**Responses of sapwood ray parenchyma and non-structural carbohydrates (NSC) of
Pinus sylvestris to drought and long-term irrigation**

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Summary

1. Non-structural carbohydrates (NSC) play a crucial role in tree resistance and resilience to drought. Stem sapwood parenchyma is among the largest storage tissue for NSC in mature trees. However, there is a limited mechanistic understanding of how NSC reserves, stem parenchyma abundance, and growth rates are interrelated, and how they respond to changing water availability.
2. We quantified NSC, ray parenchyma abundance and ring width along four successive 5-year radial sapwood segments of the stem of 40 mature *Pinus sylvestris* trees from a 10-year irrigation experiment conducted at a xeric site in Switzerland.
3. Percentage of ray volume (PERPAR) varied from 3.75 to 8.94% among trees, but showed low intra-individual variability. PERPAR responded positively to irrigation with a lag of several years, but was unrelated to %NSC. %NSC was lower in wider rings. However, wider rings still contained a larger NSC pool that was positively related to next year's ring growth.
4. Our results suggest that stem ray parenchyma does not limit NSC storage capacity, but responds to long-term environmental drivers with years of delay. The observed carbon allocation patterns indicate a prioritization of storage over growth independent of growth conditions, likely as a mechanism to ensure long-term survival. Furthermore, NSC pool size proved to be a determinant for the inter-annual auto-correlation in tree-ring growth. Our study highlights the importance of long-term multi-parameter studies to better understand tree responses to environmental variability at different time-scales.

49	Keywords:
50	Carbon allocation
51	Drought stress
52	Growth vs. storage
53	Ring width auto-correlation
54	Structure-function relationships
55	Tree-ring anatomy
56	Xylem anatomy
57	Xylem rays

Introduction

Ongoing global warming is enhancing stress across most of Earth's terrestrial biomes (IPCC 2013). Increases in the length, frequency, intensity, and spatial extent of drought episodes are expected to reduce forest productivity and increase drought-induced tree mortality rates (Breda *et al.* 2006; Allen *et al.* 2010; Carnicer *et al.* 2011). Long-term impacts include alterations in the global carbon cycling (Reichstein *et al.* 2013) and shifts in biomes and global biodiversity (Gonzalez *et al.* 2010; Mantyka-Pringle *et al.* 2015), with severe economic consequences (Hanewinkel *et al.* 2013). Understanding tree responses to drought is thus a very active field of plant science research (Lloret *et al.* 2013).

Two key processes play a major role in determining the processes of drought-induced stress and mortality: embolism-induced hydraulic failure and carbon starvation (McDowell *et al.* 2008). Yet, the current understanding of non-structural carbohydrate (NSC) mobilization during drought (Sala, Woodruff & Meinzer 2012), the recognized role of NSC in removing emboli from xylem conduits (Salleo *et al.* 2009; Johnson *et al.* 2012), and the assumed negative effect of water deficit on phloem transport (Hölttä, Mencuccini & Nikinmaa 2009; Sevanto 2014) points to the tight link between these two processes and their coupling with tree water and carbon balances (Hartmann 2015). Carbon starvation is postulated to occur during prolonged drought when long-term reduction of assimilation, typically in association with factors such as crown defoliation and mistletoe infestation, leading to NSC reserve depletion (Galiano, Martínez-Vilalta & Lloret 2011; Sala, Woodruff & Meinzer 2012; Adams *et al.* 2013; Jacquet *et al.* 2014; Yan *et al.* 2016). However, there are counterexamples showing no reduction or even increases in stored NSCs during drought (Sala & Hoch 2009; Muller *et al.* 2011; Anderegg & Anderegg 2013). Such discrepancies reveal the large variability of possible plant responses and the still modest understanding of NSCs roles for

coping with water deficit (McDowell *et al.* 2011; Sala, Woodruff & Meinzer 2012; Mencuccini 2014). Furthermore, the allocation of carbon to NSC reserves competes with structural growth (Muller *et al.* 2011), posing interesting questions about carbon allocation priority during periods of limited carbon uptake (Sala, Woodruff & Meinzer 2012; Hartmann & Trumbore 2016). For example, the availability of older NSC pools to support future growth would alleviate direct allocation trade-offs between NSC storage and structural carbon (Richardson *et al.* 2015).

NSC concentrations are generally higher in actively growing tissues such as leaves, fine roots and the phloem (Hoch, Richter & Körner 2003; Pruyn, Gartner & Harmon 2005; Gruber, Pirkebner & Oberhuber 2013). Yet, the stem sapwood – owing to the large biomass – is the most important NSC storage organ for mature temperate trees, where it accounts for 25-41% of whole-tree NSC reserves (Jacquet *et al.* 2014). NSC concentrations are not evenly distributed in the sapwood, but typically show a decrease from the outer to the inner sapwood (Saranpää & Höll 1989; Hoch, Richter & Körner 2003; but see Würth *et al.* (2005) for other patterns). In stem sapwood, NSCs are exclusively stored in parenchyma cells, which in conifers are almost entirely confined to the rays (Plavcová & Jansen 2015), a specialized storage and transport tissue which radially integrates the sapwood with the cambium and phloem (Spicer 2014; Pfautsch, Hölttä & Mencuccini 2015). The activity of rays decreases from the outer to the inner sapwood and eventually completely stops in the heartwood as parenchyma cells die (Gartner, Baker & Spicer 2000). Rays are also important for providing carbohydrates and water to refill embolized conduits (Salleo *et al.* 2009; Brodersen & McElrone 2013; Spicer 2014), the formation of heartwood (Bamber 1976), the defence against pathogens (Hudgins *et al.* 2006), wounding responses (Arbellay, Stoffel & Bollschweiler 2010; Arbellay, Fonti & Stoffel 2012), and contributing to the mechanical strength of the wood (Burgert & Eckstein 2001; Fonti & Frey 2002).

Despite the crucial role that rays play in tree functioning, our knowledge about the factors that influence ray abundance is scarce. Based on the importance of rays for NSC storage, it could be hypothesized that variations in ray volume are closely linked to the changes in NSC storage requirements (Myer 1922; von Arx, Archer & Hughes 2012), which could be referred to as “storage space constraint” hypothesis. If evidence supporting this hypothesis were found, i.e. a close relationship between percentage of NSC and the relative abundance of ray volume in the wood, time series of ray volume derived from quantitative wood anatomical analysis of tree rings would allow the reconstruction of past NSC pools. This hypothesis is further supported by several studies suggesting that higher ray abundance could be connected to greater tree vigour and / or higher growth rate (see von Arx *et al.* (2015) for a review). Furthermore, ray abundance has been shown to depend on environmental influences including climate variability (Olano *et al.* 2013), site productivity (Fonti *et al.* 2015), flooding (Arbellay, Fonti & Stoffel 2012), fire injury (Arbellay *et al.* 2014) and water availability (Esteban *et al.* 2012; von Arx, Archer & Hughes 2012).

In this study we investigated the impact of a decade-long irrigation on the abundance of ray parenchyma and the NSC reserves in mature *Pinus sylvestris* L. (Scots pine) trees growing at a xeric site in Switzerland. *Pinus sylvestris* closes stomata at relatively high xylem water potential (‘isohydric’; Irvine *et al.* 1998; Zweifel, Steppe & Sterck 2007) and therefore is a good candidate to address questions of carbon mobilization and depletion in response to drought (see Saranpää & Höll 1989; Galiano, Martínez-Vilalta & Lloret 2011; Zweifel *et al.* 2012; Poyatos *et al.* 2013). Our investigation was performed within the framework provided by the Pfynwald long-term irrigation experiment, where previous studies have reported increases in tree-ring width (Eilmann *et al.* 2011), shoot and needle length (Dobbertin *et al.* 2010), crown density (Eilmann, Dobbertin & Rigling 2013) and fine root growth and turnover rates (Brunner *et al.* 2009; Herzog *et al.* 2014). We measured NSC reserves and rays in

5-year blocks of tree rings in the stem sapwood of 40 mature trees. Our aim was to quantify the relationship among ray abundance, NSC storage and growth, and to better understand how these relationships are affected by changes in water regime. In detail, we asked: a) How do NSC levels and percentage of ray volume (PERPAR) respond to alleviation from long-term drought stress? b) How are NSC and PERPAR distributed along the stem sapwood? c) Are NSC levels related to PERPAR, *i.e.* is NSC storage constrained by PERPAR (“storage space constraint” hypothesis)? d) Does NSC availability affect secondary growth rates and does this relationship differs between irrigated and control trees?

Materials and methods

Experimental setup and site conditions

The study was performed at the Pfynwald long-term irrigation experiment, located in the driest part of the Swiss Rhone valley (46°18' N, 7°36' E, 615 m asl). The site is part of a xeric Scots pine (*Pinus sylvestris*) forest with some interspersed pubescent oak (*Quercus pubescens* Willd.) trees in the understory. Stand density is 730 stems · ha⁻¹ with a basal area of 27.3 m² · ha⁻¹ and a homogeneous tree top height of about 11 m. The climate is continental with a mean annual temperature of 10.1 °C and mean annual precipitation of 603 mm (MeteoSwiss, climate data for 1981–2010 from Sion, at 20 km distance from site). The soil is a skeletal pararendzina, with low water holding capacity. The experimental site consists of eight 25 × 40 m rectangular plots arranged side by side and separated by a 5 m buffer strip. Since 2003, four of the plots have been irrigated with sprinklers at night during the growing season (April to October). This irrigation corresponds to a supplementary rainfall of about 700 mm per year. The beginning of the irrigation treatment coincided with the extreme heat wave in summer 2003 (Schaer *et al.* 2004). Climate during the irrigated growing seasons (2003–2012) was on

average warmer (+0.80 °C) and drier (-51 mm) compared to the pre-treatment period (1993-2002, Sion, MeteoSwiss). For each tree, the level of mistletoe infestation on a four-step scale and the percentage of crown defoliation (Dobbertin, Hug & Mizoue 2004) have been annually monitored.

