Trees (2014) 28:183–191
DOI 10.1007/s00468-013-0941-6

ORIGINAL PAPER

Increasing relevance of spring temperatures for Norway spruce trees in Davos, Switzerland, after the 1950s

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Received: 30 April 2013 / Revised: 16 July 2013 / Accepted: 20 September 2013 / Published online: 9 October 2013

Abstract

Key message **Relevance of spring temperatures for tree-ring growth steadily increased since 1950s. Closely linked tree-ring growth and net CO_2 exchange driven by spring temperatures.**

Abstract We investigated long-term (over 100 years) tree-ring width (TRW) variabilities as well as short-term (10 years) variations in net ecosystem productivity (NEP) in response to climate to assess the driving factors for stem growth of Norway spruce in a subalpine forest at Davos in Switzerland. A tree-ring width index (TRWi) chronology for the period from 1750 to 2006 was constructed and linked with climate data from 1876 to 2006, and with NEP available for the period from 1997 to 2006. Based on TRWi, we found that only two out of the 257 years exhibited extreme negative TRWi, compared to 29 years with extreme positive anomalies, observed mainly in recent decades. Annual temperature, annual precipitation, as well as autumn and winter temperature signals were well preserved in the TRWi chronology over the last 130 years. Spring temperatures became increasingly relevant for TRWi, explaining less than 1 % of the variation in TRWi for the period from 1876 to 2006, but 8 % for the period from 1950 to 2006 ($p = 0.032$), and even 47 % for 1997–2006 ($p = 0.028$). We also observed a strong positive relationship between annual TRWi and annual NEP ($r = 0.661$; $p = 0.037$), both strongly related to spring temperatures ($r = 0.687$ and $r = 0.678$ for TRWi and NEP, respectively; $p = 0.028$; $p = 0.032$). Moreover, we found strong links between monthly NEP of March and annual TRWi ($r = 0.912$; $p = 0.0001$), both related to March temperatures ($r = 0.767$, $p = 0.010$ and $r = 0.724$, $p = 0.018$, respectively). Thus, under future climate warming, we expect stem growth of these subalpine trees and also ecosystem carbon (C) sequestration to increase, as long as water does not become a limiting factor.

Keywords Norway spruce · Tree-ring width · Net ecosystem productivity · Climate · Subalpine forest

Introduction

Annual changes in the environment are well recorded in tree-ring widths (TRW), since tree rings integrate physiological responses of trees to climatic and environmental changes (Schweingruber 1988; Spiecker 2002). Therefore, tree rings are often used as archives of climate change (Fritts 1976; Kozlowski et al. 1991; Schweingruber 1996; Vaganov et al. 2006), in particular because instrumental records of climatic conditions for the Northern Hemisphere older than 100 years are rare. Several dendrochronological studies have shown increases in radial stem growth related to warming in subalpine regions throughout the world

Communicated by G. Wieser.

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during the last century (e.g., Neumann and Schadauer 1995; Bolli et al. 2007), most pronounced during the last decade (Rolland et al. 1998; Paulsen et al. 2000). However, changes in the environmental conditions that trees experience do not only originate from climatic changes, but also from changes in forest stand structure due to natural disturbances or management. Thus, studies of tree-ring chronologies for the last two centuries, characterized by pronounced changes in forest, are best supplemented with historical data on forest management.

In Switzerland, temperature and water regimes have already been changing over the last decades (CH 2012). For the near future, drought is expected to increase, with unknown consequences on forest ecosystems. The relatively high mortality rate of Scots pine during the last 30 years in Valais, Southern Switzerland, and the increasing crown dieback and mortality rates of European larch during recent years have been discussed with respect to climate change (e.g., Eilmann and Rigling 2012). Thus, it is crucial to increase our understanding of how and to what degree trees—which are considered significant carbon sinks—respond to such changes.

