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– SILVICULTURE AND FOREST ECOLOGY OF THE TEMPERATE ZONES –

Picea abies and climate change – *does increasing thinning intensity prevent drought stress?*

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Content

List of Abbreviations

A	photosynthesis
A_{INT}	canopy-integrated photosynthesis
A_{max}	photosynthetic capacity
ANOVA	analysis of variance
ASWSC	available soil water storage capacity
A_s	stand sapwood area
b_t	basal area growth measured for year t
BA	basal area
BAI	basal area increment
BAI_{july}	target tree basal area increment until July
BAI_s	stand basal area
BAI_t	target tree basal area increment
C	carbon, control
ca.	circa
cf.	compare to
$\delta^{13}C$	stable-carbon isotope ratio
$\delta^{13}C_a$	stable-carbon isotope ratio of atmospheric CO_2
$\delta^{18}O$	oxygen-isotope ratio
$\Delta\ ^{13}C$	discrimination against $^{13}CO_2$
$\Delta\ W_e$	difference in extractable water
DBH	diameter at breast height
DWD	Deutscher Wetter Dienst (German Weather Service)
e.g.	for example
FS	Freising
g	stomatal aperture
gs.	growing season
g_t	basal area estimated by the Hugershoff model for year t
GG	Göggingen
ha	hectare
HT	heavy thinning
I_c	canopy interception
I_o	overstory interception
I_t	standardized growth index for year t
I_u	understory interception
LA	leaf area
LAI	leaf area index
LfL	Bavarian Institute for Agriculture
LTM	long term mean

MT	moderate thinning
MWU-test	Man-Whitney U test
N	sample number
NT	not-thinned
PDSI	Palmer Drought Severity Index
P_g	gross-precipitation, open-field precipitation
P_s	throughfall
PostDYs	year(s) after drought
PreDYs	year(s) before drought
rBAI	relative basal area increment
RH	relative humidity
REW	relative extractable soil water
REW_{crit}	critical relative extractable soil water content
REW_{60}	relative extractable soil water content down to 60 cm
T_{air}	air temperature
TDR	time domain reflectometry
R_g	groundwater runoff
Θ	volumetric soil water content
u	sap flux density per unit sapwood area
VPD	vapor pressure deficit
W_e	plant extractable soil water content
WUE_s	stand water use efficiency
WUE_t	target tree water use efficiency

List of Figures

List of Tables

Chapter 1

General Introduction

Climate Change and Forest Management

Anthropogenic climate change, including increasing surface temperatures and changes in precipitation endangers ecosystems all over the world. The period 2003-2012 revealed an overall increase in global temperature of about 0.8 °C compared to the first decade the 20th century with an even higher increase in mean annual temperature in Europe compared to the average global warming (IPCC 2007, IPCC 2013). Furthermore, the predicted increase in mean annual temperature ranges from about 2 – 5 °C until the end of the 21st century compared to the end of the 20th century (Christensen et al., 2007). Water availability is a major factor influencing the distribution and productivity of vegetation (Gholz et al., 1990). Therefore, increasing temperatures and changes in precipitation regimes will distinctly alter forest ecosystem conditions. Additionally extreme weather events such as heat waves and severe drought events are likely to become more frequent (Easterling et al., 2000; Luterbacher et al., 2004; Meehl and Tebaldi, 2004; Schär et al., 2004). Such severe drought events with exceptional high temperatures and in higher frequency became evident all over Europe during the years 2003, 2006 (Rebetez et al., 2008, 2006) and 2010 in large parts of eastern Europe and Russia (Barriopedro et al., 2011). The increased intensity and frequency of such severe drought events already led to severe consequences for forest ecosystems: a significant decrease of primary production, increasing tree mortality and even the die-back of whole stands (Allen et al., 2010; Cailleret et al., 2014; Carnicer et al., 2011; Čater, 2015; Dobbertin et al., 2007; Norman et al., 2016; Williams et al., 2010).

While the consequences of such severe drought events in terms of productivity and vulnerability are well documented for forest stands and on the single tree level, the physiological mechanisms responsible for the growth decline and tree mortality of trees are still under debate (W. R. L. Anderegg et al., 2012; Bréda et al., 2006; Chaves, 1991; Hartmann et al., 2015; Körner, 2003; McDowell et al., 2008; McDowell, 2011; Sevanto et al., 2014).

Recent research focusing on the drought response of tree species considers three main hypotheses of tree mortality: hydraulic failure, carbon starvation and/or dying via bio agents. Most likely a complex combination of the three leads to the actual death of a tree, but the process itself is still far from being fully understood (Hartmann et al., 2015; McDowell, 2011; Mcdowell et al., 2013).

Transpiration is the main driving force of water flow from the soil through the tree to the atmosphere and determines the water potential gradient of the soil-tree-atmosphere continuum (Bréda et al., 2006). At the leaf-atmosphere interface the main driver for transpiration is the evaporative demand (i.e. VPD, irradiance). Decreasing soil water content during drought leads to an increase of the hydraulic resistance at the root-soil interface and in combination with high evaporative demand on the leaf level to a decreasing water potential along the whole pathway (Bréda et al., 2006). With ongoing soil water deficit this leads to hydraulic failure (McDowell et al., 2008). In general, tree species are able to respond to decreasing soil water availability with different physiological strategies on a gradient of stomatal regulation. First, the more isohydric strategy, including stomatal regulation at earlier stages of soil water deficit which prevents a greater hydraulic safety margin (i.e. gymnosperms), and second a more anisohydric response with marginal stomatal regulation and decreasing plant water potential with decreasing soil water potential (i.e. angiosperms) and therefore a narrower safety margin to hydraulic failure (Choat et al., 2012).

In summary, though the processes are not clear yet, severe drought events have already led to a significantly decrease in primary production of forest stands and increased tree mortality (Allen et al., 2010; Cailleret et al., 2014; Carnicer et al., 2011; Čater, 2015; Dobbertin et al., 2007; Norman et al., 2016; Williams et al., 2010).

Norway spruce (*Picea abies* [L.] Karst.), a drought sensitive tree species, may be severely affected by climate change (Ammer et al., 2008; Kölling et al., 2009; Temperli et al., 2012). Norway Spruce stands cover large areas in Europe and represent the economically most important European tree species (Spiecker, 2000). In Germany, Norway spruce occupies about 2.7 million hectares and covers c. 25% of the total forest area. In the south of Germany, the percentage is even higher, with almost 40% of the total forest area and 1.4 million hectare (BMELV 2012). Centuries of forest management has led to spruce monocultures outside its natural range. i.e. in areas with higher temperatures and lower precipitation (Kahle et al., 2005; Spiecker, 2000). Due to the distribution outside of its natural range and the monoculture structure, Norway spruce is highly susceptible to abiotic stress like drought, storm, fire and snow. Preconditioned by the abiotic stress it is threatened by biotic stressors such as bark beetles leading to severe losses in forest ecosystems and timber production (Dobbertin et al., 2007; Hanewinkel et al., 2013; Schelhaas et al., 2003; Schlyter et al., 2006).

Forest management measures

“In ecosystems submitted to drought, resistance, avoidance or tolerance to stress is driven by either structural or physiological adjustments, or by a combination of both” (Bréda et al., 2006). Accordingly, the question arises which forest management measures may be used to mitigate future exacerbating drought events and the uncertainties of climate change for forest ecosystems (Ammer, 2016; Bolte et al., 2009; Bravo-Oviedo et al., 2014; Keenan, 2015; Kölling et al., 2009; Spiecker, 2003).

Altering tree composition

In general, mixing tree composition as a potential forest adaption measures include the reduction in resource competition (light, water, nutrition) (Lebourgeois et al., 2013) and the potential of facilitation within mixed stands (Holmgren et al., 1997; Pretzsch et al., 2014) by admixing broadleaf species into conifer monocultures. From a reaction pattern point of view there is evidence of increasing productivity of mixed vs. monoculture stands (Amoroso and Turnblom, 2006; Pretzsch et al., 2015, 2010), reduced economical risk (Knoke et al., 2008; Kölling et al., 2010 Neuner et al., 2015) reduced risk by biotic stress agents (Heiermann and Schütz, 2008) , an increase in biodiversity (Mielikäinen and Hynynen, 2003; Spiecker, 2003) and reduced susceptibility to drought (Metz et al. 2016). Nevertheless, recent studies revealed that the complementary effect of mixed stands under changing climate and water deficits vary in respect to site conditions (Jucker et al., 2016; Pretzsch et al., 2010), the temporal dynamics (del Río et al., 2014; Forrester, 2015), species composition (Pretzsch et al., 2015, 2014; Soares et al., 2016) and stand density with different stocking degrees (Condés et al., 2013; Forrester, 2015). The interaction and possible trade-offs of different tree species with different functional traits in mixed stands are far from being fully understood (Pretzsch et al., 2014). Nevertheless, the most promising approach seems to be the combination of tree species with different functional traits to increase the complementary effect via reducing the intra-specific competition (Ammer, 2016).