Sampling and data collection

Twenty mature pine trees per treatment (40 trees total) of similar age and size were randomly selected whilst controlling for equal numbers per plot and similar average degree of mistletoe infestation (Table 1). Thus, anomalously vital or suffering trees based on crown defoliation data were not considered to avoid results that might only apply to extreme situations. Tissue for NSC measurement was sampled from all trees by taking four 5-mm stem cores at breast height from the north, east, south and west side of each tree on March 5th 2013, *i.e.* before the onset of bud break to avoid influences by differences in phenological stage (Palacio *et al.* 2008). In any case, sampling date is not assumed to influence the outcome of the study since NSC pools in the stem sapwood of Scots pine has been shown to be comparably stable throughout the year (Fischer & Höll 1992; Hoch, Richter & Körner 2003; Oberhuber *et al.* 2011). Cores were bagged and put on dry ice in a cooler immediately after sampling. To eliminate enzymatic activity, after returning to the lab, cores were microwaved at 600 W for >90 seconds (Popp *et al.* 1996) and subsequently air-dried in an oven at 65 °C for three days. In May 2013 one 10-mm increment core was extracted adjacent to the NSC samples to quantify ring-width and ray abundance. After the 2013 growing season (December), one additional micro-core was collected per tree to quantify ring width of 2013. A single core for growth analysis was assumed sufficiently representative due to the concentric ring growth in this flat stand. Ring widths were measured using a LinTab measuring system (Rinntech,

Heidelberg, DE). The exact calendar years for all individual rings were assigned via tree-ring crossdating and subsequently verified using COFECHA (Grissino-Mayer 2001).

Ray quantification

Rays were quantified in high-resolution images of anatomical samples from all 40 cores. Therefore, cross-sections of <15 µm thickness perpendicular to the axially oriented tracheids were cut from the 10-mm cores with a sledge microtome (WSL Lab-microtome), placed on a slide, and stained with Alcian blue (1% solution in acetic acid) and safranin (1% solution in ethanol). This staining procedure results in blue unligified (parenchyma) and red ligified (tracheid) cells. Afterwards, the cross-sections were dehydrated using a series of ethanol solutions of increasing concentrations, washed with xylol, and then permanently preserved by embedding them into Eukitt glue (Kindler GmbH, Freiburg, Germany; Gärtner & Schweingruber 2013). Overlapping images covering the entire samples were captured with a Nikon D90 digital camera mounted on a Nikon Eclipse 50i optical microscope with 100× magnification and merged to a single image using PTGUI v8.3.10 Pro (New House Internet Services B.V., Rotterdam, NL; von Arx et al. 2016). All rays of the outermost 20 years (comprising 10 years before and 10 after the onset of irrigation) were then quantified in the merged images as described in (von Arx et al. 2015). In short, rays and the annual ring borders were manually outlined using a tailored clone of ROXAS v1.6 (von Arx & Dietz 2005; von Arx & Carrer 2014), a specialized image analysis tool based on Image-Pro Plus (Media Cybernetics, Silver Spring, Maryland, USA). The final sample width ranged from 7 to 9 mm, resulting in mean PERPAR values being within ±5-6% (rel. 95% confidence interval) of the true values (von Arx et al. 2015). The automatic output included the percentage of ray surface (PERPAR) for each year, which is a good estimate of the percentage of ray volume (von Arx et al. 2015).

NSC measurements

Increment cores designated for NSC measurements were cut in 5-year segments starting from the bark for the first 20 years (resulting in two pre- and two post-treatment segments), and a fifth segment including all remaining sapwood rings (between seven and 57 rings). Five-year segments were chosen to provide sufficient wood material for reliable NSC measurements, because of the generally small growth rates. The width of the sapwood segments from outer to inner sapwood were (mean $\pm$ SE) 3.6 ± 0.4 , 3.4 ± 0.5 , 5.1 ± 0.6 , 5.7 ± 0.6 and 28.7 ± 2.8 mm in control trees, and 6.1 ± 0.6 , 6.1 ± 0.8 , 3.3 ± 0.5 , 4.5 ± 0.7 and 31.3 ± 2.6 mm in irrigated trees. Corresponding segments from different cores of the same tree were then pooled and milled. Extraction of NSC followed the anthrone technique (Olano, Menges & Martinez 2006). This technique provides an estimate of NSC content per wood dry weight (%NSC), distinguishing between the contribution of soluble mono- and oligosaccharides and non-soluble carbohydrates (starch). %NSC was calculated for each tree and radial segment by adding soluble and insoluble carbohydrate contribution. A proxy for total NSC content or pool size (TNC) per sapwood segment was calculated by multiplying the basal area of each 1-cm wide sapwood segment by %NSC of the corresponding sapwood segment. TNC measurement units are thus $\text{g} \cdot \text{g}^{-1} \cdot \text{cm}^2$, which could be converted into g by multiplying by wood density and considering segment height. We use it here without units for sake of simplicity.

Statistical analysis

We established a linear mixed-effect model to assess the irrigation effect on PERPAR in the outermost sapwood segment (2008-2012). We only evaluated this segment because we considered it unaffected by any transition effects immediately after irrigation started. The

fixed term included treatment, %NSC, mean ring width of the outermost segment (as a proxy for tree growth rate), stem diameter (a surrogate for tree size), mistletoe infestation level, percentage of crown defoliation (both as indicators for tree health status), and the interactions of treatment with %NSC, mean ring width and stem diameter. Plot identity was considered as a random effect to account for pseudo-replication on plot level (Annex S1).

The factors determining PERPAR variability at annual scale were tested with a linear mixed-effect model. The fixed term included treatment and period (before *vs.* after onset of treatment) and its interactions as well as annual tree-ring width (as a proxy for tree growth rate) and stem diameter in 2012 (as a surrogate for tree size). The considered random effect terms were plot and tree identity, the latter to account for multiple measurements per tree. The initial model also included a first-order autocorrelation structure to consider year-to-year dependence of PERPAR within individual trees (Annex S1). Furthermore, as a measure for the inter-annual variability and thus sensitivity of PERPAR within individuals, we calculated the “mean sensitivity”, i.e. the mean relative change of PERPAR from year to year (Cook & Pederson 2011); and as a measure for the consistency of yearly variability in PERPAR among individuals, we calculated the mean Pearson’s correlation between the individual series (“ r_{bt} ”; Cook & Pederson 2011).

We performed a linear mixed-effect model to test the NSC “storage space constraint” hypothesis and the potential drought-release response on the outermost sapwood segment (2008-2012). The rationale behind this approach was that NSC mobilization and depletion in the outer sapwood were expected to be larger than in the inner segments (Richardson *et al.* 2013). The fixed term included PERPAR, treatment, mean ring width of the outermost segment, stem diameter, mistletoe infestation level, percentage of crown defoliation, and the

interactions of treatment with PERPAR, mean ring width and stem diameter. Plot identity was considered as a random effect (Annex S1).

The radial distribution of %NSC (total, soluble, insoluble) at the sampling date was analysed with a linear mixed-effect models. The fixed terms included segment position with five levels and treatment. The random terms included plot and tree identity. No autocorrelation structure was considered in this analysis because NSC is mobile (Annex S1).

We followed the same two-step approach to select the best model for all mixed models following Zuur *et al.* (2009). First, we compared different random terms to choose the random component that best fitted the data. The fixed part of the mixed-effect model was then selected by sequentially removing non-significant terms using dredging methods. All possible reduced models fitted by ML (maximum likelihood) were then compared based on AICc to obtain the “optimal” model. The optimal model was refitted by the REML (restricted maximum likelihood) method to obtain estimates and significances of effects. When several models showed $\Delta AICc \leq 2$, the simplest model was chosen for the sake of parsimony (see Annex S1 for details on model selection). Homoscedasticity and normality of residuals were verified graphically.

Finally, we analysed how a high vs. low level of TNC stored in the outermost segment (2008-2012) affected tree-ring growth of the following year (2013). In this analysis, it was necessary to account for individual tree growth trends, and for the strong collinearity between TNC and mean tree-ring width ($r=0.865$). Individual tree growth trends were removed by dividing the ring width of 2013 by the mean ring width of the outermost segment (2008-2012). To account for the collinearity between TNC and tree-ring width, we performed the classification into low and high TNC level separately for ring-width classes of 0.25 mm on the basis of the

respective median TNC value. The class size of 0.25 mm was chosen to balance a high spatial resolution with a robust classification of TNC level. We then compared the obtained relative growth rate between the two TNC levels using Student's t-test.

Statistical analyses were performed in R version 3.1.3 (R Development Core Team 2015) including the packages “nlme” (Pinheiro *et al.* 2016) and “MuMIn” (Barton 2016). Details about model selection are available in Appendix S1 in the Supporting Information.

Results

Trees from both treatments did not differ in age, stem diameter and number of sapwood rings (Table 1). Tree-ring width was larger in the irrigated than the control trees in the irrigation period (2003-2012; *t*-test, $t = 3.21$, $P = 0.003$), while this relationship tended to be inversed for the pre-irrigation period (1993-2002, $t = 1.82$, $P = 0.077$). This change was related to a positive treatment response in irrigated trees ($t = 2.49$, $P = 0.017$), whereas growth in control trees decreased during the treatment period ($t = 2.55$, $P = 0.015$; Fig. 1a). Furthermore, irrigated trees contained larger TNC at the end of the treatment ($t = 2.11$, $P = 0.042$; Table 1).