Moreover, tree rings can be used to deduce stem biomass increments over long periods (Landsberg et al. 2005; Spiecker 2002), providing archived information on the carbon accumulation in a forest. On the other hand, measurements of the exchange of carbon dioxide between biosphere and atmosphere using the eddy-covariance technique allow the quantification of net ecosystem productivity (NEP). Carbon accumulation in tree stems is reported to have a strong weight on NEP (Rocha et al. 2006; Gough et al. 2009; Grant et al. 2009; Ohtsuka et al. 2009; Stoy et al. 2009; Mund et al. 2010; Goulden et al. 2011; Metsaranta and Kurz 2012), although the link between tree-ring growth and net ecosystem CO_2 fluxes is not yet fully understood, and studies often show contradicting results: Rocha et al. (2006) reported tight relationships between TRW and net ecosystem CO_2 exchange ($r^2 = 0.85$). Similarly, Grant et al. (2009) found positive relationships between both approaches. However, other studies only mentioned similar orders of magnitude for both estimates (Mund et al. 2010; Metsaranta and Kurz 2012). Nevertheless, combining eddy-covariance measurements with tree-ring analyses seems very promising, using the benefits of both methods: information on high temporal resolution net ecosystem CO_2 fluxes and their drivers at the ecosystem scale with the long-term information on stem growth at the tree scale (Williams et al. 2005; Girardin et al. 2011). However, complementary data of these two independent data streams for forest sites are scarce, constraining the ability to generalize the coupling between TRW and NEP.

Here, we present results from the Davos Seehornwald forest, Switzerland, where information from different approaches is available: tree-ring width index (TRWi) chronology since 1750, instrumental climate records since 1876, and eddy-covariance measurements of forest net CO_2 exchange since 1997. Based on these data, we addressed the following questions:

1. Which climate drivers influenced Norway spruce tree-ring growth most strongly over the last 130 years?
2. To what degree is TRW—as a proxy for stem increment—related to NEP, representing a close link between TRW at the tree scale and NEP at the ecosystem scale?
3. Is there a common driver linking TRW and NEP?

Materials and methods

Study site

The study site is located in the subalpine zone of Switzerland in the Davos Seehornwald forest (46°48′N and 9°51′E, 1,639 m asl), where detailed ecophysiological measurements have been carried out since 1987 (Herzog et al. 1995), complemented by ecosystem CO_2 flux measurements since 1997 (Zweifel et al. 2010). Monthly temperature and precipitation data are available since 1876 (MeteoSwiss site at Davos; 46°49′N, 9°51′E; 1,594 m asl). These data were homogenized and corrected for dislocation of the Davos station in the early period of the measurements by MeteoSwiss using the homogenization procedure of Begert et al. (2005), which is divided into two main steps: the detection of inhomogeneities and the calculation of the adjustments. The annual mean temperature for the period from 1876 to 2006 is 3.14 °C, and the average annual precipitation is 997 mm. The typical growing season length according to Davos weather station data, when temperatures rise above 5 °C (see Fritts 1976; Schweingruber 1988, 1996), is around 5 months, starting in May and ending in September. Snow cover usually starts in early November and can last until May.

The dominant tree species growing in the Davos Seehornwald forest is Norway spruce (*Picea abies* (L.) Karst.). The vegetation has a maximum canopy height of 27 m (mean height around 18 m), and is considered to be moderately productive in the regional context at this altitude (Zweifel et al. 2010). The mean age of the co-dominant and dominant spruce trees is around 240 years, ranging between 200 and up to 450 years (Etzold et al. 2011). The understory vegetation is rather patchy, covering roughly 50 % of the ground, and is mainly composed of dwarf shrubs, primarily *Vaccinium myrtillus* L. and *Vaccinium* *gaultherioides* Bigelow as well as mosses. The remaining 50 % of the soil surface is covered by spruce litter without vegetation cover.

Dendrochronological analysis

Cross sections were taken from nine dominant living spruce trees at around 20 cm from the ground in autumn 2006, during a thinning event within regular forest management. Due to economical constraints, no tree cores at breast height (1.3 m height) could be taken. Nevertheless, it has been shown that tree-ring samples taken at lower heights yield similar results to those taken at breast height (Schweingruber 1988; Cherubini et al. 2002). Stem discs were dried and sanded, allowing a clear identification of individual tree rings. TRW were measured using semi-automatic devices (LINTAB measuring table) with 0.01 mm precision combined with the program TSAP (Rinntech, Heidelberg, Germany) for the period from 1750 to 2006. To avoid the influence of compression wood on TRW measurements, two to four different radii on each disc were measured and averaged. Mean tree diameter was 44 ± 15 cm (mean ± SD), ranging from 18 to 59 cm, taking into account growth patterns of different diameter classes, to avoid sampling biases (Cherubini et al. 1998; Brienen et al. 2012).

