

# An experimentally controlled extreme drought in a Norway spruce forest reveals fast hydraulic response and subsequent recovery of growth rates

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## Abstract

**Key message** An experimental drought treatment, exacerbated by a natural drought event, compromised growth in Norway spruce, but more cavitation-resistant xylem was produced and no long-term growth reductions were observed.

**Abstract** An experimental drought treatment in a mature Norway spruce forest that coincided with a rare drought event in southern Sweden in 1992, allowed us to study how such forests may respond to similar extreme events in the future. Immediately after the onset of the drought treatment, height and diameter growth decreased compared to control treatments. New xylem cells had smaller lumen and thicker walls, resulting in a more safety-orientated water transport system. The maximum growth and hydraulic system response of the 1990–1996 drought treatment coincided with the 1992 summer drought event. After the drought treatment ended, all measured traits recovered to control and irrigation treatment values after 3 years. While height and diameter growth recovered with delay, wood structure and hydraulic properties showed fast recovery. We conclude that a highly plastic response of the hydraulic system indicates a notable degree of resilience to droughts that are expected to become more common under climate change. Our results do not imply, however, that survival and

productivity of Norway spruce plantations would not be compromised under drier conditions in the future, and they apply to site conditions equivalent to the studied system.

**Keywords** Drought response · Resilience · Plasticity · Wood structure · Wood density · Hydraulic architecture · Norway spruce · Sweden

## Introduction

Norway spruce (*Picea abies* (L.) Karst.) naturally occurs under boreal conditions throughout Scandinavia and eastwards to the Ural Mountains. It also occurs naturally in lower montane areas of central Europe, typically in areas with relatively low temperatures and high precipitation. Because Norway spruce is a highly valued timber species it has been planted far beyond its natural range across Europe, often under drier and warmer conditions than observed in its natural range (Schmidt-Vogt 1977; Spiecker 2002). Norway spruce is not well adapted to such conditions because under drought, its relatively shallow root system cannot meet the demand of the transpiring crown (Puhé 2003), which can lead to reduced growth and a shortened growing season (Nilsson and Wiklund 1992). Recent research has shown that Norway spruce productivity is limited by water availability (e.g. Jyske et al. 2010), especially in the lowlands of southern Scandinavia (Mäkinen et al. 2001; Alavi 2002; Andreassen et al. 2006).

Productivity and health of Norway spruce plantations in central and northern Europe may be further challenged by climate trends towards warmer and drier conditions throughout Europe (Chmielewski et al. 2004). These altered growing conditions may be accompanied by the expected increase in duration and severity of drought

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conditions (Burke et al. 2006). While trees can, to some degree, acclimate to changing environmental conditions (Aitken et al. 2008), such plastic capacity may eventually be exceeded. Subsequently, changes in species distribution, namely a replacement of conifer forests with broadleaf forests, could occur (Hanewinkel et al. 2013). Norway spruce forests have already shown indications that they are becoming maladapted. Dry and warm summers have been associated with an increase in defoliation and mortality in southern Norway (Solberg 2004), and insect attacks caused severe losses in recent decades, which could indicate generally weakened trees (Schlyter et al. 2006).

In long-lived, immobile organisms, adaptation to changing environmental conditions is often accomplished through a plastic response rather than through natural selection. Increased resistance to cavitation through xylem structure changes are considered plastic responses to drought (Hacke et al. 2001; Hacke and Sperry 2001). One mechanism of failure under drought is air seeding at the interconnecting pit membranes, which causes cavitation (Tyree and Zimmermann 2002). The second mechanism of failure is the rupture of tracheid walls caused by a disequilibrium in pressure between adjunct water-filled and embolized cells (Hacke et al. 2001). Narrower conduits, a lower number of pits and thicker cell walls can decrease the probability of cavitation and ultimately increase the hydraulic safety of the system (Tyree et al. 1994; Hacke et al. 2001, 2004). However, such structural changes also decrease the efficiency of water transport. Therefore, conifers have to make a trade-off between hydraulic efficiency and safety.

Dalla-Salda et al. (2009, 2011) found that wood density is related to hydraulic conductivity in Douglas fir; specifically, trees with higher density had lower conductivity. For the same species, higher wood density was also found to be correlated with survival following the drought and heat wave of 2003 (Martinez-Meier et al. 2008). In contrast, by comparing populations of Douglas fir and Ponderosa pine east and west of the Cascade Mountain Range, Barnard et al. (2011) found higher vulnerability to cavitation on the dry eastern site of the mountain range. Similarly, Eilmann et al. (2009) found that Scots pine on a dry site in the central Alps produces few, but wide tracheids with thin cell walls. They concluded that this might be a high-risk strategy to rather maintain an efficient water conducting system by taking the risk of cavitation.