Determinants of variability in PERPAR across the sapwood

In absolute terms, ray abundance increased strongly with TNC in the outermost 5-year segment (2008-2012; Fig. 2a) due to the collinearity of both variables with ring width. However, the optimal linear model for the percentage of ray surface (PERPAR) in the outermost segment did not reveal any significant relationships with treatment, %NSC, ring width, stem diameter, mistletoe infestation level or percentage of crown defoliation (intercept $\pm$ SE: 5.796 ± 0.196 , $t = 29.590$, $P < 0.001$; Fig. 2b, 3a). Nevertheless, at an annual time scale,

PERPAR significantly increased in irrigated trees during the treatment period (2003-2012) relative to the control trees (Fig. 1b, Table 2). This treatment response occurred with a temporal lag of several years (Fig. 4b). Annual PERPAR was also strongly negatively related to ring-width (Table 2). Interestingly, in control trees, this negative relationship between PERPAR and ring width was superimposed by a concomitant decrease in both variables during the treatment period, *i.e.* the short- (annual) and long-term (decadal) responses showed opposing patterns (Table 2, Fig. 4b). The variability in PERPAR from year to year was not significantly correlated between the control and irrigated trees (*Pearson's* $r = 0.37$, $P = 0.104$) when considering the entire study period (1993-2012), but it significantly co-varied during the pre-treatment period (1993-2002; *Pearson's* $r = 0.64$, $P = 0.045$; Fig. 4b) when all trees experienced the same conditions. Despite these significant relationships, it has to be noted that the average relative change of PERPAR from one year to the next was rather low with a mean sensitivity of only 0.11 in both treatments, and the consistency among individuals was also low as reflected by the mean correlation between annual time series („r_{bt}“) of only 0.052 for control and 0.027 for irrigated trees.

The small high-frequency variability within individuals (mean sensitivity) contrasted with the large differences among individuals: PERPAR averaged over the 1993-2012 rings varied from 3.75 to 8.94%, with a mean $\pm$ SD of $5.93 \pm 1.07\%$.

Determinants of variability in NSC across the sapwood

The optimal linear model for %NSC in the outermost five tree rings only included a negative effect of tree-ring width (estimate $\pm$ SE: -0.876 ± 0.302 , $t = -2.904$, $P = 0.006$), but no significant influence by treatment, dbh, mistletoe infestation and crown transparency. The slope of this relationship thus translates into a decline in %NSC of nearly 0.9% for each

millimetre of tree-ring width (Fig. 3b). In contrast, the TNC significantly increased with tree-ring width (Fig. 3c), which is clearly due to the dependency of TNC from basal segment area.

The optimal linear mixed-effect model revealed a decrease in %NSC from the outermost (2008-2012) to the innermost (<1993) sapwood segment independent from treatment (Fig. 1c). Higher %NSC levels in the outer sapwood segment were mainly related to a drop in the soluble NSC fraction, whereas the low values in the innermost sapwood reflected a drop in insoluble NSC (Fig. 1c, Table 3).

In absolute terms, the innermost sapwood segment had the largest contribution (43 %) to TNC in both control (mean $\pm$ SE: $42.4 \pm 6.8\%$) and irrigated trees ($43.5 \pm 6.3\%$) (Fig. 1d). This is primarily a consequence of the greater number of tree-rings and the associated large basal segment area, despite the lower %NSC. The contribution to TNC by the four outer sapwood segments was rather homogeneous in the control trees (average in three middle segments: $13.3 \pm 1.0\%$, outmost segment: $17.7 \pm 2.2\%$), but was relatively larger in the outer sapwood in irrigated trees (average in three middle segments: $10.9 \pm 0.9\%$, outmost segment: $23.7 \pm 2.7\%$), mainly because of the increase in ring width (Fig. 1a).

Influence of NSC pool size on growth

TNC in the annual rings of 2008-2012 (sampled prior to the growing season in early March 2013) was strongly related to tree-ring width in the next growing season (sampled in December 2013; Fig. 5a). When relative changes in tree-ring growth vs. TNC were considered, tree rings formed in 2013 were significantly wider when TNC pool size in the previous five annual rings of 2008-2012 was larger ($t = 2.608$, $P = 0.014$; Fig. 5b).

Discussion

Ray abundance responds with delay to moister conditions, but is unrelated to %NSC

The lack of a pronounced treatment effect on the mean percentage of ray surface (PERPAR) contrasts with the strong response of other morphological and anatomical tree traits such as tree-ring growth (Fig. 4a), shoot and needle length (Dobbertin *et al.* 2010; Feichtinger *et al.* 2015), needle density (Feichtinger *et al.* 2015), fine root growth (Brunner *et al.* 2009; Herzog *et al.* 2014), resin duct production (Rigling *et al.* 2003), and cell lumen diameter and cell wall thickness (Eilmann *et al.* 2009) to irrigation in different experimental sites in the study region. In contrast, PERPAR seemed to scale mostly allometrically with other tissues to maintain a certain level of integration within the xylem (Fonti *et al.* 2015). Yet, in the control trees PERPAR declined in the last years of the experiment, simultaneously with a decrease in tree-ring width, while it remained unchanged, and thus relatively increased, in the irrigated trees (Table 2, Fig. 1b, Fig. 4b). This lagged response of PERPAR in the control trees to naturally warmer and dryer conditions possibly initiated by the extreme year of 2003 could indicate that the mean level of PERPAR might adjust to changes in general growth conditions only at the mid-term, possibly along with changes in tree vitality (Gartner, Baker & Spicer 2000). Furthermore, and in contrast to the multi-year time-scale, PERPAR and tree-ring width were negatively related on an annual time-scale (Table 2). This may indicate different determinants depending on the time-scale, i.e. contrasting short-term responses to weather conditions driving PERPAR and ring width, and similar long-term responses related to conditions improving tree vigour and thus both PERPAR and ring width (see also Fonti *et al.* 2009).

Our results do not support the hypothesis that the need for NSC storage space determines the relative amount of ray parenchyma in the stem (“storage space constraint” hypothesis). This

outcome was unexpected considering i) the importance of ray parenchyma for NSC storage, ii) the fact that species with higher %NSC in their stem sapwood such as the angiosperms (Hoch, Richter & Körner 2003) also show a greater PERPAR (Spicer 2014), and iii) the observation from other studies that more vital trees usually have a greater PERPAR (Gartner, Baker & Spicer 2000) and, likely, also a greater NSC pool (Carbone *et al.* 2013). In contrast, our findings suggest for Scots pine that NSC storage space in the stem is usually not limited, and that PERPAR in the stem might indicate, at best, the maximum potential NSC storage capacity (von Arx, Archer & Hughes 2012; Plavcová & Jansen 2015).

More generally, we were not able to explain the considerable variability in mean PERPAR among individuals. However, considering it was not related to tree size, growth rates, crown condition, mistletoe infestation and %NSC, we speculate that genetic differences among individuals may be responsible for differences in PERPAR among individuals, as already observed in other anatomical traits (Fichot *et al.* 2009). The rather low year-to-year variability within individuals might reflect the fact that once initiated, rays grow and extend to keep the connection with the cambium and phloem (Fischer & Höll 1992; Spicer 2014). The only way to control PERPAR from one year to the next is therefore by changing ray height and width and/or the initiation rate of new rays (von Arx *et al.* 2015). However, the presence of a common inter-annual variability between irrigated and control trees before treatment, but not after the onset of irrigation, is in line with the high-frequency response of ray parenchyma to environmental factors found by Olano *et al.* (2013).

Radial NSC storage patterns in sapwood indicate a gradient in ray activity and use of NSC

In line with previous studies in conifers and angiosperms (Saranpää & Höll 1989; Hoch, Richter & Körner 2003; Pruyn, Gartner & Harmon 2005), %NSC decreased from the outer to

inner sapwood (Fig. 1a). This pattern may reflect different activities of the sapwood (Pruyn, Gartner & Harmon 2002) and therefore different requirements for NSC. In the outer sapwood, NSC requirements are highest for respiration and growth (Carbone *et al.* 2013), but probably also for other demands including maintaining hydraulic integrity (Sala, Woodruff & Meinzer 2012; Sevanto 2014), a critical issue considering that the outer sapwood usually contributes most to overall sap flow (Cermak & Nadezhdina 1998). Equilibrating short-term asynchrony between carbon demand and supply (Sala, Woodruff & Meinzer 2012) leads to an intense exchange of sugars with the phloem (Richardson *et al.* 2013). In the intermediate part of the sapwood, the NSC pools are probably turned over less frequently and mainly serve as longer term reservoir and to maintain metabolic activity of the living (parenchyma) cells (Carbone *et al.* 2013). Such a gradient in NSC concentration and the observed drop in the soluble carbohydrates from the outer to the middle zone are consistent with a “last in, first out” mechanism of NSC dynamics (Richardson *et al.* 2013). The innermost part of the sapwood is generally less active with respect to water transport, respiration and storage (Cermak & Nadezhdina 1998; Gartner, Baker & Spicer 2000; Pruyn, Gartner & Harmon 2002). Yet, it maintained relatively high %NSC. This raises the question whether these reserves are still mobile or sequestered (van Bel 1990; Palacio *et al.* 2013) and/or used for heartwood formation (Saranpää & Höll 1989). Addressing this question would, however, require a higher spatial and temporal resolution of NSC measurements than performed here.

The NSC pool size (TNC) in the inner sapwood was considerable, and accounted for 43% of all NSC stored in the entire sapwood in both treatments (Fig. 1b). If these carbohydrate reserves were not accessible (Palacio *et al.* 2013), the available NSC pool for growth would be much smaller than suggested by some studies (Ryan 1989; Hoch, Richter & Körner 2003). The significant increase of the TNC and tree-ring width in the outermost two segments (*i.e.*, during the treatment) in the irrigated trees (Fig. 1b,d) indicates that supplemental water

improved tree vitality both in terms of long-term resources (TNC) and shorter term competitiveness (higher growth rates).

