None of the selected climatic variables alone was significantly

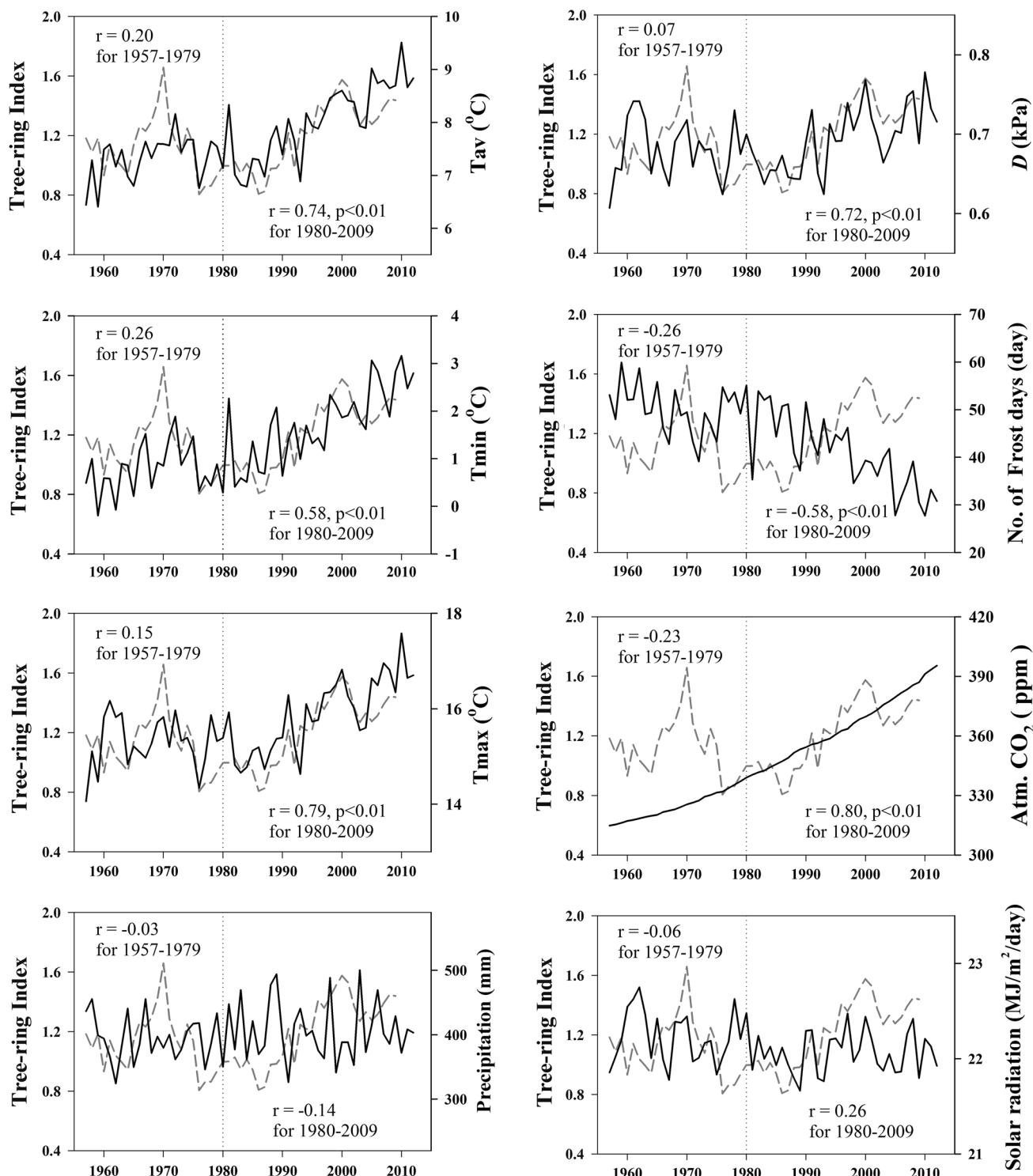


Fig. 4 Regression analyses of trends in tree-ring index and climatic variables for the two periods (1957–1979; 1980–2009). Note that none of the climatic variables were correlated significantly with the

correlated with the tree-ring index for the period 1957–1980. Since 1980, the correlation coefficients for all of the temperature variables were positive, and significant ($P < 0.01$); as was frost frequency, but with the latter

tree-growth ring index during the period 1957–1979. All but precipitation and solar radiation were significantly correlated with tree growth during the period 1980–2009

showing a negative trend ($r = -0.58$). The tree-ring index showed a strong positive correlation ($r = 0.80$) with a 48 ppm increase in the annual concentrations of atmospheric CO₂ between 1980 and 2009 (Fig. 4).