Altering stand density

While altering the stand composition of forest ecosystems may be promising on the long-term (Ammer, 2016), the conversion is not suitable for the adaption of current young Norway spruce stands on the short- to medium-term (Ammer et al., 2008; Knoke et al., 2008). Therefore, the forest management strategy of reducing interspecific competition via thinning in particular, is a frequently discussed option (Bolte et al., 2009; Lasch et al., 2002; Lindner, 2000). Although thinning as a forest management measure, was repeatedly studied on growth development and wood properties (Cao et al., 2008; Jaakkola et al., 2005; Mäkinen and Isomäki, 2004) less studies examined the potential of thinning to mitigate drought. Thinning may reduce the interspecific competition via altering the leaf-atmosphere and the root-soil interface on the tree and stand level and therefore reducing the competition for water, light and nutrients. In general, the reduced competition increases radial growth of the remaining trees during the following years and therefore may also improve tree growth in absolute terms during exceptional droughts (Brooks and Mitchell, 2011; Martínez-Vilalta et al., 2012; McDowell et al., 2003). Furthermore, thinning may increase growth resistance to drought at least on the short-term (Misson et al., 2003) and in young thinned stands (D’Amato et al., 2013) by increasing soil water availability. Additionally, thinning may decrease reported drought induced defoliation (McJannet and Vertessy, 2001), drought induced secondary pests (Netherer et al., 2015) and reduce tree mortality (Giuggiola et al., 2013). Moreover, the remaining trees in the thinned stands seem to be more resilient to drought with enhanced relative radial growth in the post-drought years compared to trees in un-thinned stands (Kohler et al., 2010; McDowell et al., 2006), which may partly be attributed to structural changes of the remaining trees. Nevertheless, it has also been shown that the radial growth of the remaining trees in thinned stands is more sensitive during drought (i.e. higher decline in radial growth during drought) compared to trees in un-thinned stands with increasing timespan between thinning and the drought event (Kohler et al., 2010; McDowell et al., 2006).

Therefore, the potential of thinning to mitigate drought stress during the drought event may depend on the possibility to increase the available soil water content. Whereas the potential of thinning to improve growth recovery after the drought may additionally depend on enhanced resource capture, greater quantities of stored reserves and increased availability of recent photosynthetic assimilates.

Nevertheless, the studies comprise different species, climatic conditions, thinning intensities and time spans between thinning and the drought events. The reaction pattern in radial growth of crop trees may differ between species, climatic conditions, thinning intensities, and time spans between the thinning interventions. Therefore, it is important to investigate the underlying variables of the water balance changed with increasing thinning intensities and additionally the drought response of the remaining trees.

The reduction of the stand leaf area index (LAI) may increase soil water availability by decreasing interception (Bréda et al., 1995a; Donner and Running, 1986; Simonin et al., 2007; Stogsdill et al., 1992), reducing stand transpiration (del Campo et al., 2014; Morikawa et al., 1986) and reduced above and belowground competition (Aussenac and Granier, 1988; McDowell et al., 2003). Nevertheless, the mentioned studies with in-situ measurements only comprise the first years after the thinning intervention and the underlying processes of increasing water availability differed between the studies. For example, in the study of Stogsdill (1992) the increased soil water availability after removing 50-75% of the basal area in a young *Pinus taeda* was more a function of reduced interception than of reduced transpiration. The reduction of LAI by thinning reduces aboveground competition (i.e. for light), which also implies an increase in insolation and wind flow at the crown level and therefore an increasing water demand on the single-tree level of the remaining stand (Bréda et al., 1995b; del Campo et al., 2014; Lagergren et al., 2008). Therefore, the benefit of thinning on the water availability may be equalized or even be off-set by the increasing water demand and leaf area of the remaining trees within a few years after the thinning intervention. The timespan with reduced water loss and increased water input may partly be dependent on the thinning intensity. For example, already in the second season after thinning, the transpiration of the thinned stand (ca. 25% of basal area removed) exceeded the reference stand in a *Picea abies* and *Pinus sylvestris* stand (Lagergren et al., 2008). Hence, potentially increasing the drought stress for the remaining trees during exceptional drought events, already in the second year after thinning. In contrast the reduction of c. 50% of the basal area in a Douglas fir stand (*Pseudotsuga menziesii* var. menziesii) improved soil water reserves during at least three subsequent years (Aussenac and Granier, 1988).

The period until equalization in stand transpiration and the different underlying processes for increased soil water availability of the thinned compared to un-thinned stands may be attributed to differences in thinning intensity. However, with increasing thinning intensity emerging ground vegetation, contributing to the water balance by increasing stand transpiration and interception could become crucial (Black et al., 1980; Cregg et al., 1990; Simonin et al., 2007; Whitehead et al., 1984). In addition, the potential of thinning on the medium to long-term mitigation effect may also depend on the plasticity and therefore, the rate by which trees are able to occupy available above- and belowground space (McDowell et al., 2003). As mentioned above the interaction of water demand on the leaf-atmosphere interface with the water delivery from the root-soil interface may be crucial for the impact of severe drought events.

Against this background the research presented in this dissertation studied the effect of increasing thinning intensities on the water balance of Norway spruce stands and the response of the remaining trees to drought along two different methodical approaches.

The leading hypotheses were the following:

- Drought stress during drought is mitigated and the recovery from drought is improved by increasing thinning intensities

- Stand transpiration and interception is reduced with increasing thinning intensities, hence improving soil water availability for the remaining trees

- The benefits of thinning on the water balance are temporary, but can be extended by increasing thinning intensity

Basic methodical approaches

Due to the lack of knowledge on the mitigation potential of thinning, the uncertainties and possible changes within the underlying processes with ongoing time after thinning, a two-tier approach was chosen. First, the possible mitigation effect of increasing thinning intensities during exceptional drought events was investigated via dendrochronology including isotopic signal analyses of tree rings. Second, an experimental thinning trial was established to improve the mechanistic understanding of tree and stand water relations altered by thinning.

Retrospective approach

In order to investigate tree response during exceptional drought years and the potential of increasing thinning intensity to mitigate drought stress two long-term thinning experiments in southern Germany were used. One stand is located near Göggingen in South-Western Germany (Baden- Württemberg) and the second stand in South-Eastern Germany (Bavaria) (see chapter 2) with similar climatic and site conditions. In 1974, at a stand age of ca. 27 years with about 5500 trees ha^{-1} both thinning experiments were established with increasing thinning intensities. To address the research question three thinning intensities were selected

1. Unthinned “Control” with no interventions;

2. “Moderate thinning” (MT) to 400 future crop trees per ha of profitable timber quality and/or dimension through 3-4 thinning interventions. (Göggingen: 1974, 1986, 1993 and 1997, Freising: 1974, 1989 and 1996) with removal of 1–2 competing trees per crop tree in each intervention

3. “Heavy thinning” (HT) to 200 future crop trees per ha through removal of all other trees in interventions (Göggingen in 1974, 1980 and 1993; Freising 1974, 1981 and 1996).

The study focused on changes in tree growth and isotopic signals of tree rings related to the exceptional pan-European drought events in 1976 and 2003. Tree growth and year ring width are known to be highly related to changes in climatic and biotic stress (Bréda and Badeau, 2008; Fritts, 1976; Hughes et al., 1982; Schweingruber, 1996, 1988). Dendroecology can take the advantage of this pattern using growth chronologies of the trees, to reveal retrospectively the tree response of different thinning intensities to severe drought events (Cescatti and Piutti, 1998; Kohler et al., 2010; Misson et al., 2003). Based on an approach suggested by (Lloret et al., 2011), the growth decline during the drought year compared to the pre-drought year(s) was defined as the resistance of the crop trees to the drought and the increase in the following year(s) as the recovery from the drought year.

Although different growth responses of trees can be used as an indicator of vitality (Dobbertin, 2005) the dendrochronological approach is solely based on a reaction pattern. Therefore, to reveal possible differences in the physiological response to drought and to get an idea of the underlying mechanism, a stable isotope analysis of year rings was included. Several studies have shown that the isotopic signal in tree rings is a useful tool to reveal plant's carbon and water relations in dependency to climatic variability (Barnard et al., 2012; Leuenberger et al., 1998; Saurer et al., 1997; Schleser et al., 1999).

Besides stomatal conductance (mainly driven by water availability and evaporative demand) the stable carbon isotope ratio ($\delta^{13}C$) in plant material depends on the rate of carbon assimilation (can also change with light/ nutrition availability) (Farquhar et al., 1989). Therefore, drought conditions causing a reduction in stomatal conductance (reduced photosynthetic discrimination against $^{13}CO_2$) as well as thinning with increasing light /nutrient availability may increase the $\delta^{13}C$ in tree rings (Powers et al., 2010; Warren et al., 2001). To attribute the response in $\delta^{13}C$ to either water availability or light availability, additionally the oxygen -isotope ratio ($\delta^{18}O$) with the dual isotope approach was used to separate changes in the stomatal conductance vs. photosynthesis (Barbour, 2007; Grams et al., 2007; Scheidegger et al., 2000).

Experimental (in-situ) approach

The vast majority of long-term thinning experiments were established to investigate the potential of different thinning intensities to increase productivity and/or timber quality. Retrospective approaches often lack in information concerning the thinning effect on stand/tree structure, physiology and morphology and even more important in data of temporal changes of these parameters after thinning interventions. Although, additional isotopic signals improve retrospective approaches, the mechanism and environmental factors underlying the isotopic composition in tree rings are not fully explored (Offermann et al., 2011; Roden and Siegwolf, 2012; Roden and Farquhar, 2012)

A thinning experiment was established in 2008 to address the physiological, morphological and structural modifications by thinnings and their potential for drought stress mitigation. The study was conducted near Landshut (48°38´20´´ N, 11°57´49´´E, Bavaria, Germany) in a 26-year-old monoculture of Norway spruce (*Picea abies* [L.] Karst.). Different thinning treatments were applied on plots with similar site condition (see chapter 3). About 430 future crop trees (target trees) per ha were selected prior to thinning.

In February 2009 three thinning intensities were conducted

1. Not-thinned "NT" with no intervention (basal area c. 42 m^2 h^{-1});
2. Moderate thinning "MT" reduced stand basal area by c. 43.0%. MT represented the thinning treatment commonly applied in Germany, i.e. thinning from above by removing two competitors per target tree on average
3. Heavy thinning "HT" On the HT plots all trees but the target trees were removed, resulting in basal area reduction of c. 67.0%.

Fostering over 400 target trees on MT was more intense compared to the fostering of about 100 target trees in the Bavarian State Forestry (Schröpfer et al., 2009).