In mature Norway spruce, trees with faster growth and lower wood density have been found to have higher hydraulic conductivity in the trunk wood, and thus, higher risk of cavitation (Rosner et al. 2008). The xylem of leader shoots of Norway spruce on the alpine timberline, however, was found to be simultaneously efficient and safe, probably through adjustments of the pits (Mayr et al. 2003). The ratio between the thickness of the double cell wall and the

conduit lumen (cell wall reinforcement) has been found to be a better predictor for cavitation resistance than wood density (Hacke et al. 2001). To overcome the negative and potentially fatal consequences of water shortages, trees may adjust their water conducting tissue to different environments by producing new tree-rings with a xylem structure more resistant to negative hydraulic pressure (Bréda et al. 2006). This process can take several years, as the sapwood consists of multiple tree-rings. Such adjustments can be retrospectively analyzed, and allow for the combination of general growth responses and wood hydraulic traits for a holistic assessment of resistance and resilience to drought.

Resistance and resilience of Norway spruce to drought has been studied experimentally with seedlings (e.g. Turtola et al. 2003), or empirically by observing growth and physiological response to inter-annual climate variation (e.g. Bryukhanova and Fonti 2013; van der Maaten-Theunissen et al. 2013). Here, we contribute data from a large-scale, long-term experiment with mature trees that was established in response to a general decline in forest health across Europe during the 1980s and 1990s, often referred to as *Waldsterben* (Schutt and Cowling 1985). We use samples from the Skogaby experimental site in southern Sweden, where water supply for a typical 30-year old commercially planted production forest was manipulated for several years through irrigation and interception of precipitation (Nilsson and Wiklund 1992). In this experiment, drought reduced radial growth by up to 60 % and height by up to 45 % compared to the control (Nilsson and Wiklund 1992).

The experimental drought treatment from 1990 to 1996 was exacerbated by a once-in-a-100-year drought event in southern Sweden in 1992, which further allows us to study how Norway spruce plantations similar to the studied system might handle extreme events that are expected to become more frequent and severe in the future. The objective of this study is to describe the adjustments in the hydraulic properties of the xylem, represented by wood density, cell wall thickness and lumen diameter, as well as derived parameters for conductivity and cell wall reinforcement under such extreme conditions. We investigate to what degree Norway spruce can adjust hydraulic properties towards a more safety-orientated water conducting system, and we assess the plastic response of various wood hydraulic traits as well as how they relate to reduction and recovery of growth traits.

## Materials and methods

### Study site and experimental design

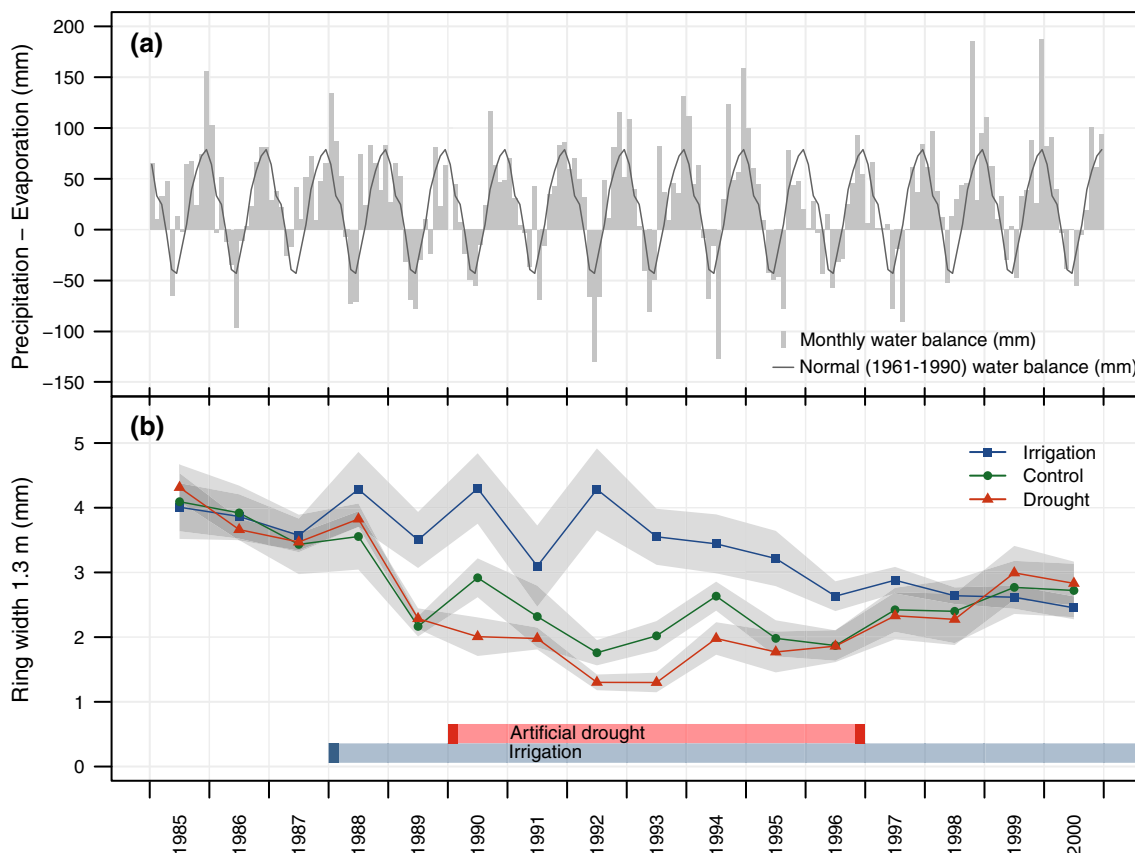
The experimental site is located about 16 km from the coast, near Skogaby in southern Sweden (Lat. 56°33'N;