The TRW time-series were visually cross-dated and dating quality was verified using the program COFECHA (Holmes 2001). The mean age of the dominant trees sampled was 230 years. The age trend in the individual (raw) TRW chronologies was removed according to the standard procedures (method of standardization) provided by the ARSTAN Software program (Cook and Krusic 2008) by selecting a negative exponential curve ($k > 0$) or a linear regression. Standardized TRWi chronology based on the average of nine trees was used for further analysis. Then, TRWi chronology was normalized to calculate TRW anomalies, with an average of zero for the whole analyzed period and to reveal so-called pointer years (i.e., extreme cold and warm years: $\pm 1.5\sigma$).

To define a threshold level of common signals among tree-ring series, the Expressed Population Signal (EPS) was calculated based on the average correlation among trees. An EPS value higher or equal 0.85 is considered to be reliable along the entire time-series (Wigley et al. 1984). In addition, the running robust average inter-series correlation (RBAR), which is independent of sample size, was used as an indicator of common variance among tree-ring series (Wigley et al. 1984; Cook and Kairiukstis 1990). EPS and RBAR were calculated among all samples using the ARS41d_xp.exe software, with a 10-year running RBAR window with a 5-year overlap (Cook and Krusic 2008). Hamming smoothing (Blackman and Tukey 1958) with an 11-year window was used to test for long-term trends of TRWi and climate data chronologies.

Net ecosystem productivity (NEP)

CO_2 exchange rates between the atmosphere and the biosphere for the years 1997–2006 were measured by the eddy-covariance technique, consisting of a triaxial ultrasonic anemometer (Solent R2 ultrasonic anemometer-thermometer; since 2006: Solent R3-50, Gill Instruments Ltd., Lymington, UK) and an infrared gas analyser (closed-path Licor 6262; since September 2005: open-path Licor 7500, Licor, Lincoln, USA), mounted on a horizontal boom attached to the top platform of a 35 m high tower, 17 m above the mean canopy height. The eddy-covariance data were measured at 20 Hz resolution, from which 30 min averages were computed according to the European standard methodology (Aubinet et al. 2012).

In addition, a correction for temperature fluctuations (Webb–Pearman–Leuning correction; Webb et al. 1980) and self-heating of the LI-7500 instrument surface was applied to the flux measurements in 2006. For the latter correction, the procedure exactly followed the one described in Rogiers et al. (2008) and validated by Järvi et al. (2009). Then, fluxes were filtered for unrealistically high values (± 50 μmol m^{-2} 30 min^{-1}) and unfavorable atmospheric conditions such as snow, heavy rain and/or dust (window dirtiness >70 %; open-path IRGA fluxes only). Insufficient turbulent mixing of the atmosphere was accounted for using a u^* filter with a threshold of $u^* < 0.2$. Gaps in the data set, due to malfunction of instruments or filtering (as described above), were filled according to gap length. Small gaps (<2 h) were linearly interpolated. Larger daytime and nighttime gaps were filled with modeled data utilizing light (Moffat 2010) and temperature response functions (Lloyd and Taylor 1994), respectively, with a moving window of variable size. Remaining gaps were filled with a running mean approach.

In this study, we calculated NEP for every month, for the four standard climatological seasons, and for each calendar year by summing up the 30 min CO_2 flux averages over the respective periods to link it with TRWi and climate data. Positive values of NEP indicate net uptake of carbon (ecosystem acting as a C sink), while negative values represent net respiratory losses of C (ecosystem acting as a C source).

Forest management

Information on forest management was taken from earlier reports on Swiss forestry (Petitmermet 1950), studies on forest development within the Davos region (Volz 1988; Günther 1984) as well as from a compilation for our forest