Prior to the thinning intervention and over seven years after the interventions all parameters concerning the water balance of the different stands were measured in-situ (for details see chapter 3+4). The continuous measurements during the years after the thinning interventions, and ongoing records of climatic variables, are essential to predict the potential of different thinning intensities to mitigate drought and to explore the structural, morphological and physiological adaption on the tree/stand level to thinning.

The two-tier approach, i.e. retrospective analyses and continuous in-situ measurements promise to provide a deeper insight in the potential and limits of adapting Norway spruce stands to drought by decreasing inter-specific competition. Moreover, it may allow to disentangling the underlying mechanisms, and providing information on temporal changes. Hence, the approach should also allow distinguishing between short- medium and long-term effects of increasing thinning intensity.

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Chapter 2

Mitigation of drought by thinning: Short-term and long-term effects on growth and physiological performance of Norway spruce (*Picea abies*)[1]

Forest Ecology and Management 308 (2013) 188–197

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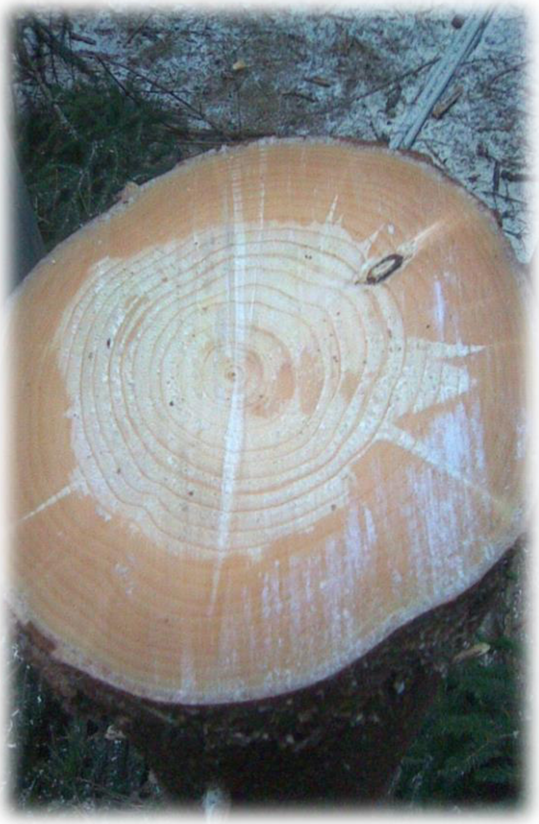

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[1] Julia Sohn and the candidate are 1st authors with equal rights. Julia Sohn and the candidate made substantial contribution to the conception and design, conducted the collection and preparation of the samples, the analysis and interpretation of data and both were lead authors of the article draft. Christian Ammer, Jürgen Bauhus and Rainer Matyssek made substantial contribution to the conception and design and the assisted the article draft. Thorsten E.E. Grams contributed substantial to the interpretation of the data and assisted the article draft. Karl-Heinz Häberle assisted sample collection and preparation.

Mitigation of drought by thinning: Short-term and long-term effects on growth and physiological performance of Norway spruce (*Picea abies*)

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Abstract

We hypothesize that reductions in stand density through thinning improve the recovery of radial stem growth in Norway spruce trees (Picea abies) from severe drought. However, thinning may not lead to higher relative radial growth during drought. Annual stem growth and stable carbon and oxygen isotopes in early- and latewood were assessed in trees from heavily thinned (HT), moderately thinned (MT) and un-thinned control stands at two sites in southern Germany. Physiological performance of trees as inferred from stable isotope analysis was used to interpret annual stem growth in response to the drought events in 1976 and 2003. Only in recently thinned stands, trees maintained growth probably through higher soil water availability during the drought year when compared to controls. In contrast, thinning improved the growth recovery in the years following the drought irrespective of the time span between thinning and drought. We conclude that thinning improves drought recovery response in the short and long term and should be considered as an effective management strategy to increase drought tolerance of Norway spruce stands.

Introduction

Global climate change will distinctly alter ecosystem conditions through rising temperatures, reduced precipitation and more frequent weather extremes (IPCC, 2007; Lasch et al., 2002; Meehl and Tebaldi, 2004). In Europe, this became evident during and after the extreme drought of 2003, which was characterized by prolonged water shortage in combination with significant heat waves (Ciais et al., 2005; Rennenberg et al., 2006; Rebetez et al., 2008). Severe drought episodes instantly affect physiological processes in trees such as transpiration, photosynthesis and carbon (C) allocation followed by resulting in increased tree susceptibility to secondary stressors such as by phytophagous insects or parasitic fungi (Bréda et al., 2006; Desprez-Loustau et al., 2006; Rouault et al., 2006). This may lead to reduced primary productivity and eventually whole-stand decline (Bréda et al., 2006; Jyske et al., 2009).

In Germany, Norway spruce (Picea abies [L.] Karst.), planted predominately in even-aged and mono-specific stands, is economically the most important tree species and occupies 30% of the total forest area (BMELV, 2008). Yet, large tracts of Norway spruce forests are growing near the perceived drought limit of the species, and with climate change, may be exposed to even more unfavorable conditions in the future (Koelling et al., 2009). As a consequence, Norway spruce has been already lost a substantial proportion of the previously cultivated area (Polley et al., 2009).

Most strategies to adapt forest ecosystems to climate change have long-term goals such as diversification of species composition or introduction of drought tolerant species (Kazda and Pichler 1998; Ammer et al., 2008). However, there are few sylvicultural adaptation approaches for immature and juvenile stands. For existing stands, intensive thinning has been discussed as an option to mitigate drought impacts (e.g. Cescatti and Piutti, 1998; Laurent et al., 2003; Martin-Benito et al., 2010).

In the short-term, thinning has been found to reduce stand transpiration (Bréda et al., 1995; Lagergren et al., 2008), interception of precipitation and competition aboveground and belowground (Aussenac and Granier, 1988; Bréda et al., 1995) so that soil water content is increased (Stogsdill et al., 1992; McDowell et al., 2003). However, increasing within-stand radiation and air flow in the canopy in recently thinned stands can also increase transpiration of remaining trees and promote the development of understory vegetation, causing a decrease in soil water availability (Bréda et al., 1995; Mueller and Bolte, 2002). In the long-term, the positive effects of thinning on soil water availability may be offset by an increased water demand of exposed trees by enlarged foliage area. For ponderosa pine in semi-arid Arizona, McDowell et al. (2006) attributed the large relative decline in basal area increment during drought and more variable gas exchange in thinned compared with unthinned stands to an enlarged foliage area per tree.

One possibility to examine short-term and long-term effects of thinning on drought response of trees is through retrospective analysis of tree growth using dendrochronological approaches (Bréda et al., 1995; Cescatti and Piutti, 1998; Laurent et al., 2003). Only recently, Lloret et al. (2011) suggested that theoretical models of tree resilience; i.e. the capacity of trees or stands to maintain/regain pre-disturbance structures (resilience) can be examined empirically by calculating indices of relative changes in tree radial growth during and after disturbance events. According to the definitions provided by Lloret et al. (2011), we define resistance as the ratio of growth levels during the drought compared to those before the drought and recovery as the ratio of growth levels after the drought compared to those during the drought.

In a previous study, intense thinning was found to improve drought recovery of radial growth in Norway spruce when compared to unthinned stands (Kohler et al., 2010). However, the relative growth reduction during the drought year was similar to that of moderately and un-thinned stands. The study, however, was based solely on dendrochronological data from one single stand so that underlying causes for the diverging growth responses during and after drought could not be ascertained.

At non-limiting sites of temperate regions tree growth often displays little or no inter-annual variation and correlation with drought-related climatic parameters (Fritts et al., 1965). Under these circumstances and owing to the strong relation between isotopic composition and water availability, stable isotope analysis has been suggested as a more reliable approach to obtain climate signals (Barnard et al., 2012). In recent years, analysis of stable isotopes in dendrochronological studies helped to infer physiological responses of trees to environmental conditions (Robertson et al., 2008).

The stable carbon-isotope ratio ($\delta^{13}C$) of plant material depends on (1) the stomatal conductance, mainly driven by water availability and evaporative demand of the atmosphere, and (2) on the rate of carbon assimilation (Farquhar et al., 1989). Drought conditions reduce stomatal aperture and thus leaf-internal CO_2 partial pressure and hence decreases photosynthetic discrimination against $^{13}CO_2$ (Farquhar et al., 1989). Likewise, $\delta^{13}C$ of plant material may increase in response to thinning as light and/or nutrient availability increases, both affecting photosynthetic capacity (e.g. Warren et al., 2001; Powers et al., 2010). Hence, responses in $\delta^{13}C$ upon thinning cannot be attributed unambiguously to either increases of water or light availability.

Oxygen-isotope ratio ($\delta^{18}O$) has been used to separate effects of stomatal aperture (g) and photosynthesis (A) on $\delta^{13}C$ by the dual- isotope approach (Scheidegger et al., 2000; Grams et al., 2007). While sharing the dependency on stomatal conductance with the $\delta^{13}C$ signature, $\delta^{18}O$ is not influenced by rubisco activity (Barbour and Farquhar, 2000). The $\delta^{18}O$ of plant material is mainly driven by the isotopic signature of source water and its evaporative enrichment during transpiration. Furthermore, the exchange rate of ^{18}O between oxygen in sucrose and later during phloem transport and stem cellulose synthesis in the developing cell has to be considered. This exchange rate is estimated in the range of 40%, but may vary during the growing season (Barbour et al., 2007; Offermann et al., 2011).