Long. 13°13'E), at an elevation of approximately 100 m a.s.l. (Nilsson and Wiklund 1992). The site is characterized by a maritime climate, with an annual mean precipitation of approximately 1,150 mm and a mean annual temperature of 7.5 °C. The growing period above 5 °C is 200 days, from the beginning of April to early November (Bergholm et al. 1995). Soil conditions of the study site are characterized by a poorly developed Haplic Podzol, with a plant available water storage capacity of around 100 mm. The stand is a single-species plantation of Norway spruce and was planted in 1966, using seedlings of two different provenances from Poland. Provenance *Isebna* was planted in blocks I–III, and *Augustow* in block IV.

The experiment was laid out as a complete randomized block design with four replications (blocks I–IV). From each block we included three treatment plots, assigned to *drought*, *irrigation* and *control*. Artificial drought was applied through roofs installed 1 m above soil (Jansson 1990). Between April 1st and September 30th, this installation prevented 2/3 of the canopy through-fall from reaching the ground (Nilsson and Wiklund 1992). The drought treatment was applied for 7 years, including the

1990 to 1996 growing seasons (Bergholm et al. 1995), after which the roofing structures were removed and trees were again exposed to natural conditions. The irrigation treatment was initiated in 1988 as a second control to detect natural water deficits in addition to the experimental drought treatments (Nilsson and Wiklund 1992). This treatment was carried out beyond the end of our observation period in 2000 (Lindberg et al. 2002). Sprinkler irrigation was applied whenever the water storage deficit exceeded 20 mm (Nilsson and Wiklund 1992). The control treatment represented the natural conditions, without any manipulation.

To quantify the amount of natural drought, a monthly climatic water balance was calculated using Hargreaves's equation, implemented in the R-package *SPEI* (Beguería and Vinte-Serano 2013). Monthly climate data were obtained from the ClimateEU database (<http://www.ualberta.ca/~ahamann/data/climateeu.html>), following the methodology described by Wang et al. (2012) and Hamann et al. (2013). Inter-annual climate variability, the normal conditions (1961–1990), and the timing of experimental drought and irrigation treatments, are shown in Fig. 1.



**Fig. 1** (a) Normal monthly water balance (line) and monthly water balance (bars) over the course of the study period and (b) corresponding ring width measurements at 1.3 m for samples representing

three experimental treatments (gray ribbons indicate the standard error of the estimate). The length of the experimental treatments is indicated by horizontal bars

## Sampling and measurements

We sampled one dominant tree from every treatment plot of the statistical design. The overall sample size was 4 blocks  $\times$  3 treatments  $\times$  1 tree = 12. Cell structure was assessed for a total of 384 tree-rings representing 2 wedges  $\times$  16 years  $\times$  12 trees. Trees were felled in spring of 2002 and height increments were measured in the field. Analysis was limited to the period of 1985–2000, as the outer tree rings were affected by insect damage. Stem disks were air-dried and four 2.5 cm wide sections were cut in north, south, east and west directions. These sections were mounted on a glass plate and the surface of the samples was prepared with an ultra-precise diamond fly cutter (Kugler F500, Kugler GmbH, Salem, Germany) as described by Spiecker et al. (2000). This technique can produce a surface quality suitable for microscopy-based measurements of cell structure and wood density (Boden et al. 2012).