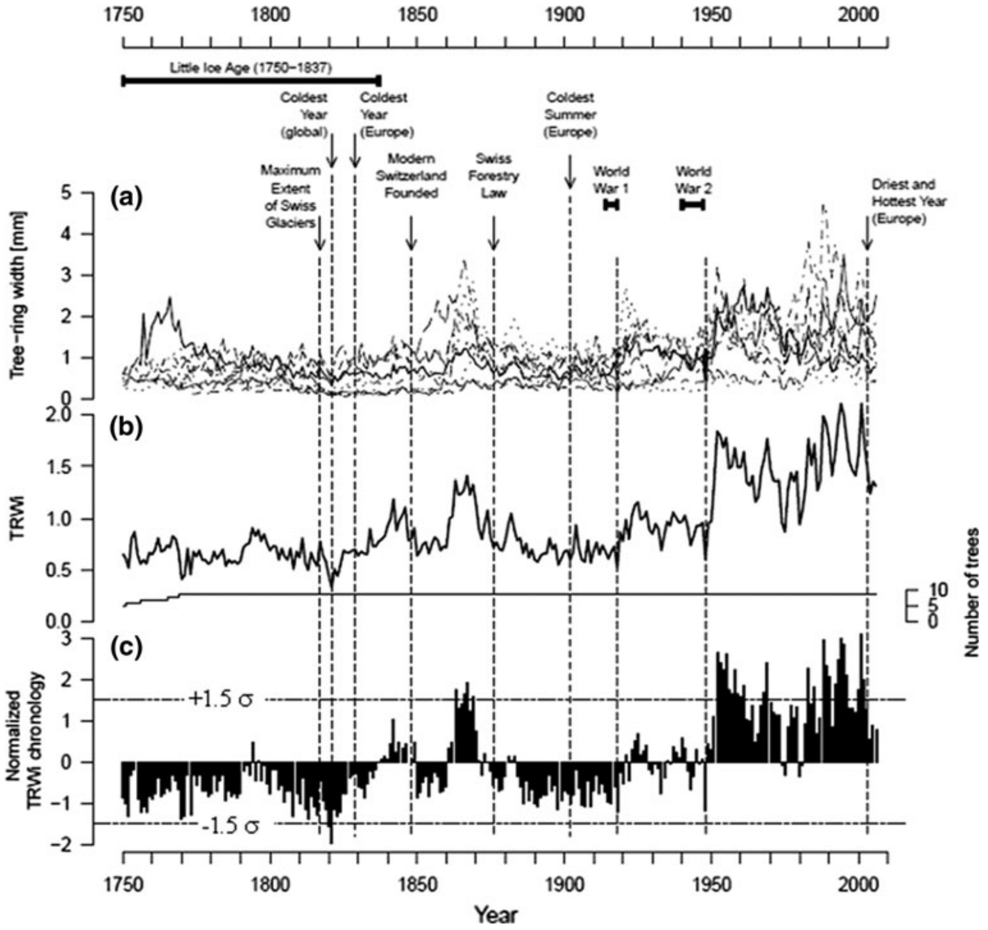

Fig. 1 Individual tree-ring width chronologies of nine trees (**a**), tree-ring width index (TRWi) and number of trees (**b**), and normalized average chronology with extreme pointer years defined as years outside the mean ± 1.5σ (*dashed lines*) (**c**) for the period from 1750 to 2006

site (Tschopp 2012). General management information dates back to the end of the nineteenth century.

Results

The mean TRW from a set of nine cross-dated individual TRW chronologies was 0.94 mm for the period 1750–2006 (Fig. 1a). Based on strong relationships among individual trees (RBAR of 0.68; EPS of 0.94), the individual TRW and the normalized average TRWi chronologies (Fig. 1b, c) were constructed. Persistently large annual width increments were observed after the 1950s.

While precipitation did not show a clear trend with time between 1876 and 2006, air temperatures have increased during these 130 years (Fig. 2b, c; Table 1). Both factors significantly influenced the TRWi of Norway spruce, in addition to winter and autumn temperatures (Fig. 2a, e, f; Table 1). Highest correlation coefficients with TRWi (unsmoothed values) were found for winter air temperatures (December to February; $r = 0.354$; $p = 0.001$) and annual mean air temperatures ($r = 0.297$; $p = 0.001$), while correlations were lower but still significant for annual precipitation ($r = 0.214$; $p = 0.014$) and autumn air temperatures (September to November; $r = 0.191$; $p = 0.029$). Spring (March to May) or summer (June to August) temperatures did not have any significant effects on the TRWi record over the 130-year period.

However, after the 1950s, among annual temperatures ($r = 0.299$; $p = 0.024$), spring temperatures became a significant climate factor ($r = 0.285$; $p = 0.032$) (Table 1). This relevance for tree-ring growth further increased when only considering the last 10 years of the long-term record. During these 10 years (1997–2006), spring temperatures showed a very tight link with TRWi ($r = 0.687$; $p = 0.028$), together with summer precipitation ($r = 0.792$; $p = 0.006$). Both climate factors, spring temperatures and summer precipitation, did increase by 0.6 °C and by 53 mm at the Davos weather station for the period from 1997 to 2006 compared to the period from 1876 to 1996, respectively.