Roden and Siegwolf (2012) recently suggested that one should interpret results of the dual isotope approach rather as changes in canopy-integrated photosynthesis ($A_{\_INT}$) and not as changes in photosynthetic capacity (A_{max}) because microclimatic variation (of light, temperature and tree water status) can alter A without influencing A_{max}. Despite multiple sources of error associated with the dual- isotope approach (Roden and Siegwolf, 2012), it has been successfully used to explain physiological mechanisms underlying differences in growth patterns among trees (Martin-Benito et al., 2010; Powers et al., 2010; Moreno-Gutiérrez et al., 2011) and so far, it remains the most powerful tool for retrospectively studying tree physiological responses in relation to climatic extremes in non-controlled environments.

The objectives of the present study are to unveil the effects of thinning on the physiological responses of stem growth to drought.
We hypothesized that:

1. The decline in radial stem growth during years of severe drought is not necessarily mitigated by thinning.

2. That the recovery of stem growth during years following severe drought is improved by thinning.

3. That differences in drought resistance and recovery of growth among treatments can be related to enhanced soil water availability and adjustment in water-use efficiency.

To examine these hypotheses, we combined analyses of radial growth of Norway spruce with carbon and oxygen isotopic information from tree rings, i.e. the dual-isotope approach, in two long-term thinning experiments from Southern Germany.

Material and methods

Study sites and thinning experiments

Trees were sampled from two thinning experiments at different sites in Southern Germany. One site, ‘‘Göggingen’’ (GG), is located in the Alpine Foreland of South-Western Germany (Baden- Württemberg) at 650 m above sea level (a.s.l.). The second site, ‘‘Freising’’ (FS), is part of the Tertiary Hill country in South-Eastern Germany (Bavaria) at an altitude of 500 m a.s.l. Both stands are situated on even terrain with similar soil types representing (endo)stagnic Cambisols and Luvisol in Göggingen and Freising, respectively. Available soil water storage capacity (ASWSC) at Göggingen was c. 150 mm m^{-1} of soil profile, whereas at Freising it reached levels of c. 250 mm m^{-1} (data extrapolated from Nikolova et al., 2009). During 1970–2006, mean annual precipitation was c. 780 and c. 790 mm along with mean annual temperatures of 7.5 and 7.9 °C at Göggingen and Freising, respectively.

At both sites, four thinning treatments and control plots were established in 1974 in 27-year-old homogeneous pure stands of Norway spruce (with a total size of c. 10 ha each). In each case c. 5500 trees ha^{-1} out of the 10,000 trees ha^{-1} initially planted had remained at the time of establishment of thinning trials. At both sites, treatments consist of two randomly assigned replicates (rectangular plots of 0.1 ha), separated by buffer zones. About 400 future crop trees per ha were selected by diameter at breast height previous to the first thinning intervention. At both sites, three treatments were investigated for the purpose of this study

- Un-thinned control (C).
- Moderate thinning (MT) to 400 future crop trees ha^{-1} of profitable timber quality and/or dimension through 3–4 thinning interventions. (Göggingen: 1974, 86, 93 and 97, Freising: 1974, 89 and 96) with removal of 1–2 competing trees per crop tree in each intervention.
- Heavy thinning (HT) to 200 future crop trees through removal of all other trees in 3 interventions (Göggingen in 1974, 80 and 93; Freising 1974, 81 and 96).

Thinning intervals ranged from six to thirteen-years and stem numbers in the respective thinning treatments were comparable between the study sites in 2006 (Table 2-1), the year of the last inventory. Natural self-thinning in control stands was more advanced at Göggingen than at Freising resulting in 1100 and 1500 trees ha^{-1}, respectively, at the end of the study period in 2006.

Table 2-1 Stem numbers per hectare (ha) for the control and the two thinning treatments after each of the four thinning interventions (T1–T4) and at the time of data collection in 2006 (Final) in Freising and Göggingen.

Site	**Treatment**	**Year**				
		Stem number per ha				
		T1	**T2**	**T3**	**T4**	**Final**
Freising		**1974**	**1981**	**1989**	**1996**	**2006**
	Control (C)	5600*	n/a	n/a	1868	1535
	Moderate Thinning (MT)	4810	n/a	n/a	1209	910
	Heavy Thinning (HT)	3240	420	n/a	243	243
Göggingen		**1974**	**1980**	**1986**	**1993**	**2006**
	Control (C)	5200*	3050	1950	1600	1100
	Moderate Thinning (MT)	4970	2790	1560	1240	757
	Heavy Thinning (HT)	3110	393	393	211	211

* Data representative for the whole initial stand.

Sampling and tree-ring analyses

Dendrochronological data from Göggingen were obtained from Kohler et al. (2010), who had collected stem discs at breast height (1.3 m) from the HT (11 trees) and MT (9 trees) plots in early spring 2007. In the same year, 8 trees per control plot had been sampled at breast height with two increment cores oriented in North and West direction each. In Freising, two increment cores (oriented North and West) were extracted at breast height in summer 2009 from 10 trees per treatment (C, MT, HT). At both sites, stem discs and cores were collected from (co-) dominant trees, which appeared healthy and uninjured. Mean annual basal area increments (BAI, mm^2 year^{-1}) of trees were calculated from annual radial increments (mm). We averaged eight radii per disc or two cores per tree, assuming cross-sectional incremental areas of concentric shape in the absence of site inclination. Resulting BAI curves (1974–2006) were standardized to eliminate tree size effects using the following formula (ARSTAN software of the University of Arizona, http://www.ltrr.arizona.edu):

$$I_t=b_t/g_t \qquad (1)$$

where I_t is the relative growth index for year t, b_t is the basal area growth increment measured for year t, and g_t represents the basal area estimated by the Hugershoff model (Cook, 1985) for year t. The model accounts for the long-term growth trends of tree individuals, so that variation in It, is mainly due to short-term fluctuations of climatic factors. Standardized growth series of each treatment and site produced by ARSTAN are based on a robust estimation of annual means of I_t minimizing the effect of outliers (Cook, 1985).

For analyzing drought responses, the two pan-European droughts of 1976 and 2003 were selected by data of Palmer Drought Severity Index (PDSI), precipitation and vapor pressure deficit (VPD) during early summer (May–June) and late summer (July–August) from each site. Despite the strong growth decline visible in all tree-ring series, we decided against analyzing tree response to the 1992 drought. This decision was based on this year coinciding with a heavy masting event, which we expected might have caused additional background noise in our isotope data. Similar to the indices suggested by Lloret et al. (2011), resistance to and recovery from drought was calculated as ratios of standard growth indices (It) using either one year or the mean of two or three years as reference periods:

Resistance 1 = I_t DY / I_t PreDY and Resistance 2 = I_t DY / Mean I_t 2 or 3 PreDYs (2&3)

Recovery 1 = I_t PostDY / I_tDY and Recovery 2 = I_t Mean 3 PostDYs/DY (4&5)

where DY is the drought year, PreDY is DY-1, PostDY is DY+1, Mean 2 or 3 PreDYs is ((DY-1)+(DY-2))/2) or ((DY-1)+(DY-2)+(DY-3))/3, and Mean 3 PostDYs is ((DY+1)+(DY+2)+(DY+3))/3.

Analyses of stable carbon and oxygen isotopes

At each site and treatment, five representative sample trees were selected for tree-ring analysis of carbon and oxygen isotope ratios ($\delta^{13}C$ and $\delta^{18}O$, respectively). We sampled two years before and 3–5 after the drought years (1976 and 2003) from the North-orientation and separated earlywood from latewood. For a subsample, we compared isotope values in bulk wood with those in cellulose in order to determine the necessity to extract cellulose in our trees. This methodological study suggested that bulk wood and extracted cellulose displayed significant correlations in $\delta^{13}C$ and $\delta^{18}O$ (Fig. 2-1a and b) confirming earlier findings in Pinus species (Barbour et al., 2001) and in Norway spruce (Jaggi et al., 2002).

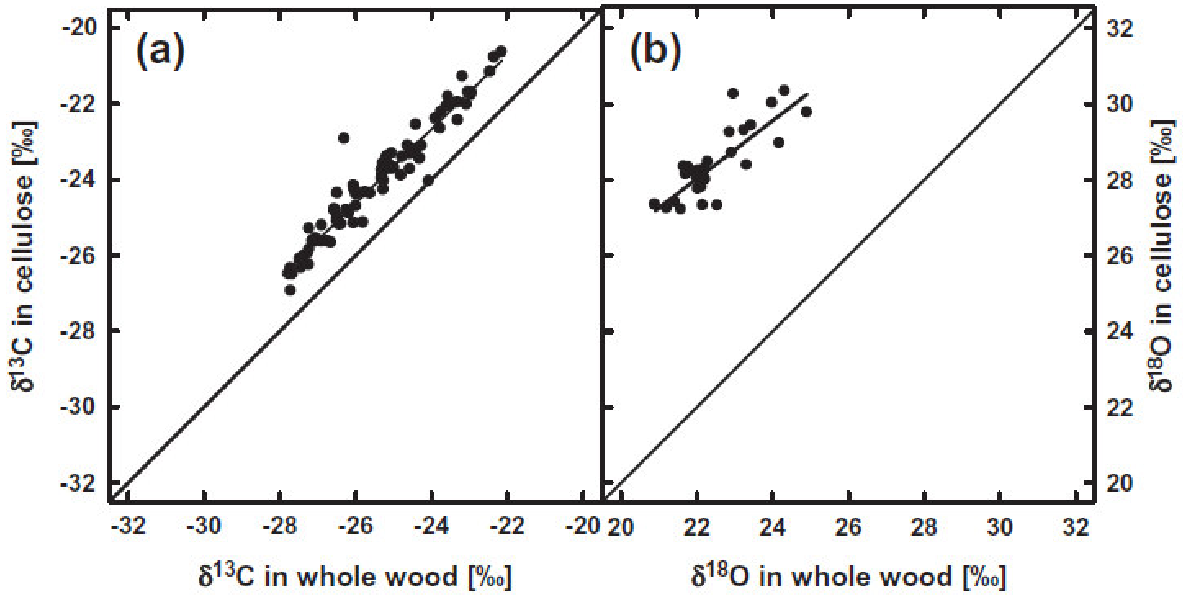

Figure 2-1 Comparison of $\Delta^{13}C$ (a) and $\delta^{18}O$ (b) in whole wood and wood cellulose of annual growth rings. Linear regression models gave a goodness of fit of (a) R2 = 0.92 ($P < 0.001$, N = 60) and (b) R2 = 0.67 ($P < 0.01$, N = 30).