Wood density and tree-ring width were assessed on all four wedges using high-frequency (HF) densitometry (Schinker et al. 2003). This method measures the dielectric properties of wood by emitting and receiving electromagnetic waves, and results are highly correlated with wood density. We used a  $65 \times 680 \mu\text{m}$  probe and  $28.12 \mu\text{m}$  spacing between data points. Wood density and tree ring measurements were implemented in a two-pass approach: first, the sample wedge was fixed on a moving table (Physik Instrumente M-126.DG, Physik Instrumente GmbH & Co. KG, Karlsruhe, Germany), repeatedly photographed in constant intervals at  $25\times$  magnification to record tree-ring width and angles of ring borders relative to the sample wedge. The photographs were then merged and tree-rings were measured with digital image analysis software described in Spiecker et al. (2000). Subsequently, the tree-ring data were used for cross-dating wood density records. Based on the recorded angle of the tree-ring border, an automatic adjustment of the probe was applied in case of skewed ring borders.

Within tree-rings, cell structure was measured in two of the four sample wedges obtained for each tree: north and south directions at 1.3 m. After cross-dating, we evaluated tree-rings prior to the drought and irrigation treatments (1985–1989 and 1985–1987, respectively), during the treatment (1988–2000 for the irrigation treatment and 1990–1996 for the drought treatment) and 4 years after the end of the drought treatment (1997–2000). Tree-rings were photographed at high magnification using a black and white CCD digital camera (UK1158-M). The camera was installed on a reflected light microscope (Zeiss AxioTech vario 25 HD, Carl Zeiss AG, Jena, Germany). Photos were taken at  $500\times$  magnification with a  $1,360 \times 1,024$  image size for an effective resolution of 4.95 pixels per  $\mu\text{m}$ .

Using an in-house developed semi-automatic image analysis software (*Zellstruktur*), the successive images were re-assembled to create a seamless array for every tree ring (Spiecker et al. 2000). Rows of comparatively small tracheids indicate that they were cut closer to their tapered ends, and further from their longitudinal center (DeSoto et al. 2011). Therefore, we have excluded rows of tracheids which had lumen diameters below  $2/3$  of the largest lumen diameter found on the respective image.

Radial diameter of cells and cell lumen, cell wall thickness, and the number of cells were measured along three radial rows per section, resulting in six rows per tree ring. Cell wall thickness was calculated as the sum of half of the two adjunct cell walls of each cell. To calculate the proportion of latewood of each annual ring, cell structure data were separated into early- and latewood following Mork's definition, where a cell gets classified as latewood if its cell wall thickness multiplied by 2 is equal or greater than half of its radial lumen diameter (Denne 1988). Hydraulic conductivity was calculated following the law of Hagen–Poiseuille as the sum of cell lumen diameters of each tree ring to the power of four ( $\sum d^4$ ). Cell wall reinforcement was calculated following Hacke et al. (2001) as  $(t/b)_n^2$ , where  $t$  is the double cell wall thickness and  $b$  is the hydraulic conduit diameter ( $d_h$ ). To estimate the hydraulic conduit diameter, the formula  $\sum d^5 / \sum d^4$  provided by Kolb and Sperry (1999) was used.

## Statistical analysis

To test for significance of treatment effects on the dependent variables, repeated measures ANOVAs were performed in the R programming environment (R Development Core Team 2013) using the *lmer* function for mixed models of the package *lme4* (Bates et al. 2012). The drought, control and irrigation treatments were specified as a fixed effect, and block and year were specified as random effects to account for auto-correlation in repeated tree-ring measures within trees. Post-hoc tests were performed using the *glht* function implemented in the *multcomp* package (Hothorn et al. 2008) with a Bonferroni adjustment to experiment-wise  $p$  values to allow for multiple inference. To account for the initial differences between drought, irrigation, and control treatments, the mean difference between treatments and control in three common years prior to treatment was subtracted from the drought and irrigation series.

While cell structure is often analyzed separated into earlywood and latewood (e.g. Park and Spiecker 2005), we show complete profiles of cell lumen diameter and cell wall thickness, which allows for a more detailed assessment of within-ring variation. Mean profiles were calculated in two steps: first, the series of measurements from an individual

sample was linearly interpolated to a common interval number according to the mean number of cells within treatments and within treatment years, using the *approx*-function of the R base-package. Secondly, arithmetic mean profiles were calculated across all samples per tree and all trees per treatment and treatment year.