Annual TRWi and annual NEP for the period from 1997 to 2006 were significantly correlated ($r = 0.661$; $p = 0.037$) (Fig. 3a), indicating a large contribution of stem growth to ecosystem C sequestration. In turn, both TRWi and NEP were significantly related to spring

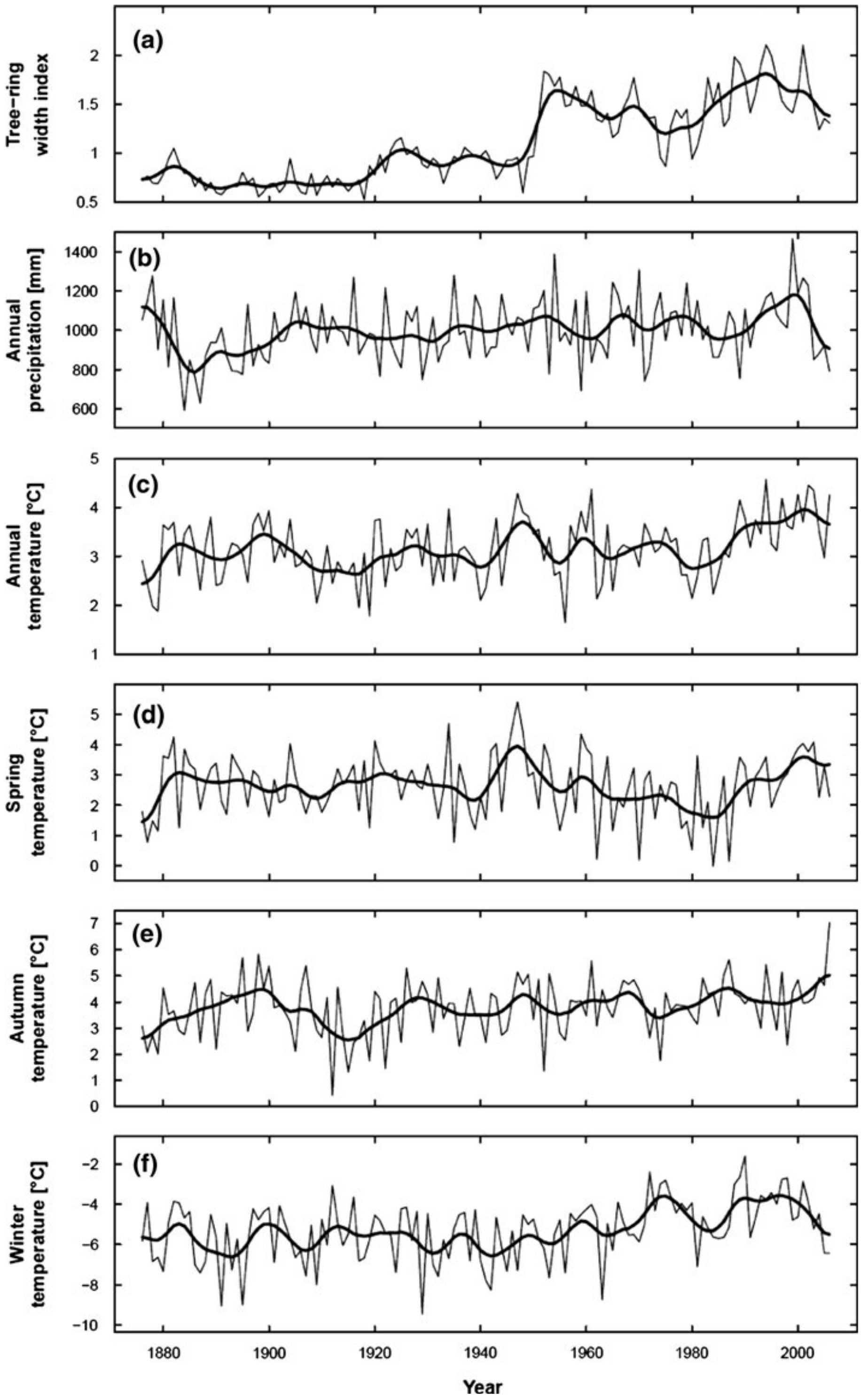

Fig. 2 Tree-ring width index (TRWi) (**a**), annual precipitation (**b**), annual temperature (**c**) as well as spring (**d**), autumn (**e**), and winter (**f**) air temperatures for the period from 1876 to 2006. The bold black curves are smoothed by a 11-year Hamming window