Sensitivity analysis with 3-PG model under averaged climatic conditions

Sensitivity analyses indicated that the θ_{\max} could vary from 50 to 300 mm (Table 1) under averaged climatic conditions (Table 2) without any effect on P_G (simulations not shown). Similarly, a 20 % increase in growing season D had no influence on P_G . A decrease in T_{opt} from 10 to 9 °C would increase P_G by <2 % under averaged climatic conditions, and had a similar or lesser effect on the results of the comparison of exchanging 1980 with 2009 growing season temperatures shown in Table 4. Reducing T_{\max} from 40 to 30 °C would increase P_G by 10 % with a T_{opt} of 20 °C (2 °C above T_{av} of the warmest month). It is unlikely that a 1.73 °C increase in growing season average temperature contributed significantly to the 60 % increase in tree-ring growth between 1980 and 2009 (Table 3).

The largest response in P_G was generated with a change in the frequency of frost during the growing season from the beginning to the end of the last period (1980–2009).

When we reduced frost frequency by 18 days in the 1980 growing season to that predicted in 2009 (i.e., from 51 to 33 days), P_G was predicted to increase by 42 % (Table 4). On the other hand, reversing the situation in 2009 would reduce P_G by 27 %. There is a strong interaction between frost and CO₂. With a 48 ppm increase in CO₂ under typical 1980 climatic conditions, a 20 % increase in P_G was predicted (Table 4). Reversing the situation for 2009, with only 33 days of growing season frost compared to 51 in 1980, and a predicted reduction in CO₂ from 385 to 337 ppm, would cause a 27 % reduction in P_G according to our simulations (Table 4).

Analysis with continuous variation in climatic conditions and atmospheric CO₂

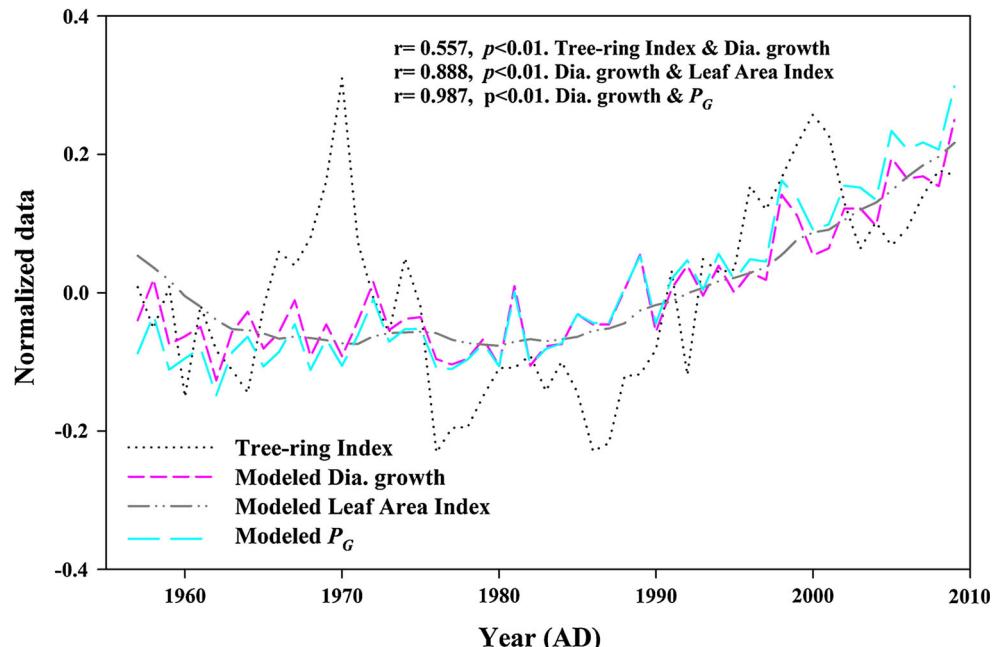
To provide a year-to-year comparison of tree-ring analyses with diameter growth predicted by 3-PG, we activated a subroutine “Vary Block” below which entries into the columns “Age” and “CO₂” were made for the period