On average, $\delta^{13}C$ in cellulose was 1.35‰ higher than that in bulk wood, which is similar to the difference of 1.34–1.37‰ found by Borella et al. (1998) for the same species. Mean $\delta^{18}O$ in cellulose was 5.9‰ higher than in bulk wood, being consistent with the 5.5‰ in needles of adult spruce trees (Grams et al., 2007). Based on these findings, we used bulk wood samples rather than extracted cellulose for isotope analysis as sample sizes were limiting. Quantities of 0.2–1.0 mg per sample were weighed into tin ($\delta^{13}C$) and silver ($\delta^{18}O$) capsules. For analyses of $\delta^{13}C$, wood samples were combusted in an elemental analyser (NA 2500; CE Instruments, Milan, Italy) coupled to an isotope-ratio mass spectrometer (IRMS, Delta- Plus, Finnigan MAT

GmbH) by a Conflo II interface. For $\delta^{18}O$ analysis, samples were pyrolised in a high temperature conversion/ elemental analyser (TC/EA; Finnigan MAT GmbH, Bremen, Germany), which was linked to an IRMS (DeltaPlus XP, Finnigan MAT GmbH) by a Conflo III interface (Finnigan MAT GmbH). The $\delta^{13}C$ of wood was corrected for the decline in $\delta^{13}C$ of atmospheric CO_2 ($\delta^{13}C_a$) over the study period (McCarroll and Loader, 2004) and discrimination against $^{13}CO_2$ ($\Delta^{13}C$) was calculated as follows (Farquhar et al., 1989):

$$\Delta^{13}C\ [‰] = (\delta^{13}C_a - \delta^{13}C)/\ (1+ \delta^{13}C_a) \qquad (6)$$

To facilitate interpretation of changes in $\delta^{18}O$ as primarily influenced by stomatal conductance the following prerequisites have to be fulfilled: A major assumption is that source water $\delta^{18}O$ is similar among trees so that the majority of $\delta^{18}O$ variation in organic matter is driven by the evaporative enrichment (Barbour, 2007; Grams et al., 2007; Roden and Siegwolf, 2012). In addition, $\delta^{18}O$ of atmospheric vapor, relative air humidity and leaf temperature must be constant over time and similar between the treatments. Source water $\delta^{18}O$ (i.e. xylem water) depends on the $\delta^{18}O$ of soil water, thus varies with soil depths and precipitation. In our case, the latter varied by more than 2‰ from year to year and by more than 10‰ between different months (data not shown). Since variations are hard to quantify in retrospective studies against this background noise, we derived thinning effects on $\delta^{18}O$ of wood as the difference between thinned and control plots (cf. Brooks and Mitchell, 2011) assuming that trees took up water with a similar isotopic signature. This assumption is justified by the lack of slope at both sites and similar vertical distributions of fine root biomass among plots at Göggingen (Omari, 2010). Thus, $\delta^{18}O$ in wood of each tree in the thinned plots was related to the mean of $\delta^{18}O$ of the control trees for each year and site. Along this line, we also assumed leaf temperature, relative humidity and $\delta^{18}O$ of water vapor to be similar among our treatments, considering the well coupled canopy in mature stands of Norway spruce. However, having not measured these parameters, we acknowledge that in particular differences in leaf temperature may add some variation that we could not account for.

Statistical analyses

We used the Man-Whitney U test (MWU-test) (a < 0.05) to test for differences in resistance and recovery of growth indices between treatments. Regression analysis was performed to model the effects of year, site, thinning treatment, wood type (earlywood or latewood), or interactions (e.g. site times treatment) on the relationship between $\Delta^{13}C$ and $\delta^{18}O$. Orthogonally contrasted dummy variables were used coding site, thinning treatment and wood type. In order to detect significant inter-annual changes in $\Delta^{13}C$ and $\delta^{18}O$ relative to the control, repeated measures ANOVA followed by pairwise comparisons was performed separately for trees from each site, wood type and thinning treatment. The same statistics were used to identify interactions between year (within-subject factor) and thinning treatment (between-subject factor) in isotope series. Correlation analysis was conducted to examine relationships between carbon and oxygen isotopes in earlywood and latewood of each thinning treatment and site. Quantitative statistics were performed using the software package SPSS 2008 (SPSS Statistics 17.0, Inc., Chicago IL.).

Results

At both sites, thinning altered the trajectory of the relationship between the basal area (BA) and basal area increment (BAI) of trees (Fig. 2-2). Maximum BAI increased with BA and thinning intensity. The BAI peaked at about 30, 35 and 70 cm^2 $year^{-1}$ in control, moderate thinning (MT), and heavy thinning (HT), respectively. At Freising, 32 years after the first thinning, i.e. in 2006, the average accumulated BA amounted to 800 cm^2, 1000 cm^2 and 1700 cm^2 for control, MT and HT trees, respectively. At Göggingen, maximum basal area of MT trees did not differ from the control (c. 900 and 1000 cm^2, respectively) and reached 1550 cm^2 for HT trees. In total, 66% the variation in $\delta^{18}O$ could be explained by the variables discrimination against ^{13}C, i.e. $\Delta^{13}C$, site and year (Table 2-2). Based on these results, we decided to analyze drought response of radial growth and isotopes separately for each site and the two periods 1974–1981 and 2001–2006.

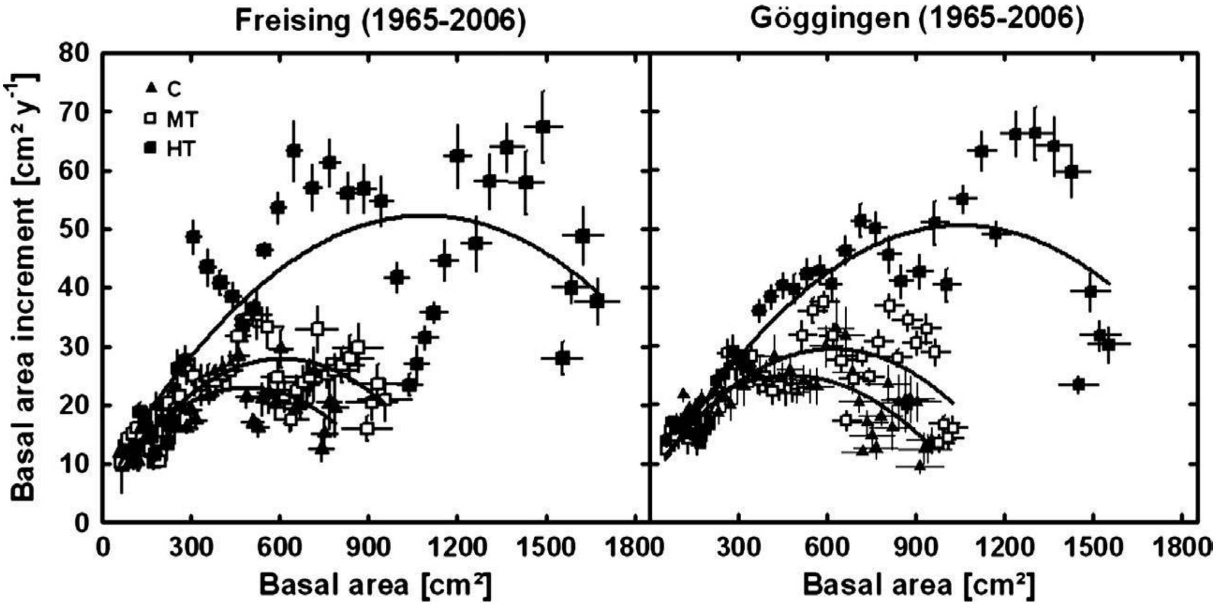

Figure 2-2 Relationship between basal area (BA) and basal area increment (BAI) of dominant and co-dominant trees from three different thinning treatments for the period 1965– 2006 at two sites (N = 8–11). Closed triangles represent control (C), open squares moderate (MT) and closed squares heavy thinning (HT). Vertical and horizontal bars indicate ± 1 standard error for means of BAI and BA, respectively. Curves result from fitting of a second order polynomial function for each series (R^2 = 0.5–0.7).

Table 2-2 Summary of the dummy regression model for the dependent variable δ18O. Only predictors that increased R by at least 5% are shown.

Model predictors	R	Adjusted R^2	Std. Error of the Estimate	Changes of R^2
$\Delta^{13}C$	0.47a	0.22	1.87	0.22
$\Delta^{13}C$, Site	0.76b	0.57	1.38	0.35
$\Delta^{13}C$, Site, Year	0.82c	0.66	1.24	0.09

Drought response of radial growth

In 1976, i.e. two years after the first thinning, drought during spring and early summer led to the formation of false year rings at both the Göggingen and the Freising site (cf. Kohler et al., 2010). During this drought event, standardized growth (It) of control trees at Freising declined by c. 25% compared to the previous year (resistance 1) or previous two years (resistance 2) (Table 2-3, Fig. 2-3) indicating lower drought resistance than in MT (resistance 1 and 2) and

HT (resistance 2) trees, which were hardly affected. At the same site, growth recovery in the first year following drought (recovery 1) and the three years following drought (recovery 2) was fastest in HT trees, with standardized growth (It) increasing by up to 60% compared to values of the drought year while this was no more than 20–35% in control and MT trees. At Göggingen, the standardized growth index (It) of control trees decreased only by 5–15% in 1976 compared to the previous year(s). Drought resistance was similar among treatments (Table 2-3, Fig. 2-3). However, growth recovery of HT trees was slower relative to MT trees (recovery 1 and 2) and control trees (recovery 2) by c. 20%. During the drought of 2003, the growth index of control trees dropped by c. 50% compared to 2002 (Table 2-3, Fig. 2-3). A similar response was found for MT trees whereas growth decline was even higher for HT trees (up to 60% at Göggingen). Correspondingly, drought resistance in trees from HT plots was lowest at both sites (Table 2-3). Growth recovery in 2004 (recovery 1) was stronger by c. 20–40%, albeit far from being complete, in HT trees when compared to MT and control trees at both sites.