temperatures ($r = 0.687$ and $r = 0.678$; $p = 0.028$ and $p = 0.032$ for TRWi and NEP, respectively; 1997 to 2006; Table 1). Furthermore, high correlations were found between TRWi and monthly NEP of February ($r = 0.729$; $p = 0.017$) (data not shown) and monthly NEP of March ($r = 0.912$; $p = 0.001$) for the last 10 years (Fig. 3a). At the same time, strong positive responses of both TRWi and NEP to March air temperatures were observed ($r = 0.767$, $p = 0.010$ and $r = 0.724$, $p = 0.018$, respectively).

Table 1 Correlation coefficients between climate data and annual (unsmoothed) tree-ring width index (TRWi) and net ecosystem productivity (NEP) for the periods from 1876 to 2006, 1950 to 2006, and 1997 to 2006

Period	Parameter	Temperature					Precipitation				
		Annual	Spring	Summer	Autumn	Winter	Annual	Spring	Summer	Autumn	Winter
1876–2006	TRWi	**0.297**	0.019	−0.005	**0.191**	**0.354**	**0.214**	0.131	0.134	0.110	0.091
		$p = 0.001$	$p = 0.834$	$p = 0.960$	$p = 0.029$	$p = 0.001$	$p = 0.014$	$p = 0.135$	$p = 0.127$	$p = 0.212$	$p = 0.302$
1950–2006	TRWi	**0.299**	**0.285**	0.176	0.067	0.154	0.087	0.163	0.125	−0.004	−0.049
		$p = 0.024$	$p = 0.032$	$p = 0.189$	$p = 0.619$	$p = 0.253$	$p = 0.522$	$p = 0.225$	$p = 0.353$	$p = 0.976$	$p = 0.715$
1997–2006	TRWi	0.236	**0.687**	−0.025	−0.340	0.559	0.540	0.319	**0.792**	0.503	−0.205
		$p = 0.511$	$p = 0.028$	$p = 0.946$	$p = 0.337$	$p = 0.093$	$p = 0.107$	$p = 0.369$	$p = 0.006$	$p = 0.139$	$p = 0.569$
	NEP	0.028	**0.678**	−0.061	−0.182	−0.042	0.366	0.022	0.254	0.380	0.362
		$p = 0.939$	$p = 0.032$	$p = 0.987$	$p = 0.615$	$p = 0.908$	$p = 0.298$	$p = 0.950$	$p = 0.479$	$p = 0.279$	$p = 0.304$

Significant values are in bold

Discussion

Long-term tree-ring and climate chronologies

Only few years before 1950 were classified as extreme years, i.e., falling outside the $\pm1.5\sigma$ range around the overall mean (Fig. 1c, horizontal dashed lines). Of these extreme years, only two showed negative growth anomalies, i.e., 1820 and 1821, which is in close agreement with the Alpine climate reconstruction by Frank and Esper (2005), who identified 1821 as the year with the lowest summer (June to August) temperatures during the period 1600 to 2000. All other pointer years showed positive growth anomalies, larger than average long-term growth, i.e., in the 1860s (1863, 1866, 1867, 1869), most of the 1950s (1952–1961), 1968, 1969, and during 12 out of 20 years between 1983 and 2002 (1983, 1985, 1988–1990, 1992–1996, 2000, 2001). Such positive growth anomalies since the 1950s as in our study have also been reported by Rolland et al. (1998) for *Picea abies*, *Larix decidua*, *Pinus cembra* and *Pinus uncinata* near the alpine timberline and by Paulsen et al. (2000) studying tree rings along elevational transects at and below the upper treeline in the European Alps.

While some years with negative growth anomalies clearly showed the response to climatic anomalies (namely in 1948 or during the period of the Little Ice Age from 1750 to 1837 which includes very cold years such as 1821), others rather showed the response to severe weather events (see also Babst et al. 2012a). For example, low tree-ring growth in 1980 was probably due to the exceptionally high snow loads in September 1979, reported by Volz (1988).