Carbon allocation to growth and storage depends on available resources

Our results indicate different carbon allocation strategies depending on available resources. First, wider tree rings showed a lower %NSC, but higher TNC irrespective of treatment (Fig. 3b,c). In other words, more vigorous trees allocated relatively more NSC into ring growth than storage, while still increasing their NSC pool size. Such a carbon allocation pattern that depends on tree vitality and growth conditions could be an evolutionary strategy to balance short- and long-term fitness. If a vigorous tree allocates proportionally and absolutely more carbon to growth, it increases its short-term competitive ability, while concomitantly building up a larger NSC pool that likely increases long-term safety and resilience (Sala, Woodruff & Meinzer 2012), thus fostering future tree performance. On the other hand, if tree vitality is low and/or carbon might become limited, prioritizing carbon allocation to storage over tree-ring growth is consistent with a “bet-hedging” strategy to reduce short-term risks and improve long-term fitness (Stearns 1976; Chapin, Schulze & Mooney 1990; Wiley & Helliker 2012). An evergreen species as Scots pine with several active sapwood rings certainly has more degrees of freedom in this respect, because it can survive with barely or even without any (ring) growth in a specific year (Rigling *et al.* 2002), as long as the leaf area and therefore the required water-conducting tissue do not change (Zweifel *et al.* 2006), and sufficient carbohydrates are available for vital functions (Pruyn, Gartner & Harmon 2002; Zha *et al.* 2004; Sala, Woodruff & Meinzer 2012). If this pattern would only show in control trees, one could argue that water deficit will limit cell division and enlargement (Hsiao & Acevedo 1974), NSC mobilization and transport in the phloem (Sevanto 2014), but the same relationship between %NSC, TNC and ring width showed in the irrigated trees for which we

can reasonably exclude any significant water limitation. Our results thus suggest an active control of carbon storage as opposed to a passive overflow storage of carbon not used for growth (Sala, Woodruff & Meinzer 2012; Saffell *et al.* 2014).

Our second important finding in this context – the positive effect of a larger NSC pool size (TNC) on next year's growth (Fig. 5a,b) – supports the aforementioned view, but is also exciting in another respect: it suggests a physiological role of TNC in explaining the auto-correlation of tree-ring growth. In a year following ample carbon accumulation, rings are wider, and here we found direct and novel evidence that the concomitant increase in the TNC carries over to the growth of the following year. Consistently, the irrigated trees with a larger NSC pool size also showed a stronger and longer auto-correlation in ring width (Fig. 5c). Although larger cells would also result in wider rings without requiring more carbon, evidence from other conifer species showed a correlation of $r \geq 0.97$ between ring width and number of cells (Olano *et al.* 2012, Gricar *et al.* 2015). Our interpretation is also supported by correlations between NSC levels and secondary growth (Desoto, Olano & Rozas 2016), as well as evidence found by Carbone *et al.* (2013) for a link between NSC pool size (and age) and ring growth using ^{14}C methods in red maple trees.

Conclusion

A reasonable assumption is that ray abundance, NSC reserves and growth rate are all linked and respond to environmental drivers in synchrony to maintain homeostasis in tree functioning. However, our results show that ray abundance in the stem sapwood of Scots pine is a rather constant characteristic that shows low-frequency responses to long-term changes in external conditions delayed by several years, and that does not seem to be controlled by NSC storage demand. From the tree functional point of view, it is puzzling to observe that ray

abundance varies that much among trees, given the pivotal role of rays for tree carbon and water cycle. The high low-frequency variability in ray abundance, coupled with the only weak coherence among individual times-series, suggests a high intrinsic, i.e. genotypic control of ray abundance – a hypothesis that still needs to be tested. From a methodological point of view, our results highlight the different perspectives obtained by performing NSC analyses on tree-ring compared to metric levels. We also found it was relevant to consider both NSC concentration and NSC pool size. While the NSC concentration seems to be the relevant metrics for processes on tissue level such as respiration, transport and maintenance of hydraulic integrity, the NSC pool size likely reflects the carbon allocation to growth *vs.* storage. From a life-history strategy point of view, the carbon allocation patterns observed here rather support a prioritization of storage over growth (“active storage”) than passive overflow storage in the isohydric Scots pine. Overall, we encourage to perform more research on – long-term – ray variability within and among individuals, including the internal and environmental drivers of this variability, and how rays vary in other tree organs, notably branches and roots, in order to improve the mechanistic understanding of the role that this vital tissue plays for tree functioning and performance.

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Data Accessibility

All data used in this manuscript are present in the supporting information (Table S1-S5).

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Tables:

Table 1. Characterization of the sampled *Pinus sylvestris* trees from the control and irrigated plots at the Pfywald experimental site (means $\pm$ SE; bold face – significant differences between treatments based on *t*-test, $P \leq 0.05$).

Treatment	Control	Irrigation
Number of trees	20	20
Tree age [yrs.]	83.3 $\pm$ 7.0	95.2 $\pm$ 3.5
Stem diameter (DBH) [cm] 2003	19.3 $\pm$ 1.3	22.0 $\pm$ 1.1
Crown defoliation [%] 2003-2012	28.8 $\pm$ 1.6	28.9 $\pm$ 2.6
Mistletoe infestation level [levels: 0-3] 2003-2012	1.48 $\pm$ 0.21	1.71 $\pm$ 0.21
Number of sapwood rings	51.8 $\pm$ 3.7	57.2 $\pm$ 2.5
Sapwood area [cm ²]	187.9 $\pm$ 22.7	258.4 $\pm$ 27.3
Mean tree-ring width [mm] 1993-2002	1.08 $\pm$ 0.12	0.78 $\pm$ 0.12
Mean tree-ring width [mm] 2003-2012	0.71 $\pm$ 0.09	1.22 $\pm$ 0.13
NSC concentration in all sapwood [%]	2.83 $\pm$ 0.07	2.87 $\pm$ 0.05
NSC pool size in all sapwood	5.30 $\pm$ 0.66	7.42 $\pm$ 0.82
% Ray surface 1993-2002	6.01 $\pm$ 0.25	5.99 $\pm$ 0.25
% Ray surface 2003-2012	5.79 $\pm$ 0.27	5.92 $\pm$ 0.24

819 **Table 2.** Results of the linear mixed-effect model to explain the annual percentage of ray
 820 surface (PERPAR) in the period 1993-2012 for *Pinus sylvestris* trees growing at the Pfywald
 821 experimental site.

Fixed effects	Estimates	SE	<i>P</i>	Random	SD	Phi
Intercept	0.811	0.020	<0.001	Tree ID	0.083	0.471
Treatment (irrig.)	-0.012	0.027	0.653			
Period (2003-2012)	-0.033	0.008	<0.001			
Ring width	-0.041	0.006	<0.001			
Treat. × Period	0.046	0.012	<0.001			

822 SE: standard error of fixed effect estimates, SD: standard deviation of random factor, Phi:
 823 autocorrelation coefficient
 824 PERPAR log-transformed to meet normality criteria.

Table 3. Results of the linear mixed-effect models explaining NSC concentration (%NSC; overall, soluble, insoluble) in the sapwood of *Pinus sylvestris* trees growing at the Pfywald experimental site.

Response	Fixed effects	Levels	Estimates	SE	P	Random	SD
%NSC	Intercept	–	0.347	0.013	<0.001	Tree ID	0.031
	Segment	Segment ≤1992 ^a	0	0.013	<0.001		
		1993-1997 ^b	0.147	0.017			
		1998-2002 ^b	0.168	0.017			
		2003-2007 ^b	0.171	0.017			
		2008-2012 ^c	0.326	0.017			
%NSC soluble	Intercept	–	-0.071	0.018	<0.001	Tree ID	0.047
	Segment	Segment ≤1992 ^a	0	0.018	<0.001		
		1993-1997 ^b	0.071	0.023			
		1998-2002 ^b	0.113	0.023			
		2003-2007 ^c	0.176	0.023			
		2008-2012 ^d	0.455	0.023			
%NSC insoluble	Intercept	–	0.130	0.016	<0.001	–	–
	Segment	Segment ≤1992 ^a	0	0.016	<0.001	–	–
		1993-1997 ^{bc}	0.189	0.023			
		1998-2002 ^{bc}	0.202	0.023			
		2003-2007 ^b	0.165	0.023			
		2008-2012 ^c	0.213	0.023			

SE: standard error of fixed effect estimates, SD: standard deviation of random factor

All response variables log-transformed to meet normality criteria.

Different superscript letters for segment estimates indicate significant differences at $P < 0.05$.

Figures:

Fig. 1. Mean tree-ring width (a), percentage of ray surface (PERPAR) (b), NSC concentration (%NSC) (c), and NSC pool size (TNC) (d) in the stem sapwood of *Pinus sylvestris* growing at the Pfynwald irrigation experiment (Salgesch, Switzerland) in radial 5-year segments from 1993-2012 and all remaining sapwood (≤ 1992 ; control: 31.8 ± 3.7 yrs., irrigated: 37.2 ± 2.5 yrs.). The dashed vertical lines indicated the onset of the irrigation treatment (2003). Values are means of 20 individuals per treatment ± 1 SE. Check [Table 3](#) for significance of segment differences.

Fig. 2. Relationship between NSC levels and ray abundance in the outer sapwood (2008-2012) of *Pinus sylvestris* growing at the Pfynwald irrigation experiment (Salgesch, Switzerland). (a) NSC pool size (TNC) vs. total ray surface, (b) NSC concentration (%NSC) vs. percentage of ray surface (PERPAR). Each symbol represents data from one tree (n=20 for each treatment). r – Pearson correlation coefficient. No correlation coefficient reported for TNC vs. total ray surface because both are based on basal segment area.