Climate data suggest that no water limitation for tree development occurred during the two vegetation periods preceding the selected drought years (Fig. 2-4 – 2-7g and h). Thus, observed reductions of radial growth can be related to the distinct droughts in the years 1976 and 2003 and respective preceding radial growth in the absence of water limitations can be used as reference for the calculations of drought resistance.

Table 2-3 Effects of thinning intensity (moderate thinning (MT), heavy thinning (HT) on the resistance and recovery of standardized growth (I_t) for drought years 1976 and 2003. Resistance relates the growth in the drought year to that of the previous year (resistance 1) or the previous 3 years (resistance 2). Recovery relates the growth of one (recovery 1) or 3 (recovery 2) years following drought to the drought year.

Drought year	**Growth indices**	**Freising**			**Göggingen**		
		Control	**MT**	**HT**	**Control**	**MT**	**HT**
1976	Resistance 1	**0.78a**	**1.05b**	0.94ab	0.95a	1.00a	0.91a
	Resistance 2	**0.75a**	**1.02b**	**1.03b**	0.86a	1.07a	0.91a
	Recovery 1	**1.37a**	**1.20a**	**1.61b**	1.12ab	**1.20a**	**1.02b**
	Recovery 2	1.29ab	**1.13a**	**1.38b**	**1.06a**	**1.09a**	**0.88b**
2003	Resistance 1	0.53ab	**0.56a**	**0.43b**	0.46a	0.47a	0.40a
	Resistance 2	**0.57a**	**0.60a**	**0.46b**	0.45ab	**0.45a**	**0.39b**
	Recovery 1	**1.17a**	**1.32a**	**1.50b**	**1.39a**	**1.33a**	**1.70b**
	Recovery 2	1.41a	1.39a	1.58a	1.60a	1.27a	1.48a

Different letters indicate significant differences between treatments at $P < 0.05$, N = 8, 9 and 11 for control, moderate thinning and heavy thinning, respectively.

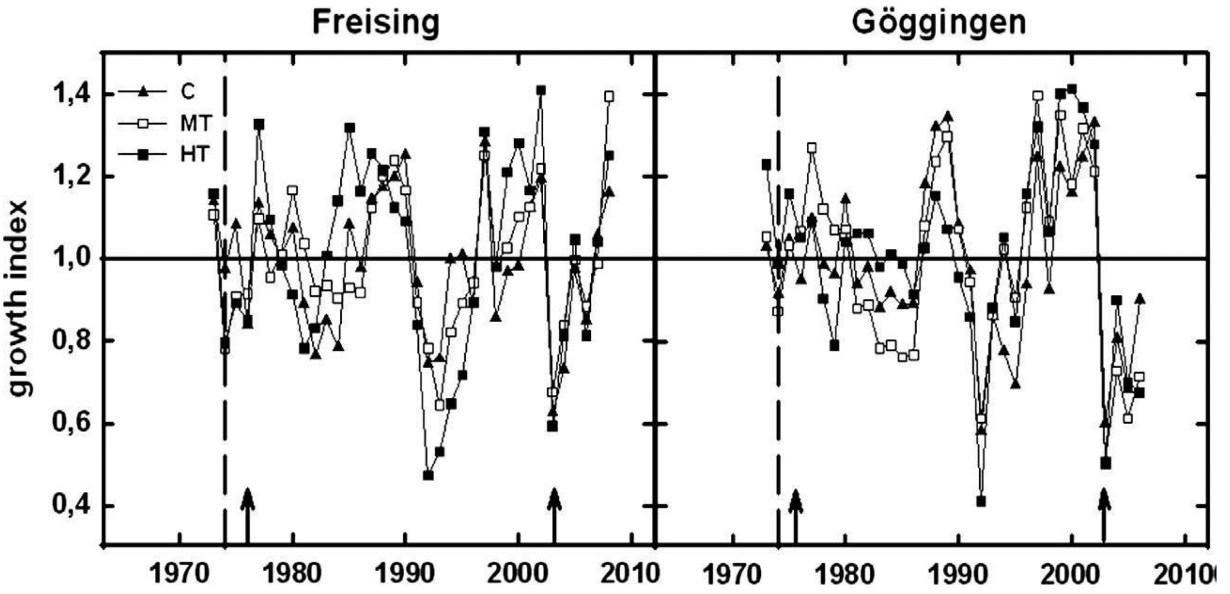

Figure 2-3 Dimensionless growth indices (I_t) at Freising and Göggingen: BAI of the post-thinning period 1974–2006 was detrended using the Hugershoff growth functions in ARSTAN. Closed triangles: control (C), open squares: Moderate thinning (MT) and closed squares: heavy thinning (HT). Dashed lines indicate year of first thinning and arrows point to drought events of 1976 and 2003.

Isotopes

At both sites and across treatments, $\Delta^{13}C$ in earlywood was (marginally) significantly correlated ($P < 0.01$) with $\Delta^{13}C$ in latewood of both the same and the preceding year (Table 2-4). The same was found for $\delta^{18}O$, except for control trees in Göggingen, where the correlation was weaker between earlywood and latewood of same years ($P < 0.05$) and not significant between earlywood and latewood of the previous years

Table 2-4 Correlation coefficients (Pearson-R) of $\Delta^{13}C$ and $\delta^{18}O$ in earlywood of current year with latewood of both previous and current year under the three treatments (control, moderate thinning (MT), heavy thinning (HT) at both sites (Göggingen and Freising).

		Earlywood / Freising			**Earlywood / Göggingen**		
	Latewood	**Control**	**MT**	**HT**	**Control**	**MT**	**HT**
$\Delta^{13}C$	**Previous year**	0.50	0.62	0.42	0.89	0.76	0.86
	Current year	0.49	0.60	0.31	0.86	0.73	0.87
$\delta^{18}O$	**Previous year**	0.71	0.53	0.38	0.10	0.59	0.49
	Current year	0.68	0.49	0.41	0.25*	0.64	0.46

All correlations are significant at $P < 0.001$, except for * where $P < 0.05$ and the italic number where $P > 0.05$ ($N = 65–80$). Significance levels were calculated using Fischer-P, two-tailed test.