## Results

### General growth patterns and response to treatments

The climatic water balance between 1985 and 2000 is displayed by gray bars in Fig. 1a): positive values indicate a water surplus while negative values represent water deficits. The dark line overlaying these gray bars represents the mean water balance calculated from the standard 1961–1990 climate baseline period. Particularly unusual water deficits are therefore revealed when observed water deficits fall below this normal range. Climatic conditions during the field experiment were generally constant, with slightly wetter conditions in the beginning and the end of the observation period and somewhat drier summers and higher moisture deficits from 1989 to 1995 (Fig. 1a). The year 1992 stood out with an almost complete lack of precipitation for a period of 8 weeks in June and July, representing the most severe drought event in southern Sweden in the last 100 years (Nilsson 1997). The water deficit exceeded the normal conditions threefold in June of 1992, exacerbating the experimental drought treatment to an extreme level. The years from 1998 to 2000 had only marginal water deficits during the growing season.

In general, the radial growth response at 1.3 m followed moisture availability in the control and drought treatments, while the irrigation treatment appears largely unaffected by moisture limitations. Overall, ring width declined from the beginning to the end of the observation period (Fig. 1b). Within this general trend, ring width appears to show a limited response to particularly dry years including 1989 (all treatments), 1992 (drought and control) and 1995 (control). The onset of the drought treatment shows an immediate effect (deviation of control and drought treatment in 1990), whereas the onset of the irrigation treatment had some effect in 1988, but diverged substantially during the year with naturally drier conditions, starting 1989 (Fig. 1a). The generally positive response of the irrigation treatment indicates that the experimental site is a water-limited system.

Standard errors of the estimates imply sufficient precision to evaluate treatment effects, although high variability among trees of the irrigation treatment is apparent as well (Fig. 1b). Statistical analysis suggests significant response to drought and irrigation treatments in all measured traits,

at an experiment-wise  $\alpha$ -level of 0.05 (Table 1). Growth traits, as measured by ring width at 1.3 and 10 m as well as height increments, were negatively affected by drought and positively influenced by irrigation. Under drought, trees had smaller cell diameters, a larger proportion of latewood, smaller cell lumen and thicker cell walls. The hydraulic conductivity was reduced, and cell walls reinforced. As a result, mean wood density was lower for the irrigated trees and higher for trees under drought treatment. Significantly more and larger cells were produced under the irrigation treatment than under the control and drought treatment, accounting for the observed increase in ring width.

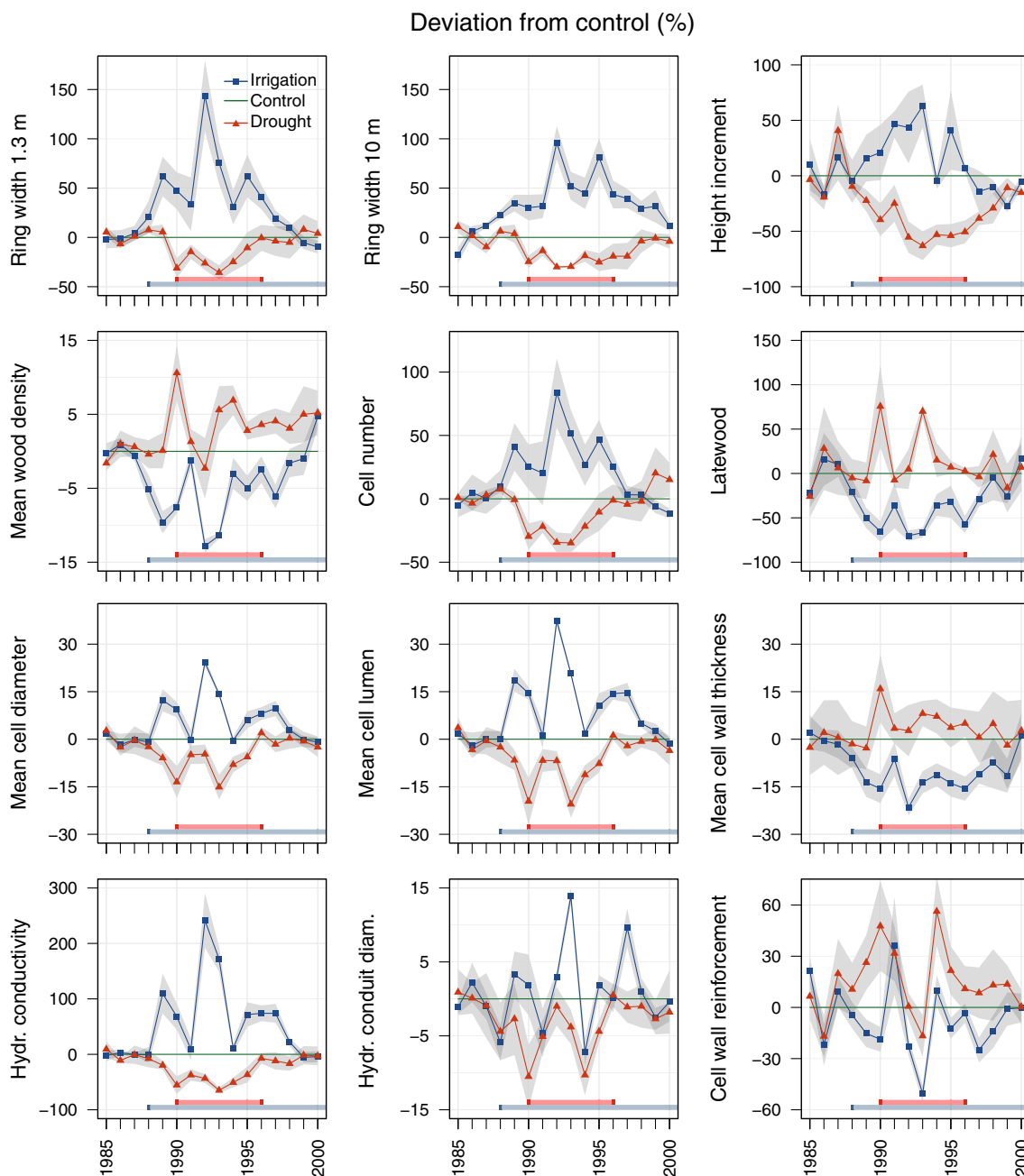
### Timing of plastic response and recovery