The influence of climate on TRWi

Focusing on the period between 1920 and 1970, Babst et al. (2012b) also found higher correlations of TRWi with temperatures than with precipitation for the Alpine region, and a clear dominance of temperature on TRWi for Norway spruce in this time window. While annual temperature and precipitation are known to affect plant growth (Larcher 1995), high autumn (September to November) and mild winter temperatures (December to February) at this subalpine site might have two effects; (1) less frost damage, when winter and spring average temperatures are close to their norm temperatures and not anomalies and (2) less intensive frost hardening and therefore earlier and larger tree-ring growth. (1) Milder winters with less severe frost periods will reduce the risk of frost damage. This means that the water-conducting xylem vessels are less likely to be destroyed (Larcher 1995), and hence stem dehydration and embolism will become less severe (Sperry and Sullivan

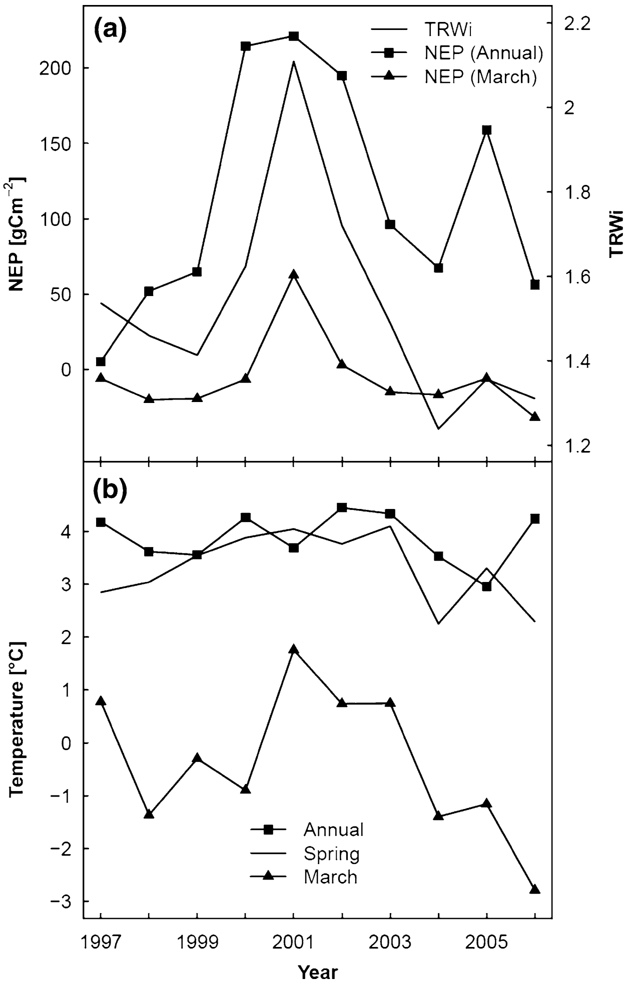

Fig. 3 Time courses of tree-ring width index (TRWi), annual net ecosystem productivity (NEP) and net ecosystem productivity of March (**a**) as well as annual average temperature, average spring and average March air temperatures (**b**) for the period from 1997 to 2006

1992; Mayr et al. 2002). Also impacts on phloem cells in the bark (Zweifel and Häsler 2000) and cell death in general will become less likely during mild winter conditions. Thus, frost-related cell repair will be less C consuming and consequently growth and biomass production can start earlier in the following spring. Thus, mild temperatures during the winter season are clearly advantageous for tree-ring growth. (2) Furthermore, frost hardening might have been impacted by increasing temperatures over the last decades. Once plants are frost hardened, their metabolic activities are highly reduced and cell division is shut down (Sakai 1970; Sakai and Larcher 1987, and literature therein). The lower the temperatures and the longer the cold winter periods, the more intensive is the frost hardening and its persistence, with negative consequences for spring metabolic activities. With increasing winter temperatures, frost hardening will not be as intensive and the de-hardening process can start earlier in spring (Sakai 1970), also contributing to increased tree-ring growth.