Table 4 Predicted changes in gross photosynthesis (P_G) in 1980 and 2009 from 3-PG

Variable	Simulated change	% change in P_G
GS temperature ^a	1980 climate with 2009 GS temperatures	-3
GS temperature	2009 climate with 1980 GS temperatures	2
CO ₂ effect	1980 climate with 2009 CO ₂	20
CO ₂ effect	2009 climate with 1980 CO ₂	-14
Frost effect	1980 climate with 2009 GS frost	42
Frost effect	2009 climate with 1980 GS frost	-27

^a GS growing season (May through September)

Fig. 5 Over the period from 1957 to 2009, modeled gross photosynthesis, P_G as closely correlated with simulated growth in diameter ($r = 0.985$, $P < 0.01$) and with Leaf Area Index, L ($r = 0.888$, $P < 0.01$), but less so with the measured tree-ring index ($r = 0.557$, $P < 0.01$)



1957–2009. In addition to diameter growth, values of P_G and L were generated to compare with tree-ring growth index values. To compare deviations from the mean for the four variables, we first normalized the annual entries as a fraction of the maximum recorded, then subtracted them from the mean (ranging between 0.74 and 0.78 of the maximum).

The results of the analysis are presented in Fig. 5, showing normalized values of P_G and diameter growth deviated from averaged values in nearly identical fashion ($r = 0.985, P < 0.01$). The normalized tree-ring index and 3-PG predictions of diameter growth both show a steady increase since 1980, ($r = 0.701, P < 0.01$) along with an increase in simulated L . There is little agreement, however, between the two variables in the period from 1957 to 1979 ($r = 0.168, P \text{ NS}$).

There are no changes in the eight meteorological variables that might account for such large variation in the tree-ring chronology before 1980 (Fig. 4). As noted by Li et al. (2014), variation among trees from different dominant classes may contribute to such a varying signal in growth rings. It is unlikely that a major disturbance to the canopy would result in a marked increase in ring growth. There is a possibility that the simulated trend in L (Fig. 5), which correlate well with projected diameter growth and P_G ($r = 0.888, P < 0.01$) can be assessed by further analyses of tree cores, an option that will be discussed in the next section.

Discussion

There are two main points that come from our analysis: (1) interpretation of simple correlations with weather data and tree growth can be misleading, and (2) by deriving a more complete set of climatic variables, it is possible to use process-based growth models to help identify causal responses in growth rates to changing environmental conditions. For example, since 1980, both D and mean maximum growing season temperatures [as well as July temperatures (Gao et al. 2015)] increased significantly ($P < 0.01$) in parallel with tree-ring indices (Fig. 4), but there was as yet no cause for a reduction in stomatal conductance or P_G because D remained <1 kPa by 2009 (Oren et al. 1999). Most spruces however are extremely sensitive to increases in D (Waring et al. 1975; Watt et al. 1976; Marchand 1984; Brubaker and Hinckley 1985), particularly at low soil temperatures (DeLucia and Smith 1987). Recently observed canopy reduction and dieback of *P. crassifolia* at lower elevations elsewhere in its range (Yu et al. 2015) are likely a response, at least initially, to increasing humidity deficits associated with warming climatic conditions.

In contrast, CO_2 , which has been rising steadily long before 1957, only began to appear to affect Qinghai spruce growth at the study site after 1980. This is probably because, before that time, the frequency of subfreezing nights during the growing season equaled or exceeded 40 % (i.e., ≥ 60 days out of 150) and severely damped any growth response to rising atmospheric concentrations of CO_2 (Fig. 4). If climatic warming continues, we can extrapolate by applying Eq. (1) that once mean monthly minimum temperatures during the growing season exceed 6 °C, that frost will no longer limit P_G . At that time, the growing season should expand to more than 5 months (Table 2). Without frost, the maximum temperature is likely to continue to rise, increasing the evaporative demand, which, although reducing photosynthesis immediately, could still increase transpiration rates from 2 to over 3 mm day⁻¹, eventually leading to drought-stressed spruce without a reduction in growing season precipitation (simulations not shown).