Changes to wood traits, cell hydraulic traits and growth traits appear to be pronounced and immediate at the onset of the drought treatment (Fig. 2, divergence of red lines in 1990). Peak effects of the drought treatment were observed in 1992, corresponding to the general drought, or during the subsequent 1993 growing season. In contrast, the irrigation treatment had strong effects for most traits starting in 1989, coinciding with general water limitations due to reduced precipitation. The largest effects of the irrigation

**Table 1** Comparison of treatment effect on growth and cell structure variables based on treatment years (1990–1996)

Trait	Drought	Control	Irrigation
Ring width 1.3 m (mm)	1.74 (0.10)a	2.21 (0.12)b	3.50 (0.20)c
Ring width 10 m (mm)	2.72 (0.15)a	3.53 (0.15)b	5.33 (0.20)c
Height increment (cm)	24.0 (2.43)a	46.3 (3.40)b	60.2 (4.25)c
Wood density (Volts)	5.12 (0.06)a	4.92 (0.08)b	4.61 (0.03)c
Cell number	51.1 (2.73)a	66.8 (3.53)b	92.3 (5.21)c
Latewood proportion (%)	21.3 (1.24)a	17.8 (1.67)a	8.52 (1.03)b
Mean cell diameter ( $\mu\text{m}$ )	29.7 (0.51)a	32.0 (0.59)b	34.6 (0.31)c
Mean cell lumen diam. ( $\mu\text{m}$ )	23.2 (0.53)a	25.9 (0.74)b	29.4 (0.33)c
Mean cell wall thickn. ( $\mu\text{m}$ )	6.43 (0.14)a	6.04 (0.20)a	5.19 (0.09)b
Hydraulic conductivity ( $\mu\text{m}^4$ )	4.5e+7 (4.4e+6)a	8.0e+7 (8.94e+6)b	1.4e+8 (7.9e+6)c
Hydraulic conduit diam. ( $\mu\text{m}$ )	36.8 (0.49)a	38.8 (0.66)b	39.1 (0.38)b
Cell wall reinforcement ( $(t/b)_h^2$ )	0.032 (0.002)a	0.028 (0.004)ab	0.023 (0.001)b

Standard errors are provided in parentheses. The same lower case letter among treatments within a row indicates that there is no significant difference ( $\alpha$ -level = 0.05)



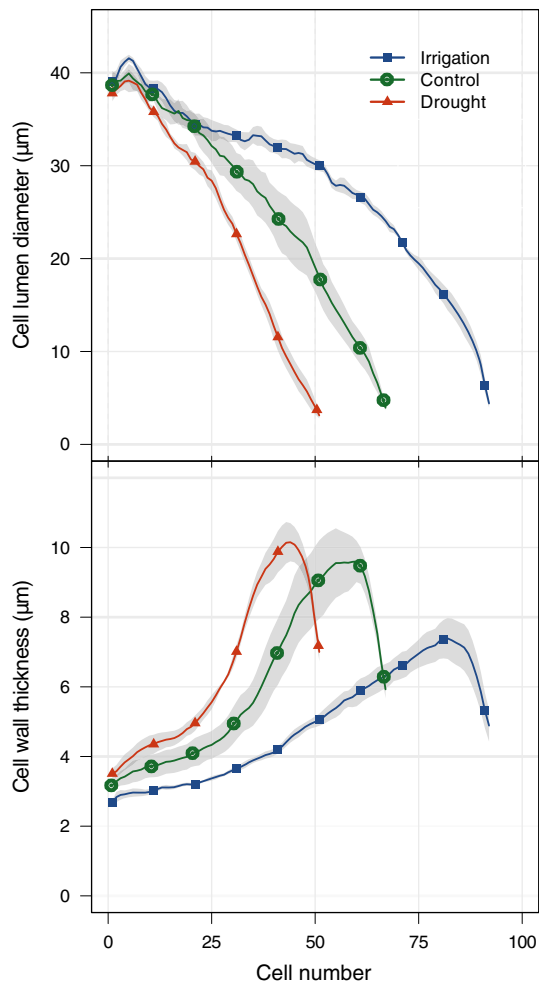
**Fig. 2** Inter-annual variation, treatment response, and recovery for 12 traits. Units for all measurements are percent deviation from the control treatment. *Gray ribbons* indicate the standard error of the