Fig. 3. Relationships between percentage of ray surface (PERPAR; a) NSC concentration (%NSC; b) and NSC pool size (TNC; c) with mean tree-ring width in the outer sapwood (2008-2012) of *Pinus sylvestris* growing at the Pfynwald irrigation experiment (Salgesch, Switzerland). Each symbol represents data from one tree (n=20 for each treatment). The triangle symbols in (b,c) indicate an outlier tree that was excluded from analyses because it showed abnormally lower %NSC in the outer than the middle segments. r – Pearson correlation coefficient.

Fig. 4. Chronologies of ring width (a) and percentage of ray parenchyma (PERPAR; b) $\pm$ 95% confidence intervals for the 10 years before (1993-2002) and the 10 years after (2003-2012) the onset of irrigation for *Pinus sylvestris* growing at the Pfynwald irrigation experiment (Salgesch, Switzerland). Means are based on 20 individuals for each treatment. Note the truncated y-scale in (b). Vertical lines separate the pre- from the post-irrigation period. Horizontal lines give mean values for each treatment and period. Ring-width showed a significant decrease (control) and increase (irrigated) from the pre- to the post-treatment period (t -test, $P \leq 0.001$), whereas PERPAR decreased significantly only in the control trees (t -test, $P = 0.020$).

Fig. 5. Relationship of tree-ring width 2013 to total NSC content (TNC) as quantified in the previous year in the outermost sapwood rings (2008-2012). (a) tree-ring width 2013 vs. TNC 2008-2012, (b) ratio of tree-ring width 2013: 2008-2012 for low and high TNC 2008-2012 (see Methods for details to the low vs. high TNC classification); the size of the symbols reflect tree-ring width in 2013, the dashed horizontal reference line indicates identical tree-ring width for 2013 and 2008-2012. Each symbol represents data from one tree (n=20 for each treatment). (c) Auto-correlation of ring width for control and irrigated trees. Data from control and irrigated trees were pooled in panel (b).

Supporting Information

Appendix S1. Details on statistical model selection.

a) Determinants of PERPAR in outmost segment (2008-2012)

Initial linear-mixed effect model:

Response	Fixed effects	Random effect
PERPAR	Treat. × %NSC + Treat. × MRW + Treat. × DBH + Crown transp. + Mistletoe inf.	Plot ID

Checking for best random structure, if any (selected model in bold italics):

Random structure	AICc
None	154.5
Plot ID	158.6

Best linear models ($\Delta AICc \leq 2$, selected model in bold italics):

Fixed effects	AICc
None	134.0
DBH	135.3
RW	135.6
Treat.	135.9
Mistletoe inf.	135.9

b) Determinants of annual PERPAR across the sapwood

Initial linear-mixed effect model:

Response	Fixed effects	Random effect
Log ₁₀ (PERPAR)	Treat. × Period + RW + DBH	Plot ID, Tree ID

Checking for best random structure, if any (selected model in bold italics):

Random structure	AICc
Tree ID	-2261.9
Plot ID, Tree ID	-2259.9
Plot ID	-1537.4
None	-1488.2

Checking for need of first-order auto-correlation structure model (selected model in bold italics):

Response	Fixed effects	Random effect	Auto-correlation	AICc
Log₁₀(PERPAR)	Treat. × Period + RW + DBH	Tree ID	Year Tree ID	-2403.6
Log ₁₀ (PERPAR)	Treat. × Period + RW + DBH	Tree ID	–	-2261.9

Best linear mixed-effect models ($\Delta AICc \leq 2$, selected model in bold italics):

Fixed effects	AICc
Treat. × Period + RW	-2404.9
Treat. × Period + RW + DBH	-2403.6

c) Determinants of %NSC in outmost segment (2008-2012)

Initial linear-mixed effect model:

Response	Fixed effects	Random effect
%NSC	Treat. × PERPAR + Treat. × MRW + Treat. × DBH + Crown transp. + Mistletoe inf.	Plot ID

Checking for best random structure, if any (selected model in bold italics):

Random structure	AICc
None	139.1
Plot ID	143.2

Best linear models ($\Delta AICc \leq 2$, selected model in bold italics):

Fixed effects	AICc
MRW	119.1
MRW + Mistletoe inf.	120.5
MRW + Crown transp.	120.5
MRW + PERPAR	120.8

d) Determinants of %NSC across the sapwood

Initial linear-mixed effect model:

Response	Fixed effects	Random effect
Log ₁₀ (%NSC)	Segment + Treat.	Plot ID, Tree ID

Checking for best random structure, if any (selected model in bold italics):

Random structure	AICc
Tree ID	-430.8
Plot ID, Tree ID	-428.6
Plot ID	-424.0
None	-426.1

Best linear mixed-effect models ($\Delta AICc \leq 2$, selected model in bold italics):

Fixed effects	AICc
Segment	-432.9
Segment + Treatment	-430.8

e) Determinants of %NSC soluble across the sapwood

Initial linear-mixed effect model:

Response	Fixed effects	Random effect
Log ₁₀ (%NSC sol.)	Segment + Treat.	Plot ID, Tree ID

Checking for best random structure, if any (selected model in bold italics):

Random structure	AICc
Tree ID	-270.3
None	-267.8
Plot ID, Tree ID	-265.0
Plot ID	-262.5

Best linear mixed-effect models ($\Delta AICc \leq 2$, selected model in bold italics):

Fixed effects	AICc
Segment	-296.3
Segment + Treatment	-296.0

f) Determinants of %NSC insoluble across the sapwood

Initial linear-mixed effect model:

Response	Fixed effects	Random effect
Log ₁₀ (%NSC insol.)	Segment + Treat.	Plot ID, Tree ID

Checking for best random structure, if any (selected model in bold italics):

Random structure	AICc
<i>None</i>	-342.4
Tree ID	-340.2
Plot ID, Tree ID	-340.6
Plot ID	-262.5

Best linear models ($\Delta AICc \leq 2$, selected model in bold italics):

Fixed effects	AICc
Segment + Treatment	-342.4
<i>Segment</i>	-341.8

942 **Table S1.** Annual mean tree-ring width and basal segment area of all study trees.

	ID	Plot	Tree-ring width [mm]						Basal segment area [mm ²]				
			YYYY-1992 *	1993-1997	1998-2002	2003-2007	2008-2012	2013	YYYY-1992 *	1993-1997	1998-2002	2003-2007	2008-2012
Control	8	1	1.39	1.70	1.64	1.20	0.98	0.63	14102	4384	4650	3683	3166
	41	1	1.01	0.80	0.82	0.49	0.63	0.41	6168	1422	1558	992	1329
	52	1	1.16	1.98	1.26	0.69	1.26	1.3	10065	4087	2912	1710	3307
	64	1	1.02	1.37	1.29	0.58	0.48	0.95	1557	2833	2929	1407	1196
	131	1	0.84	0.86	0.65	0.44	0.55	0.38	8677	1851	1469	1030	1336
	470	4	0.94	0.94	0.66	0.58	0.88	1.02	5700	1682	1272	1172	1882
	497	4	2.05	2.03	1.65	1.32	1.16	1.27	4236	3072	2986	2687	2595
	505	4	0.99	0.69	0.48	0.25	0.36	0.47	4452	978	727	388	581
	533	4	0.98	1.16	1.15	0.60	0.65	1.31	18388	4045	4232	2290	2537
	561	4	0.40	0.66	0.57	0.32	0.41	0.32	9615	1643	1459	847	1109
	597	5	0.46	0.97	0.77	0.39	0.60	0.9	10851	2711	2248	1180	1853
	607	5	2.56	2.10	2.13	2.06	1.81	NA	7876	4246	5007	5515	5406
	624	5	1.50	1.48	1.17	0.66	0.88	1.1	8617	2779	2426	1472	2054
	630	5	0.65	0.38	0.37	0.27	0.34	0.5	12214	902	900	679	870
	644	5	0.73	0.54	0.63	0.34	0.33	0.52	25692	1946	2306	1286	1273
	950	8	0.69	0.92	0.94	0.79	0.61	0.65	5723	1566	1731	1573	1280
	974	8	1.03	1.32	1.17	0.92	0.73	0.89	28895	4391	4108	3372	2781
	976	8	0.90	1.79	1.80	0.94	1.00	0.74	3671	2202	2721	1624	1872
	1026	8	0.90	0.88	0.85	0.57	0.62	1.11	6729	1619	1694	1190	1353
	1072	8	0.33	0.25	0.35	0.25	0.30	0.51	6046	485	709	508	623
Irrigated	153	2	0.47	0.89	0.41	0.22	0.23	0.24	5032	1815	873	477	507
	154	2	0.60	0.48	0.10	0.17	0.30	0.55	7124	1014	223	369	662
	166	2	0.61	0.25	0.28	0.87	0.75	0.32	7944	567	642	2112	1903
	225	2	0.74	0.56	0.52	1.22	1.19	0.93	6164	858	847	2154	2315
	255	2	0.60	0.68	0.77	2.50	1.03	1.22	12946	1801	2127	7537	3395
	371	3	2.09	2.24	1.64	2.38	2.44	2.31	3520	3354	2955	5030	6096
	389	3	1.03	1.37	1.27	1.81	1.35	1.34	13564	3734	3741	5768	4633
	395	3	0.65	0.83	0.56	1.03	1.02	0.81	7595	1673	1194	2313	2464
	398	3	0.59	0.34	0.40	1.09	1.44	2.03	10621	1014	1202	3391	4768
	403	3	1.01	0.71	0.34	0.76	0.73	0.93	14550	2231	1083	2502	2501
	744	6	0.64	0.35	0.32	0.75	1.09	1.81	14143	1022	944	2298	3513
	753	6	0.60	0.36	0.31	0.44	0.80	1.32	23147	1350	1166	1696	3151
	759	6	0.56	0.55	0.37	0.50	0.81	0.88	7982	1371	937	1308	2190
	764	6	1.24	0.94	0.85	1.44	1.00	1.25	18550	2656	2533	4531	3325
	775	6	0.94	0.58	0.50	1.25	1.22	1.56	21145	1721	1538	3987	4141
	818	7	1.07	1.24	0.87	1.72	1.94	1.69	22074	4210	3112	6475	7869
	824	7	1.14	0.47	0.65	1.46	1.67	1.19	33180	1787	2537	5931	7186
	934	7	1.08	1.16	0.73	1.63	1.56	NA	15023	3580	2355	5588	5734
	995	7	1.26	2.65	1.72	2.26	2.21	2.15	17403	7729	5607	8066	8670
	999	7	1.24	1.19	0.72	1.03	1.47	1.38	16022	3332	2130	3168	4840

943 * YYYY – starting from innermost sapwood ring

944 **Table S2.** % Ray parenchyma and basal segment ray parenchyma area of all study trees.