The simulated 20 % increase in P_G between 1980 and 2009 (Table 4) associated with a 48 ppm increase in CO_2 is more than what might be expected to affect photosynthetic efficiency or tree growth (Norby et al. 2005). This additional enhancement of growth results, in the model, because the Qinghai spruce stand is assumed to have an $L < 3.0$; where small increases make a big difference in the fraction of light intercepted by the canopy (Beer's Law, Eq. 2). Under 1980 climatic conditions, an increase from ambient levels of CO_2 (337 ppm) to 2009 concentrations (385 ppm) was predicted to increase L from 1.95 to 2.32, equivalent to a 10 % increase in light interception by the canopy, and accounted for 50 % of the total simulated increase in P_G associated with the increase in atmospheric CO_2 over the period (Table 4). The predicted increase of L is within the most sensitive range of passive remote sensing instruments (White et al. 1997; Smettem et al. 2013). Such a response to increasing concentrations of CO_2 is well documented (Norby et al. 2005). The full impact of rising concentrations of atmospheric CO_2 upon forest ecosystems is complicated as it affects not only foliage production and turnover, but also nitrogen cycling and the partitioning of growth below ground (Norby and Luo 2004; Norby and Zak 2011). In areas where climatic warming is accompanied by drought and high vapor pressure deficits, photosynthesis will be increasingly limited, eventually leading to species replacement, regardless of the beneficial effects of increasing CO_2 and reduced frequency in frost (Choat et al. 2012).

In general, it is easier to model the growth response of a forest stand than that of individual trees. Unfortunately, most dendrochronological studies do not provide information that foresters and process models require to characterize stands. It would be highly desirable to determine

the sapwood cross-sectional areas and tree diameters for all species sampled within a specified plot area. With this additional information, the leaf growth efficiency, a measure of tree vigor, and stand L can be assessed (Kaufmann and Troendle 1981; Waring 1983; Marchand 1984).

We were fortunate that *P. crassifolia* has been fairly well studied at a site where both L (<3.0) and foliar nitrogen content were notably low ($<0.8\%$). Also, through sensitivity analyses, we were able to conclude that the observed recent increase in D is probably still ineffectual, and that with normal summer precipitation θ_{\max} could vary between 50 and 300 mm without effect on P_G or diameter growth. We feel that the frost effect is conservatively estimated, because a subalpine spruce in Taiwan already shows much reduced photosynthesis at temperatures slightly above freezing (Weng et al. 2005). At the same time, the Taiwan spruce exhibits a very broad temperature optimum between 2 and 11 °C (Weng et al. 2005), supporting our interpretation that growth responses since 1980 are unlikely to be attributed to increases in mean growing season temperatures. We have less confidence in our assessment of the CO₂ effect, particularly without more direct estimates of L . Although all models are simplifications of reality, they can still be helpful in separating correlations from causation. As we demonstrate, sensitivity analyses are useful in evaluating the relative importance of variables, and in identifying thresholds where effects become important.

The real goal should be the prediction of above-ground growth, which require the inclusion of allometric relations with tree diameter (Hember et al. 2015) and the recognition of possible interannual variation in wood density (Bourlaud et al. 2015), both variables specified in Table 1. Clearly, it would be advantageous to have direct measurements for all of the parameters required to initialize 3-PG or any other process-based model. When such is the case, above-ground growth can be predicted accurately even in fast-growing plantations that differ by >20-fold in productivity (Rodríguez et al. 2002, 2009) or have recently been fertilized and irrigated (Stape et al. 2004). In the future, we hope that process-based modeling can be applied to more sites with other tree species in China with an effort to quantify stocking density, mean tree diameters, ages, and L .

Although not observed at the study site, high elevation forests are becoming more vulnerable to outbreaks of native insects and pathogens where conditions are wetter and warmer, or much drier than historically was the case. Older trees, although they may have deeper root systems, are particularly vulnerable because their hydraulic systems are less efficient than trees still growing rapidly in height. Although growing conditions for Qinghai spruce appear to be improving above an elevation of 3000 m, it is unlikely that such old trees will be resistant to attack if massive

outbreaks of insects occur with further warming (Bentz et al. 2010). The hybrid approach presented in this paper offers valuable insights that indicate thresholds beyond which the effects of climatic change may shift from beneficial to conditions that may impair tree growth and threaten survival.

Author contribution statement LG conducted the field work, analyzed the tree-ring cores, and created all but Fig. 2. RW wrote the manuscript, created Fig. 2, all the tables, and did the modeling with 3-PG.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interests.

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