estimates, and the length of the experimental treatments is indicated by *horizontal bars* as in Fig. 1

treatment on all growth and cell hydraulic traits coincided with the 1992 drought event.

After the drought treatment ended in late 1996, most growth traits showed a fast recovery to the level of the control treatment (Fig. 2). For ring width at 1.3 m, drought-treated trees recovered immediately to values comparable to the control trees. In the 10 m stem disks, the recovery appears to be more delayed after the end of the

drought treatment. Recovery of annual height increments seems particularly slow, while measured with good precision. In contrast, parameters describing cell structure and including cell diameter, cell number, cell lumen and hydraulic conductivity which could also be measured with high precision, show fast recovery rates after the drought treatment ended. Our data are somewhat inconclusive for other traits including cell wall thickness, cell wall



**Fig. 3** Within-tree-ring profiles of cell wall thickness and cell lumen diameter. The graphs represent the distribution of cells types throughout individual tree rings, averaged over the common experimental treatment period (1990–1996). *Gray ribbons* indicate the standard error of the estimates

reinforcement, hydraulic conduit diameter, latewood proportion, and wood density, which showed high standard errors toward the end of the study period.

#### Within-tree-ring response

The mean course of growth within the growing season is represented by the cell lumen and cell wall thickness profiles in Fig. 3. The first data point represents the beginning of cell division while the last data point shows the end of the production of new cells. The three curves show a general gradient from wet (irrigation) to dry (drought treatment). Under the drought treatment, trees produced cells with thicker cell walls and smaller lumen diameters. In contrast, irrigated trees produced cells with thinner cell walls and larger lumen diameter. This effect is visible starting with the first cell produced at the beginning of the

growing season. The slope of cell wall thickness and cell lumen curves is steeper for the drought treatment than for the irrigated trees. This is accompanied by a different length of the curves, caused by an increased number of produced cells through better water supply for the control and irrigated trees. Strong differences are visible between maximal and minimal cell wall thickness. While drought-treated trees had a high proportion of cells with thick cell walls, few cells with large lumen were produced. On the contrary, irrigated trees had generally thinner cell walls, but larger lumen diameters.

## Discussion

### Growth response to drought

The growth response to the irrigation treatment was not apparent in the first year, indicating that growing conditions were not water-limited at the onset of the experiment. In all subsequent years, however, the strong positive response to irrigation relative to the control treatment implies that forest growth was drought limited, even without the experimental intercept of precipitation. Note that the general decline in growth includes an age effect as new wood is allocated to a larger circumference. Therefore, growth response should primarily be evaluated among treatments rather than over time. As expected, the onset of the drought treatment caused immediate negative effects on diameter and height growth, which conforms to similar studies with experimentally controlled water supply in different locations in Europe (e.g. Bergh et al. 1999; Jyske et al. 2010).

All traits describing hydraulic efficiency and safety suggest that the drought treatment caused the production of a water conducting system orientated towards safety. This becomes evident especially by comparison with the irrigation treatment, where trees produced xylem with twice the hydraulic conductivity. The profiles of within-tree-ring variation of cell lumen diameter and cell wall thickness suggest that this pattern holds true from the first cell onwards. The hydraulic response observed in our study does not conform to Eilmann et al. (2009), who studied adaptation of Scots pine (*Pinus sylvestris* L.) xylem structure. Under xeric conditions these authors found a decreased number of cells in combination with thinner cell walls but increased lumen diameter. They concluded that this may be a strategy to use scarce carbon to produce an efficient water conducting system at the expense of higher cavitation risk. Indications for a similar strategy were found for Douglas fir and Ponderosa pine (Barnard et al. 2011). Our data suggest that this high-risk strategy does not apply to Norway spruce in the studied system. Instead, we

observed a more safety-orientated wood structural response, at the expense of lower efficiency of the water conducting system, and temporary reduction of growth rates. The result conforms to Park and Spiecker (2005) and Bryukhanova and Fonti (2013), confirming a safety oriented drought resilience strategy in Norway spruce.