	ID	Plot	% Ray parenchyma				Basal segment ray parenchyma area [mm ²]			
			1993-1997	1998-2002	2003-2007	2008-2012	1993-1997	1998-2002	2003-2007	2008-2012
Control	8	1	5.30	5.25	5.35	5.60	232.6	244.1	197.2	177.3
	41	1	6.20	5.96	4.80	5.34	88.2	92.9	47.6	70.9
	52	1	9.53	9.06	8.89	8.27	389.7	263.8	152.1	273.5
	64	1	5.31	5.74	6.49	6.33	150.3	168.0	91.3	75.7
	131	1	6.52	6.23	5.97	5.88	120.8	91.5	61.5	78.5
	470	4	5.72	5.38	5.16	4.39	96.3	68.5	60.4	82.7
	497	4	6.62	8.26	6.64	7.05	203.4	246.7	178.3	182.8
	505	4	4.85	5.24	5.01	4.49	47.4	38.1	19.5	26.1
	533	4	5.79	5.43	5.21	4.56	234.0	229.8	119.4	115.7
	561	4	6.03	5.92	4.93	5.50	99.1	86.4	41.8	61.0
	597	5	6.03	5.29	6.24	5.15	163.4	118.9	73.6	95.4
	607	5	5.93	6.15	6.38	5.65	251.8	308.0	351.7	305.6
	624	5	4.51	4.40	3.99	4.14	125.4	106.8	58.8	85.1
	630	5	7.13	6.52	6.33	6.04	64.4	58.7	43.0	52.5
	644	5	5.51	5.52	5.34	5.83	107.3	127.3	68.7	74.2
	950	8	5.76	5.64	5.97	5.05	90.2	97.7	93.9	64.6
	974	8	6.52	6.19	6.11	7.06	286.2	254.5	206.1	196.3
	976	8	6.01	6.88	7.74	6.65	132.2	187.1	125.6	124.4
	1026	8	4.19	3.99	3.62	3.25	67.9	67.6	43.0	43.9
	1072	8	7.01	7.00	7.91	7.26	34.0	49.6	40.2	45.2
Irrigated	153	2	5.50	5.82	6.80	5.69	99.7	50.8	32.5	28.9
	154	2	5.64	6.17	6.98	6.07	57.2	13.8	25.7	40.2
	166	2	5.75	5.21	5.14	5.48	32.6	33.4	108.6	104.3
	225	2	6.73	6.17	6.08	5.65	57.7	52.2	131.0	130.8
	255	2	4.72	4.45	5.28	4.98	84.9	94.6	397.9	169.2
	371	3	5.65	5.42	5.05	5.33	189.6	160.1	254.2	325.1
	389	3	5.90	6.15	6.42	7.86	220.2	230.0	370.2	364.1
	395	3	7.59	7.38	7.42	7.18	127.0	88.1	171.6	176.8
	398	3	6.25	6.19	6.07	4.98	63.4	74.4	205.8	237.3
	403	3	8.91	8.83	6.71	8.55	198.8	95.7	168.0	213.8
	744	6	5.93	6.35	5.19	4.41	60.6	59.9	119.3	155.0
	753	6	6.30	5.70	5.66	4.91	85.1	66.4	96.0	154.8
	759	6	4.04	3.85	3.98	3.81	55.4	36.1	52.0	83.5
	764	6	5.86	6.96	5.59	6.16	155.6	176.3	253.1	204.7
	775	6	6.67	7.17	7.16	7.68	114.9	110.2	285.5	318.1
	818	7	6.39	6.75	6.42	7.28	268.9	210.2	416.0	573.3
	824	7	5.93	6.14	6.34	6.50	106.0	155.9	376.2	467.3
	934	7	5.63	5.45	6.10	5.69	201.7	128.3	341.0	326.5
	995	7	6.25	5.80	5.94	6.06	482.9	324.9	479.4	525.5
	999	7	3.93	3.99	4.05	4.08	131.1	84.9	128.2	197.4

946 **Table S3.** % NSC, insoluble NSC and soluble NSC per sapwood segment of all study trees.

	ID	Plot	% NSC					% Insoluble NSC					% Soluble NSC				
			YYYY-1992 *	1993-1997	1998-2002	2003-2007	2008-2012	YYYY-1992 *	1993-1997	1998-2002	2003-2007	2008-2012	YYYY-1992 *	1993-1997	1998-2002	2003-2007	2008-2012
Control	8	1	2.97	2.62	3.40	3.90	6.65	2.19	1.70	2.14	2.45	3.59	0.78	0.92	1.26	1.45	3.06
	41	1	2.37	3.06	3.76	3.08	4.63	1.62	1.96	2.82	1.70	1.92	0.76	1.09	0.94	1.38	2.71
	52	1	1.67	2.24	2.42	2.99	3.74	1.14	1.35	1.50	1.86	2.07	0.53	0.89	0.93	1.13	1.66
	64	1	2.03	2.81	3.44	5.49	5.72	1.31	1.52	2.17	4.15	2.73	0.72	1.29	1.27	1.34	2.98
	131	1	2.14	3.94	2.94	5.39	3.40	1.26	3.06	1.91	2.78	2.20	0.88	0.89	1.03	2.61	1.20
	470	4	2.06	2.79	3.34	2.92	4.76	1.39	1.94	2.33	1.67	1.86	0.67	0.84	1.02	1.25	2.90
	497	4	2.47	2.58	2.52	3.26	5.03	1.61	1.84	1.55	1.99	2.41	0.86	0.75	0.97	1.27	2.62
	505	4	1.85	2.63	3.59	3.73	6.51	1.15	1.70	2.24	2.30	3.43	0.70	0.93	1.35	1.44	3.08
	533	4	2.13	4.27	3.32	4.17	5.89	1.27	2.87	2.18	2.63	2.00	0.86	1.40	1.14	1.54	3.89
	561	4	2.28	3.12	3.45	3.18	2.45	1.27	1.74	2.08	1.47	2.06	1.01	1.39	1.38	1.71	0.40
	597	5	2.39	2.58	2.93	3.03	5.53	1.77	1.63	1.86	2.14	2.06	0.62	0.95	1.07	0.89	3.48
	607	5	2.40	3.21	2.55	2.52	3.47	1.38	2.54	1.70	1.60	1.65	1.02	0.67	0.85	0.92	1.82
	624	5	1.98	2.75	2.76	3.10	4.83	1.35	1.84	1.73	2.17	2.01	0.63	0.91	1.03	0.94	2.81
	630	5	1.80	4.52	3.67	5.07	5.84	0.84	3.37	2.60	3.71	2.17	0.96	1.15	1.07	1.36	3.68
	644	5	2.16	4.01	3.77	4.10	6.90	1.30	2.60	2.42	2.86	2.44	0.86	1.41	1.35	1.23	4.45
	950	8	2.70	2.64	3.27	2.56	4.42	1.76	1.99	2.23	1.67	2.27	0.93	0.65	1.04	0.89	2.14
	974	8	2.22	3.30	3.46	3.84	4.37	1.23	2.26	2.08	2.67	2.07	0.99	1.04	1.37	1.17	2.29
	976	8	2.21	3.21	2.55	2.61	6.09	1.33	2.31	1.56	1.63	3.53	0.88	0.91	1.00	0.99	2.56
	1026	8	2.60	3.25	2.55	2.85	3.85	2.04	2.54	1.56	1.90	1.81	0.56	0.71	0.99	0.95	2.04
	1072	8	2.03	3.65	3.59	3.59	5.50	1.06	2.75	2.52	2.45	2.94	0.98	0.90	1.07	1.15	2.56
Irrigated	153	2	2.75	3.06	3.58	3.45	6.18	1.56	2.11	2.64	2.34	3.00	1.18	0.95	0.94	1.11	3.18
	154	2	2.60	3.64	3.63	4.41	6.86	1.71	2.13	1.92	2.57	2.67	0.90	1.51	1.71	1.84	4.20
	166	2	1.77	5.54	3.55	3.11	4.48	1.01	4.04	2.31	1.91	2.10	0.76	1.50	1.25	1.20	2.38
	225	2	1.85	4.11	3.55	2.82	4.64	1.21	3.08	2.68	1.77	2.18	0.64	1.03	0.87	1.05	2.47
	255	2	2.31	2.99	3.19	2.55	4.57	1.31	2.11	2.37	1.24	1.95	1.00	0.88	0.82	1.31	2.62
	371	3	2.19	2.92	2.16	2.84	3.79	1.48	2.16	1.24	1.89	1.96	0.71	0.76	0.91	0.95	1.83
	389	3	2.42	2.32	2.49	2.88	4.52	1.55	1.53	1.45	1.53	1.60	0.87	0.79	1.04	1.35	2.92
	395	3	2.29	2.87	4.14	2.97	4.86	1.45	1.79	2.71	1.34	1.97	0.84	1.07	1.43	1.63	2.89
	398	3	2.08	3.61	3.58	3.12	6.53	1.01	2.23	2.08	1.65	3.03	1.07	1.38	1.50	1.47	3.50
	403	3	2.14	3.25	3.62	4.00	6.27	1.19	2.07	2.34	1.74	2.77	0.95	1.17	1.29	2.26	3.50
	744	6	2.11	3.56	3.47	3.49	4.47	1.40	2.27	2.44	2.20	2.63	0.71	1.29	1.03	1.29	1.84
	753	6	2.28	3.52	3.69	3.00	3.32	1.11	2.61	2.59	1.62	1.76	1.16	0.91	1.09	1.38	1.56
	759	6	1.82	3.18	3.53	2.90	4.08	1.17	2.41	2.59	2.08	1.86	0.66	0.76	0.95	0.82	2.22
	764	6	2.16	2.81	3.67	3.56	4.73	1.10	1.76	2.32	2.03	2.61	1.06	1.06	1.34	1.52	2.12
	775	6	2.14	3.28	3.63	2.67	3.97	1.21	2.30	2.70	1.60	2.07	0.93	0.97	0.93	1.08	1.90
	818	7	2.23	2.84	3.69	2.95	4.47	1.19	1.75	2.74	1.49	2.15	1.04	1.09	0.95	1.46	2.33
	824	7	3.05	3.46	3.29	3.27	4.00	2.07	2.09	1.86	1.87	1.58	0.98	1.37	1.43	1.40	2.43
	934	7	2.09	2.64	3.51	3.16	3.86	1.28	1.52	2.28	1.77	1.57	0.81	1.11	1.23	1.39	2.29
	995	7	2.54	2.16	3.81	2.94	3.56	1.37	1.22	2.87	1.27	1.53	1.17	0.94	0.93	1.68	2.03
	999	7	2.39	2.29	3.20	2.91	4.56	1.39	1.46	2.20	2.02	2.07	1.00	0.83	1.00	0.89	2.49