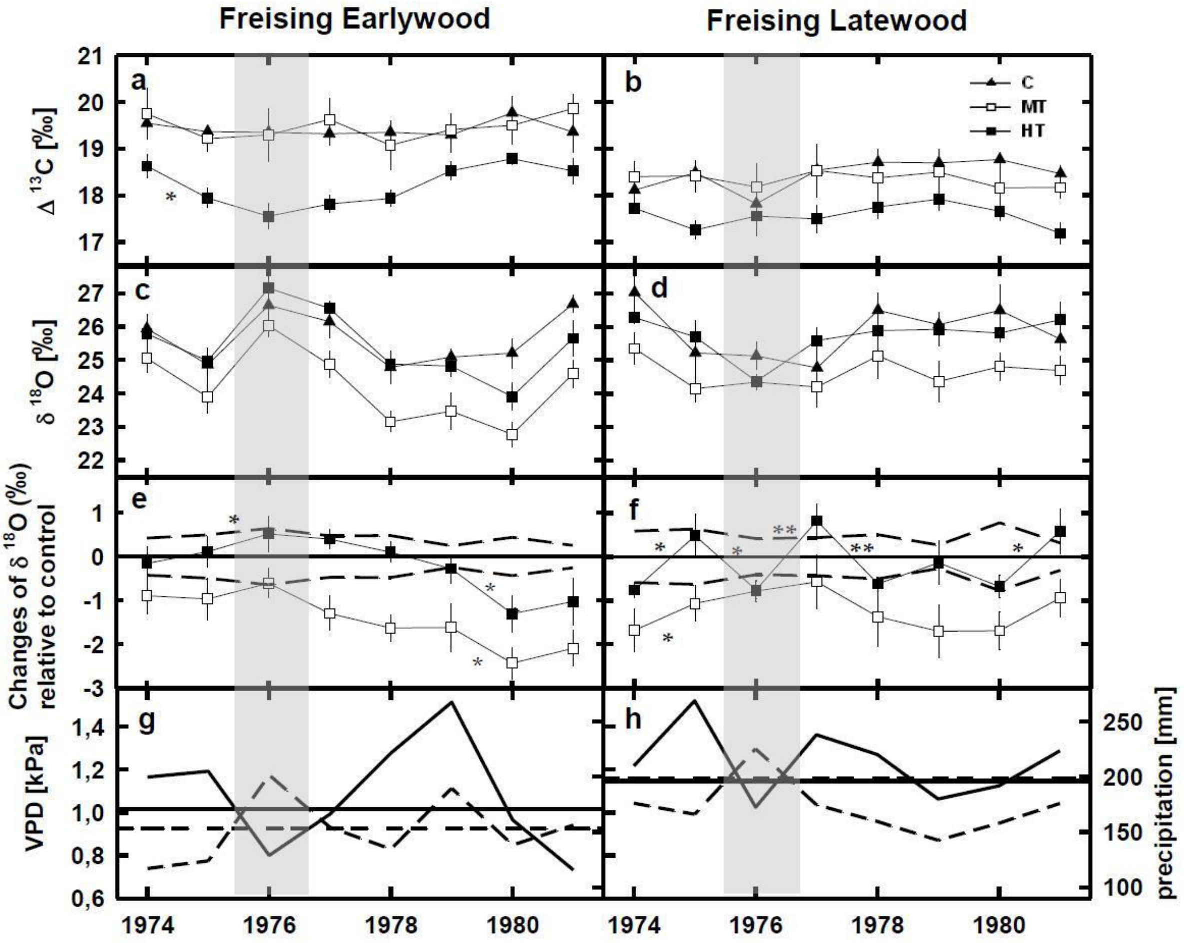

Figure 2-4 a–f Means (±SE) of $\Delta^{13}C$ (a and b), and $\delta^{18}O$ (c and d) for the post-thinning period of 1974–1981 in earlywood (a and c) and latewood (b and d) in control (closed triangles), moderate (open squares) and heavy thinning (closed squares) at Freising (N = 5 each). Differences of MT and HT trees in $\delta^{18}O$ relative to control trees are given for earlywood (e) and latewood (f). Dashed lines in e-f indicate ± 1 standard error of control trees. One and two stars indicate significant differences between subsequent years at $P < 0.05$ and $P < 0.01$, respectively (repeated measures ANOVA). (g and h) Long-term (1973–2006) and annual (1974–1981) means of VPD (at 2 pm; dashed lines) and precipitation (solid lines). Data are averaged for Mai to June (g) and from July to August (h) for comparison with early- and latewood, respectively; grey area shows drought event of 1976.

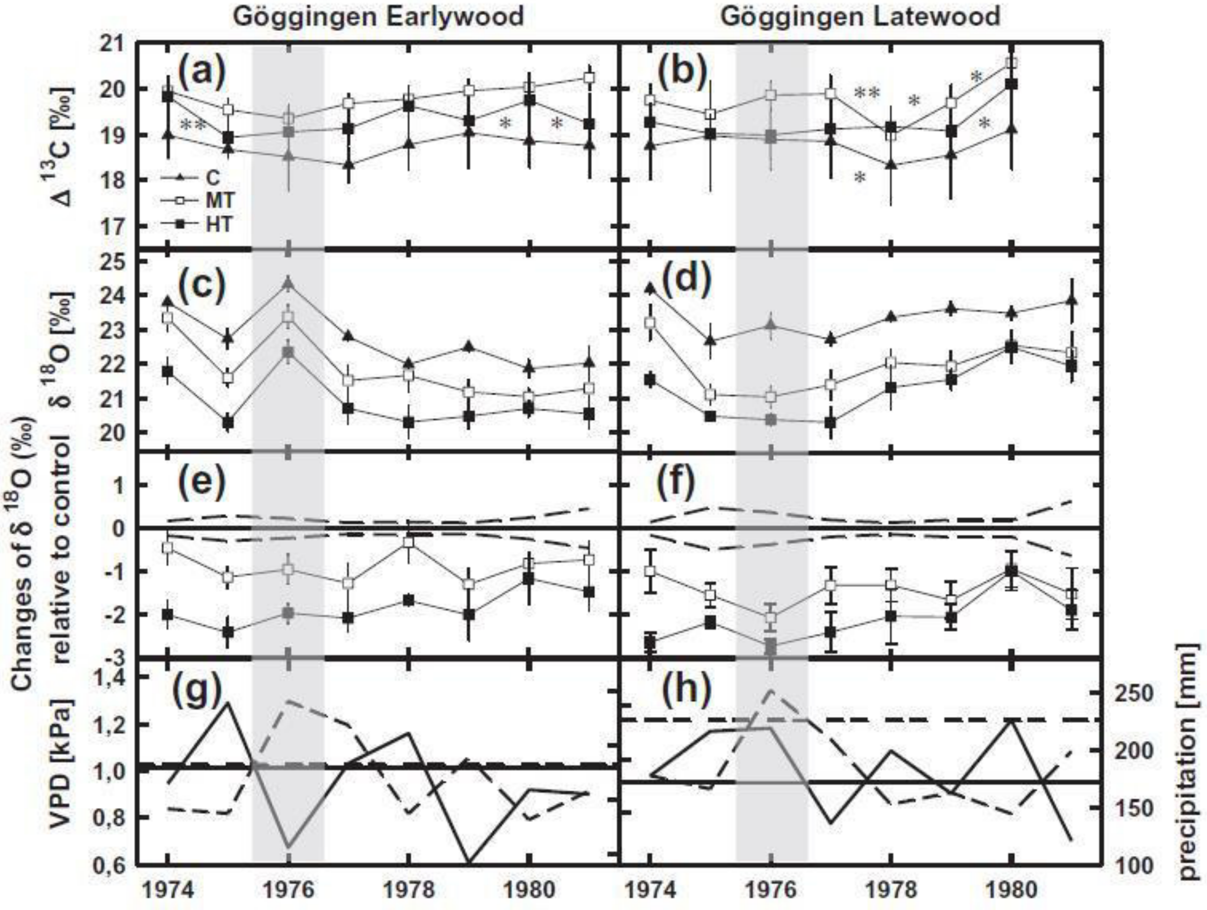

Figure 2-5 a–f Means (±SE) of $\Delta^{13}C$ (a and b), and $\delta^{18}O$ (c and d) for the post-thinning period of 1974–1981 in earlywood (a and c) and latewood (b and d) in control (closed triangles), moderate (open squares) and heavy thinning (closed squares) at Göggingen (N = 5 each). Differences of MT and HT trees in $\delta^{18}O$ relative to control trees are given for earlywood (e) and latewood (f). Dashed lines in (e–f) indicate ±1 standard error of control trees. One and two stars indicate significant differences between subsequent years at $P < 0.05$ and $P < 0.01$, respectively (repeated measures ANOVA). (g and h) Long-term (1973–2006) and annual (1974–1981) means of VPD (at 2 pm, dashed lines) and precipitation (solid lines). Data are averaged for Mai to June (g) and from July to August (h) for comparison with early- and latewood, respectively; grey area shows drought event of 1976.

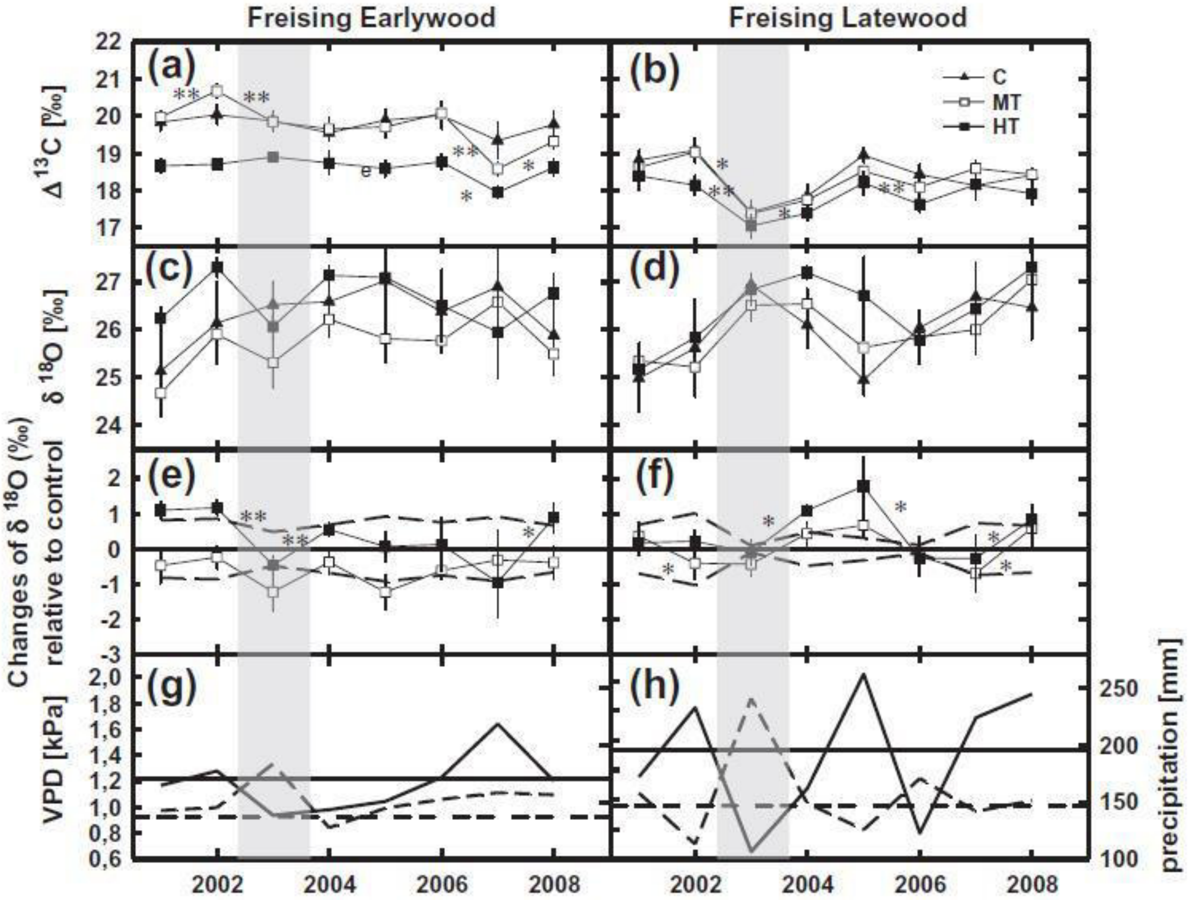

Figure 2-6 a–f Means (±SE) of $\Delta^{13}C$ (a and b), and $\delta^{18}O$ (c and d) for the post-thinning period of 2001–2008 in earlywood (a and c) and latewood (b and d) in control (closed triangles), moderate (open squares) and heavy thinning (closed squares) at Freising (N = 5 each). Differences of MT and HT trees in $\delta^{18}O$ relative to control trees are given for earlywood (e) and latewood (f). Dashed lines in e–f indicate ± 1 standard error of control trees. One and two stars indicate significant differences between subsequent years at $P < 0.05$ and $P < 0.01$, respectively (repeated measures ANOVA). (g and h) Long-term (1973–2006) and annual (2001–2008) means of VPD (at 2 pm, dashed lines) and precipitation (solid lines). Data are averaged for Mai to June (g) and from July to August (h) for comparison with early- and latewood, respectively; grey area shows drought event of 2003.