#### Resilience through plastic response

Our results of rapid plastic response in wood hydraulic traits further conform to Bryukhanova and Fonti (2013), where trees quickly adjusted their hydraulic system to inter-annual variations. Plasticity can also be observed intra-annually, as shown by Rozenberg et al. (2002), where wood density of Norway spruce followed water availability throughout the growing season. High plasticity of hydraulic properties indicates a mechanism of acclimation to rapidly changing environmental conditions. In turn, this could allow for successful colonization of sites with a broader range of moisture regimes. Despite the strong effect on productivity, mature trees investigated in this study have also proven to be remarkably resilient, fully recovering to growth rates of the control within about 1–3 years after an experimental drought that was exacerbated by a once-in-a-100-year extreme drought event. Jyske et al. (2010) found a similar rapid recovery in a drought experiment on Norway spruce. The data suggest that drought events associated with climate change may compromise productivity, but may not easily induce mortality under studied site conditions. Instead, trees showed a remarkable plasticity in wood and cell structural traits to quickly acclimate to varying levels of water availability under realistic field conditions.

Dendrometer data acquired on the same site by Nilsson and Wiklund (1992) suggest that the artificial drought shortened the growing period of the sample trees, seemingly causing less matter produced through photosynthesis. In the course of the treatment, trees might have adjusted their shoot/root ratio by reduced height growth and increased litter fall, as well as higher fine root mortality (Nilsson and Wiklund 1992). These adjustments might account for the prolonged recovery phase of height and diameter growth at 10 m after the end of treatment. Wood density of drought-treated trees, however, remained high until the end of our observation period (the year 2000). Relatively large standard errors for cell wall thickness near the end of the experiment do not clearly indicate whether wood density is due to thicker cell walls or changes in cell wall chemistry.

#### Implications for climate change

Future climate change according to the CMIP3 multi-model projections for southern Sweden predict a slight

average increase in summer precipitation of +3 mm by 2080, with values ranging from –92 mm to +109 mm across 16 climate models and three scenarios (B1, A1B, A2) (Wang et al. 2012; Hamann et al. 2013). Projected increases in mean annual temperature range from 1.8 to 4.5 °C by the end of the century, depending on the model and scenario used, with an overall average of 2.9 °C. Such temperature shifts lead to higher evaporation and, correspondingly, a reduction in the water balance of 48 mm by the 2050s and by 59 mm by the 2080s. This change might initially appear small in absolute terms (e.g. Fig. 1a), but the consequence becomes apparent when comparing this change to the typical inter-annual variation in water balance during the 1961 to 1990 climate normal period. This period had a water balance mean of 440 mm, and a standard deviation of 31 mm. Since the water balance is projected to decrease by 48 mm, this represents a change of 1.5 standard deviations (48 mm/31 mm). This in turn shifts the probability of a once-in-a-100-year drought event from 1 % (99th percentile) to 20 % (80th percentile), implying a 1 in 5-year frequency of severe drought by the 2050s. By the 2080s, the equivalent calculation yields a 1 in 3-year drought frequency.

Our findings suggest that Norway spruce is able to acclimate to some degree of drought stress and recover within several years from exceptional drought conditions. Therefore, it may initially remain a suitable tree species under climate change, but we should not presume that these resilience mechanisms can protect plantations if climate shifts such as those outlined above occur. Many studies have already shown that Norway spruce productivity is water-limited, and a projected high frequency of severe droughts toward the end of the century may also compromise survival by increasing the susceptibility of trees to secondary damage through insects, pathogens and wind-throw (Turtola et al. 2003; Schlyter et al. 2006). Drought response has been suggested as being under at least partial genetic control in Norway spruce (Rozenberg et al. 2002). By implication, it is important to assess the extent of genetic control over drought response in Norway spruce populations in order to select the most appropriate planting stock for a changing climate.

We should also emphasize that our results are limited to conditions represented by the study site and stand. The study site at Skogaby was carefully chosen to represent typical environmental conditions where production forests of Norway spruce would be planted in north and central Europe. Site characteristics include anthropogenic pollution and a relatively unfavorable nutrient regime because the species is often planted on soils that have been depleted by centuries of agricultural use (Spiecker 2002). Nevertheless, one should be careful to generalize our results to all types of Norway spruce plantations. Because long-term



experiments in mature stands are expensive and are unlikely to be sufficiently replicated to make landscape-scale inferences, our research needs to be interpreted in the context of other empirical studies and monitoring efforts.

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

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