* YYYY – starting from innermost sapwood ring

948 **Table S4.** Annual tree-ring width [mm] of all study trees.

	ID	Plot	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012
Control	8	1	1.4	1.7	2.2	1.5	1.4	1.2	2.0	1.4	1.6	1.7	0.9	1.3	1.1	0.9	1.4	1.3	1.1	1.1	0.5	0.5
	41	1	0.7	0.8	0.8	0.6	1.0	0.7	1.2	0.7	0.7	0.7	0.4	0.5	0.4	0.4	0.7	0.7	0.6	0.8	0.4	0.5
	52	1	2.0	2.4	1.7	1.9	0.8	0.4	1.5	1.1	1.1	1.1	0.5	0.7	0.7	0.4	1.1	1.4	1.3	1.4	0.8	1.1
	64	1	1.1	1.4	1.9	1.2	1.3	1.0	1.5	1.4	1.3	1.1	0.7	0.6	0.6	0.5	0.5	0.6	0.6	0.5	0.2	0.3
	131	1	0.8	0.9	1.0	0.9	0.8	0.4	0.9	0.6	0.6	0.7	0.4	0.4	0.4	0.3	0.7	0.8	0.7	0.8	0.3	0.3
	470	4	0.8	0.8	1.1	0.9	1.0	0.7	0.8	0.6	0.6	0.6	0.4	0.8	0.6	0.4	0.8	0.7	0.9	1.2	0.8	0.8
	497	4	2.0	2.2	2.0	1.9	2.4	2.3	1.5	1.4	1.6	1.4	1.1	1.4	1.4	1.1	1.3	1.5	1.1	1.2	0.8	0.8
	505	4	0.9	0.6	0.6	0.6	0.7	0.5	0.5	0.4	0.5	0.4	0.2	0.3	0.3	0.2	0.2	0.3	0.4	0.6	0.3	0.3
	533	4	0.9	1.0	1.6	0.8	1.3	0.8	1.2	1.3	1.4	1.1	0.7	0.5	0.7	0.5	0.6	0.7	0.6	1.0	0.5	0.3
	561	4	0.4	0.7	1.0	0.5	0.6	0.4	0.6	0.4	0.7	0.8	0.3	0.3	0.3	0.3	0.4	0.4	0.5	0.6	0.2	0.3
	597	5	0.7	0.8	1.2	1.0	0.9	0.5	0.9	0.8	0.8	0.8	0.4	0.4	0.3	0.3	0.5	0.5	0.5	0.8	0.4	0.5
	607	5	1.6	2.0	2.4	2.1	2.4	1.8	2.5	2.2	2.2	2.0	1.7	2.1	2.4	1.8	2.0	1.9	1.8	2.4	1.3	1.9
	624	5	1.5	1.3	2.0	2.1	1.6	0.9	1.4	1.2	1.2	0.9	0.7	0.6	0.7	0.5	0.7	1.1	0.8	1.1	0.5	0.6
	630	5	0.3	0.4	0.5	0.4	0.4	0.2	0.5	0.3	0.4	0.4	0.2	0.2	0.3	0.3	0.4	0.4	0.3	0.5	0.3	0.2
	644	5	0.5	0.4	0.7	0.5	0.7	0.5	0.6	0.6	0.6	0.7	0.3	0.4	0.4	0.3	0.4	0.4	0.3	0.5	0.2	0.2
	950	8	0.8	0.9	1.0	0.8	0.6	0.3	0.6	0.8	1.3	1.3	0.7	0.9	0.9	0.6	0.6	0.7	0.8	0.7	0.3	0.4
	974	8	1.0	1.2	1.6	1.2	1.4	0.9	1.2	1.3	1.4	1.1	0.8	1.0	1.0	0.8	1.1	0.9	0.8	1.1	0.6	0.4
	976	8	1.4	1.6	2.2	2.1	1.9	1.3	2.2	2.0	2.0	1.7	0.7	0.7	1.1	0.9	1.3	1.4	1.2	1.2	0.7	0.7
	1026	8	0.9	0.8	1.0	0.8	0.8	0.6	0.9	0.8	0.9	0.9	0.4	0.7	0.6	0.5	0.7	0.5	0.7	0.8	0.4	0.6
	1072	8	0.2	0.2	0.3	0.2	0.3	0.2	0.3	0.4	0.5	0.4	0.2	0.3	0.2	0.2	0.3	0.3	0.3	0.3	0.2	0.3
Irrigated	153	2	0.9	1.3	0.9	0.7	0.2	0.1	0.7	0.3	0.5	0.4	0.1	0.2	0.4	0.2	0.2	0.2	0.4	0.2	0.1	0.2
	154	2	0.8	1.0	0.8	0.6	0.6	0.4	0.6	0.6	0.4	0.4	0.2	0.1	0.1	0.2	0.3	0.3	0.6	0.4	0.2	0.3
	166	2	0.1	0.2	0.3	0.3	0.2	0.3	0.2	0.3	0.2	0.3	0.4	0.8	1.0	1.2	1.2	1.1	0.9	0.6	0.5	0.5
	225	2	0.8	0.7	0.5	0.3	0.4	0.2	0.6	0.5	0.6	0.6	0.5	1.0	1.5	1.4	1.5	1.4	1.6	1.1	0.8	0.8
	255	2	0.6	0.9	0.5	0.6	0.4	1.0	0.6	0.9	1.0	0.7	2.3	3.3	3.0	2.6	1.4	1.2	0.9	0.5	0.8	0.2
	371	3	1.8	1.9	2.8	2.4	2.3	1.2	2.1	1.9	1.8	1.4	1.1	2.1	2.1	2.5	4.2	3.0	2.8	2.4	2.1	2.2
	389	3	1.1	1.3	1.9	1.5	1.4	0.9	1.4	1.2	1.9	1.4	0.9	1.9	2.0	2.1	2.5	1.7	1.7	1.3	0.9	1.4
	395	3	0.7	1.0	1.1	0.8	0.9	0.3	0.8	0.5	0.7	0.5	0.3	0.8	1.6	1.3	1.6	1.3	1.2	1.1	0.8	1.1
	398	3	0.3	0.4	0.5	0.3	0.2	0.2	0.5	0.5	0.5	0.5	0.3	1.0	1.1	1.5	1.8	1.5	1.2	2.3	1.3	2.5
	403	3	0.6	0.8	0.9	0.5	0.5	0.3	0.6	0.3	0.3	0.2	0.2	0.4	0.7	1.1	1.1	0.9	0.8	0.8	0.4	0.5
	744	6	0.3	0.4	0.5	0.3	0.3	0.2	0.3	0.2	0.4	0.4	0.2	0.8	0.6	1.1	0.9	0.8	0.8	1.4	1.0	1.3
	753	6	0.3	0.4	0.5	0.2	0.3	0.2	0.4	0.3	0.3	0.4	0.2	0.3	0.5	0.6	0.6	0.7	0.7	1.0	0.7	0.7
	759	6	0.5	0.6	0.7	0.5	0.6	0.3	0.5	0.3	0.2	0.2	0.2	0.3	0.5	0.6	0.7	0.6	0.9	1.1	0.7	0.7
	764	6	0.9	0.8	1.1	0.7	0.9	0.6	0.9	1.2	0.7	0.8	0.5	1.0	2.2	1.5	1.5	1.2	1.0	1.0	0.7	0.8
	775	6	0.4	0.5	0.8	0.4	0.5	0.3	0.4	0.5	0.6	0.6	0.4	1.1	1.6	1.3	1.9	1.8	1.3	1.1	1.0	0.8
	818	7	1.2	1.1	1.8	0.9	1.2	0.6	1.1	1.2	0.8	0.8	0.9	1.6	1.5	2.0	2.5	1.9	2.0	2.1	1.5	1.7
	824	7	0.3	0.5	0.7	0.4	0.5	0.4	0.6	0.9	0.7	0.7	0.5	1.3	1.5	1.5	2.3	2.0	2.1	1.6	1.3	1.2
	934	7	1.1	1.1	1.7	0.7	0.9	0.4	0.7	0.7	0.9	0.8	0.6	1.4	1.4	1.9	2.4	1.8	1.5	1.5	1.2	1.3
	995	7	2.9	2.8	3.0	2.0	1.8	1.6	1.7	1.7	1.6	1.4	1.7	2.1	2.3	2.1	2.5	2.6	2.4	2.3	1.6	1.5
	999	7	0.8	1.1	1.7	0.9	1.1	0.6	0.8	0.7	0.8	0.6	0.5	0.8	1.0	1.1	1.7	1.5	1.4	1.5	1.3	1.3

950 **Table S5.** Annual % ray parenchyma of all study trees.