Changes in management recorded in tree rings between 1876 and 2006

In general, forest management in Switzerland has been obliged to adopt the sustainability concept, since the Swiss Federal Forestry Law entered into force in 1876, thus forest use should not have exceeded tree growth, although reinforcement did not start until some decades later (Petitmermet 1950). Until mid-twentieth century, forest use in Switzerland consisted of tree harvests for multiple purposes (e.g., timber, fencewood, firewood, litter); in addition, forest grazing by cattle, sheep, and goats was common (Günther 1984; Volz 1988). However, both litter raking and forest grazing strongly decreased until the 1950s (Volz 1988). During and after World War II, tree harvests in Swiss forests, particularly during the period from 1940 to 1946, were higher than usual, with about double the harvest amounts as compared with previous years (Petitmermet 1950). Forest harvests (carried out in winters) only resumed to "normal" magnitudes in winter 1946/1947. Overall, Swiss forests during the last two centuries were rather overexploited until sustainable management was reinforced around 1900 (Günther 1984; Volz 1988; Tschopp 2012); they were strongly impacted by wood demand during the two world wars (Petitmermet 1950), and are currently rather underused, with increasing wood stocks accumulating in Swiss forests (Brändli 2010; Tschopp 2012).

For the Davos forests, Tschopp (2012) reported an average harvest rate of 1.9 m^3 ha^{-1} $year^{-1}$ during the period from 1924 to 1964, which drastically decreased to an average 0.8 m^3 ha^{-1} $year^{-1}$ thereafter from 1964 to 1983. However, our TRWi data clearly show a very fast transition from average annual growth rates to increased stem biomass production (positive TRWi anomalies) in the early 1950s, which suggests that this transition in management intensities occurred already a decade earlier in the Davos Seehornwald forest compared to forests in the larger Davos region. Moreover, Tschopp (2012) analyzed aerial photographs from this period and found evidence of increasing density of the forest canopy already in the period from 1954 to 1985.

Tree-ring growth, net ecosystem productivity and climate variability

Based on mean monthly flux rates, highest net CO_2 uptake of the Davos Seehornwald forest was found in April and May compared to the rest of the year (for the years

1997–2009; Etzold et al. 2011). Similarly, Metsaranta and Kurz (2012) reported warm spring temperatures increasing net primary production (NPP) of boreal forests, pointing to the high relevance of spring conditions on tree growth and thus carbon sequestration in forests. Furthermore, the tight positive relationship between tree-ring growth and NEP found at the Davos Seehornwald forest site (Fig. 3) is supported by high-resolution point-dendrometer measurements (Zweifel et al. 2010), showing a strong link between radial diameter increments and NEP. Similar patterns were also reported by Rocha et al. (2006) who showed a highly significant relationship between TRWi and NEP for an old black spruce stand in Canada (about 150 years old), and by Jassal et al. (2010) who reported increased TRWi and simultaneously net ecosystem exchange (NEE) for three relatively young Douglas fir stands in the Pacific Northwest after 2 years of fertilization (7, 19 and 59 years old). Since no management interventions had taken place during the period from 1997 to 2006 at our site, we can exclude respective influences on such a spring-driven link.

Conclusions

In this study, we have been able to identify the high relevance of increment growth and its contribution to ecosystem C sequestration based on the combination of different approaches and data streams, i.e., long-term tree-ring growth chronology, forest management information, instrumental climate records, and high temporal resolution net ecosystem CO_2 fluxes, which would not have been possible with one approach alone. The increasing relevance of spring temperatures over time on stem growth suggests that C sequestration in woody biomass in our subalpine Davos forest might increase substantially under future climatic warming, as long as soil moisture does not become a growth-limiting factor in spring. Potential mechanisms for increased stem growth might be a combination of less frost damage and reduced frost hardening. Nevertheless, information on the long-term soil C sequestration is needed to predict the fate of the total C sequestration of this subalpine forest under future climate conditions.

Acknowledgments This work was supported by a Faculty-Exchange Grant within the Scientific and Technological Cooperation Programme Switzerland-Russia. We acknowledge the use of digital long-term climate data provided by the MeteoSwiss IDAWEB data base. We thank Rudolf Häsler who started and established the eddy covariance flux measurements at Davos Seehornwald, and Magdalena Noetzli from WSL, Switzerland, for providing tree-ring measurements. Thanks also go to Roman Zweifel for very valuable comments on an early version of the manuscript. Nina Buchmann and Werner Eugster acknowledge funding within the projects GHG-Europe (EC FP7, GA No. 244122), Carbo-Extreme (EC FP7, GA 226701) and SNSF project PDFMP3_132562/1.

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