	ID	Plot	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012
Control	8	1	5.1	5.5	5.1	4.9	5.9	5.5	5.0	6.4	5.0	4.4	5.5	5.4	5.6	5.0	5.3	5.1	5.1	5.5	5.5	6.8
	41	1	7.4	5.9	5.5	5.9	6.3	5.0	5.3	7.0	5.8	6.7	5.0	4.8	4.3	5.1	4.8	4.7	5.7	6.0	6.0	4.4
	52	1	9.4	9.0	10.2	9.4	9.7	10.0	8.5	8.4	9.5	9.0	9.8	8.5	9.0	9.0	8.1	8.0	8.0	8.0	9.4	8.0
	64	1	4.8	6.2	4.5	5.1	5.9	6.1	5.1	5.9	6.1	5.6	5.7	6.4	7.0	6.4	6.9	7.4	6.4	5.8	6.3	5.8
	131	1	6.2	6.4	6.5	7.1	6.4	6.7	6.0	5.8	6.3	6.5	6.3	5.6	5.8	6.2	6.1	6.4	5.8	5.2	6.1	6.0
	470	4	5.4	5.4	5.8	6.3	5.7	5.8	5.0	5.5	5.2	5.5	5.2	5.7	4.8	4.8	5.4	5.7	5.0	3.7	3.4	4.1
	497	4	7.7	5.6	7.7	6.3	5.8	8.0	9.4	8.2	7.1	8.7	7.0	5.3	6.0	6.8	8.1	6.2	7.3	7.3	7.3	7.1
	505	4	5.4	4.9	4.5	4.6	4.9	5.9	5.1	5.5	4.9	4.9	5.8	5.6	4.7	4.3	4.6	5.1	5.0	3.9	4.0	4.4
	533	4	6.2	6.4	5.9	5.5	5.0	5.4	5.0	4.1	6.1	6.7	6.2	5.7	5.3	4.6	4.3	4.2	4.7	4.2	4.5	5.3
	561	4	6.4	5.8	5.2	5.9	6.8	6.3	6.2	5.8	5.8	5.5	5.0	5.2	4.6	4.9	5.0	4.8	5.6	5.7	5.8	5.6
	597	5	6.2	6.0	5.2	6.0	6.8	5.8	6.2	5.1	4.3	5.1	6.4	6.0	5.5	6.1	7.2	5.5	5.4	4.4	5.9	4.6
	607	5	6.1	6.7	6.5	5.8	4.7	6.6	5.7	6.7	5.6	6.2	6.5	5.8	6.8	6.5	6.3	5.6	6.0	5.9	6.1	4.7
	624	5	4.9	4.0	4.4	4.6	4.7	4.9	4.8	3.7	4.0	4.5	3.8	4.0	4.0	4.2	4.0	3.9	4.2	3.1	4.8	4.7
	630	5	7.2	6.9	6.9	7.6	7.1	6.1	6.5	6.8	6.7	6.5	6.5	6.1	6.1	6.5	6.4	6.6	6.1	5.7	5.7	6.1
	644	5	5.5	6.2	5.2	5.3	5.4	5.4	5.8	5.8	5.4	5.3	5.5	5.5	5.2	5.5	5.0	5.2	5.3	6.2	6.4	6.0
	950	8	4.7	5.8	5.6	6.0	6.7	7.3	6.1	5.2	4.4	5.2	5.6	5.3	5.5	6.1	7.4	6.6	5.2	4.5	4.8	4.0
	974	8	5.8	7.0	7.5	6.6	5.7	7.0	6.0	6.1	5.6	6.2	5.6	7.0	6.3	5.8	6.0	7.5	6.9	5.7	7.4	7.9
	976	8	5.5	5.3	5.5	6.4	7.4	6.8	6.4	6.9	6.4	7.9	7.8	7.4	6.2	8.7	8.7	7.7	7.0	5.7	5.8	7.0
	1026	8	4.4	4.0	4.3	4.2	4.0	4.4	3.5	4.2	4.3	3.5	3.9	3.5	3.2	3.1	4.4	3.4	2.9	3.7	3.7	2.2
	1072	8	6.6	6.5	6.6	7.8	7.5	6.4	6.1	6.9	7.7	7.9	8.3	7.1	6.7	7.6	10.0	8.7	7.6	7.4	6.3	6.3
Irrigated	153	2	6.7	5.5	5.9	4.5	5.0	5.3	5.5	5.8	5.8	6.7	7.7	7.6	6.4	6.1	6.2	5.0	5.3	6.1	6.6	5.4
	154	2	5.9	5.4	5.1	6.4	5.5	6.7	5.5	5.4	6.3	7.0	7.3	7.5	7.2	6.5	6.3	6.9	6.3	5.4	5.2	6.6
	166	2	7.3	5.7	5.1	5.0	5.7	5.4	5.1	4.9	5.5	5.2	4.5	5.5	5.5	5.4	4.8	6.5	5.0	6.0	5.1	4.8
	225	2	6.8	7.1	5.9	7.0	6.8	7.2	6.7	6.1	5.7	5.2	6.7	6.5	5.5	5.9	5.8	6.3	5.4	5.9	5.5	5.2
	255	2	4.7	3.9	5.1	4.9	5.0	3.4	4.3	4.3	5.3	4.9	4.9	5.3	5.6	5.4	5.3	5.0	6.2	5.5	4.8	3.5
	371	3	5.0	6.0	5.5	5.7	6.0	6.3	5.1	4.9	5.0	5.8	5.9	5.1	4.6	4.8	4.8	6.4	5.1	4.1	5.4	5.8
	389	3	5.5	5.8	5.7	6.1	6.3	7.2	5.3	6.7	5.5	6.0	6.8	6.2	6.1	5.8	7.3	7.7	7.0	8.9	9.1	6.6
	395	3	8.6	7.9	7.0	7.1	7.5	7.9	7.6	8.1	6.7	6.6	7.3	8.3	6.7	8.0	6.8	7.0	7.0	6.7	7.4	7.9
	398	3	6.9	4.6	5.8	6.6	7.3	7.4	6.0	5.2	5.7	6.6	7.5	6.6	5.5	5.8	5.0	5.3	4.4	5.9	5.4	3.9
	403	3	9.8	8.6	8.0	8.8	9.3	9.3	9.0	8.9	8.6	8.4	6.8	7.6	6.6	5.9	6.7	8.1	8.3	8.3	9.6	8.5
	744	6	5.3	6.0	6.1	5.9	6.3	7.7	6.0	6.3	6.1	5.7	6.0	5.0	5.2	4.8	5.0	5.1	4.9	4.1	4.0	4.1
	753	6	6.0	5.8	5.7	7.1	6.9	6.5	5.6	5.3	5.9	5.7	5.9	5.3	5.8	5.5	5.7	5.4	4.9	4.7	4.9	4.7
	759	6	4.0	4.7	3.8	4.4	3.3	4.3	4.8	3.6	3.1	3.5	3.9	3.5	4.5	4.5	3.5	3.1	3.9	3.8	3.8	4.4
	764	6	6.1	5.9	5.3	5.8	6.2	7.0	8.2	7.5	6.9	5.2	5.3	5.4	5.3	5.8	6.2	5.7	6.5	5.9	6.4	6.3
	775	6	7.6	7.3	5.7	6.4	6.4	6.7	7.2	6.7	7.5	7.7	8.1	6.0	6.8	8.1	6.8	6.7	8.9	8.5	7.6	6.7
	818	7	7.1	7.2	5.8	6.1	5.7	6.7	5.8	6.9	7.2	7.2	6.1	6.2	5.5	6.7	7.5	7.6	6.2	7.7	8.0	7.0
	824	7	5.8	5.5	5.4	6.9	6.1	6.7	6.0	5.8	6.4	5.8	7.2	6.5	5.4	6.6	6.1	6.6	4.9	7.8	7.1	6.1
	934	7	5.8	5.0	4.6	6.5	6.4	6.0	5.1	5.5	4.9	5.8	8.0	6.4	5.8	4.7	5.6	5.6	6.0	5.6	5.6	5.7
	995	7	6.7	6.4	6.0	6.2	5.9	5.7	5.9	6.4	5.8	5.2	7.1	5.7	5.9	5.2	5.8	5.9	6.1	6.5	5.9	5.9
	999	7	3.9	4.0	4.3	4.4	3.2	3.4	4.2	4.4	4.2	3.7	4.1	4.5	3.4	3.9	4.4	3.8	3.7	4.3	4.3	4.3