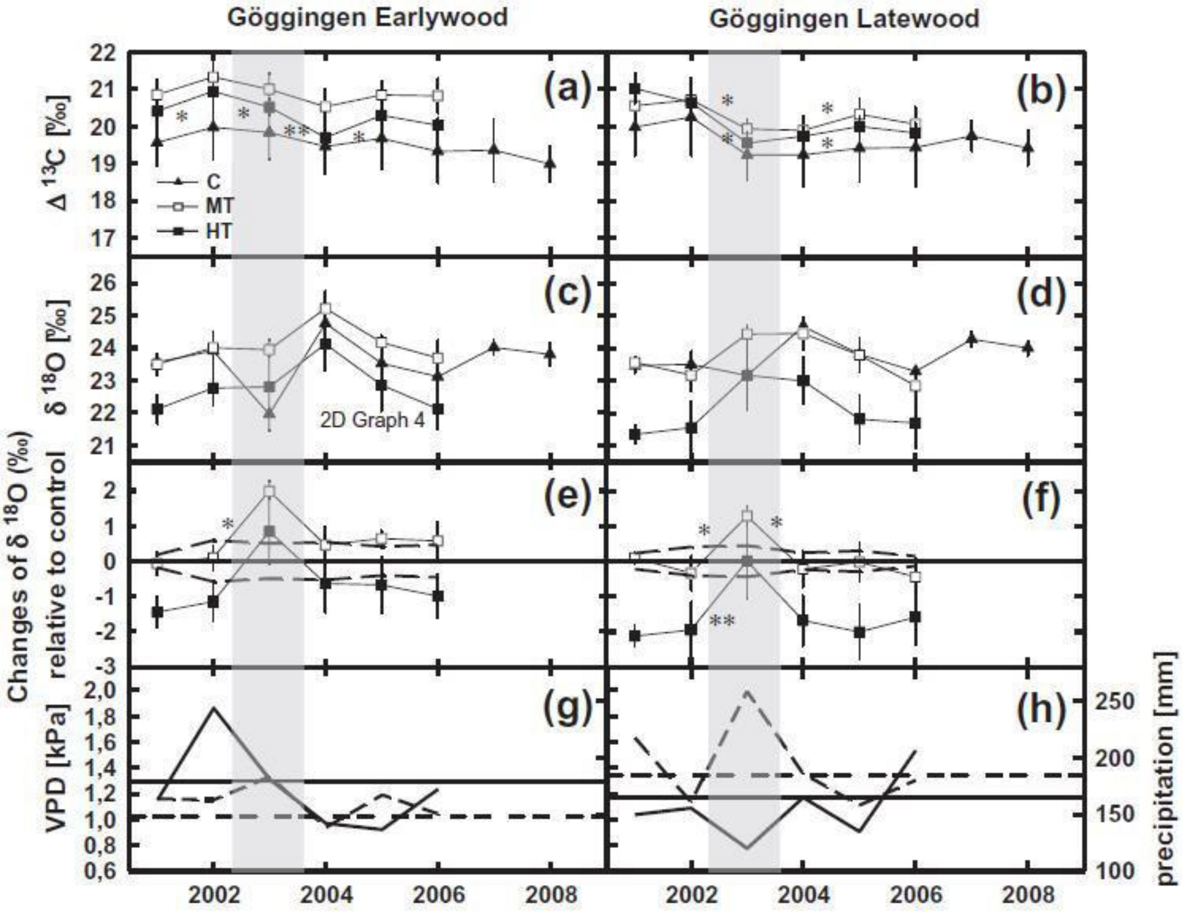

Figure 2-7 a–f Means (±SE) of $\Delta^{13}C$ (a and b), and $\delta^{18}O$ (c and d) for the post-thinning period of 2001–2006 in earlywood (a and c) and latewood (b and d) in control (closed triangles), moderate (open squares) and heavy thinning (closed squares) at Göggingen (N = 5 each). Differences of MT and HT trees in $\delta^{18}O$ relative to control trees are given for earlywood (e) and latewood (f). Dashed lines in e-f indicate ± 1 standard error of control trees. One and two stars indicate significant differences between subsequent years at $P < 0.05$ and $P < 0.01$, respectively (repeated measures ANOVA). (g and h) Long-term (1973–2006) and annual (2001–2006) means of VPD (at 2 pm, dashed lines) and precipitation (solid lines). Data are averaged for Mai to June (g) and from July to August (h) for comparison with early- and latewood, respectively; grey area shows drought event of 2003.

At Freising, during the drought year 1976, i.e. two years after the initial thinning, $\Delta^{13}C$ in latewood of control trees tended to decrease by about 1 ‰ ($P = 0.07$), whereas no significant drought effects were found in $\Delta^{13}C$ in latewood of MT and HT trees and in any of the three earlywood series (Fig. 2-4a and b). In earlywood $\delta^{18}O$ of HT trees increased significantly relative to controls during the drought year 1976 (Fig. 2-4c and e). In latewood $\delta^{18}O$ of the same trees decreased significantly during the drought and subsequently increased significantly in the following year relative to controls (Fig. 2-4d and f). In Göggingen, during the 1976 drought and following years, we found no significant inter-annual changes either in $\Delta^{13}C$ or $\delta^{18}O$ relative to controls in earlywood or latewood (Fig. 2-5). The increases in $\delta^{18}O$ in earlwood of 1976 are similar in all treatments (Figs. 2-4c and 2-5c) and are likely caused by enriched $\delta^{18}O$ of precipitation (data not shown).

During the 2003 drought, $\Delta^{13}C$ in latewood decreased (significantly) by ca. 1–2‰ at both sites and for all treatments (Figs. 2-6b and 2-7b). In the following year, a small positive trend (significant for MT trees) was observed in Freising but values did not recover to pre-drought levels until 2005 (Fig. 2-6b). At Göggingen, no changes occurred in latewood $\Delta^{13}C$ in the first post-drought year but one year later, values of MT and HT trees increased significantly (Fig. 2-7b). The corresponding decrease of $\Delta^{13}C$ in earlywood during 2003 was somewhat smaller at both sites (significant for MT trees in Freising and HT trees in Göggingen) and continued at least for one more year (Figs. 2-6a and 2-7a).

The developments of $\delta^{18}O$ in earlywood and latewood at the two sites showed no consistent pattern during the 2003 drought. At Freising, $\delta^{18}O$ relative to controls significantly decreased in2003 in earlywood of HT trees (Fig. 2-6c and e). In the following year, the same trees showed a significant increase in $\delta^{18}O$ relative to control in both early and latewood (Fig. 2-6e and f). At Göggingen, in contrast, we found a (significant) increase in earlywood and latewood $\delta^{18}O$ relative to the control in trees of the MT and HT treatments during the 2003 drought and a (significant) decrease in the following year (Fig. 2-7c–f).

Discussion

The present study assessed the effects of thinning on the drought response of stem growth in Norway spruce from two thinning experiments in Southern Germany. We hypothesized that thinning (1) does not mitigate the growth reduction, i.e. increase resistance, during a drought year, but (2) enhances recovery of stem growth during following years. These hypotheses were corroborated through our analysis for the 2003 drought, but not in all cases for 1976. To facilitate retrospective inference of physiological drought responses of trees, the different growth resistance to and recovery from drought are interpreted on the basis of tree ring isotope data (hypothesis 3) by means of the conceptual models using the dual isotope approach (Scheidegger et al., 2000; Grams et al., 2007; Roden and Siegwolf, 2012).

Growth response to drought in 1976

In contrast to our hypothesis 1 that thinning does not increase growth resistance to drought, we found a significantly higher resistance in 1976 in trees from thinned compared to unthinned stands at Freising. At the second site, Göggingen, there were no differences in resistance among treatments. However, this outcome must be seen within the context of the moderate growth suppression in 1976 of control trees at Göggingen by 5–15% compared to 25% at Freising. Considering the normal to wet climatic conditions during the two preceding years at both sites (Figs. 2-4g, h and 2-5g, h), it is unlikely that control trees at Freising had a higher predisposition to succumb to drought than at Göggingen. However, the larger growth reduction at Freising may be related to a longer duration of drought during the 1976 growing season at this site compared to Göggingen. Rainfall during late summer was still below average at Freising whereas it was higher than the long-term average at Göggingen (Figs. 2-4 and 2-5h).

It is likely that the higher drought resistance of trees from thinned compared to control stands at Freising resulted from the short time period since the initial thinning in 1974. During earlywood formation when drought peaked, the model of Scheidegger et al. (2000) suggests that trees responded with a reduction of both stomatal conductance (g) and assimilation (A) (i.e. no change in $\Delta^{13}C$ and increase in $\delta^{18}O$ relative to control) compared to the pre-drought year. This effect was strongest in HT trees. For recently thinned Douglas Fir stands on

Vancouver Island, a similar isotopic response in earlywood formed during drier spring seasons was related to a decrease of g along with a decrease in relative humidity and/or increase in leaf temperature (Brooks and Mitchell, 2011). However, we cannot rule out that the increase in $\delta^{18}O$ in HT relative to control stands during the drought may have been at least partly related to more enriched source water in open stands due to comparably more evaporation loss of more exposed soils in recently thinned stands (cf. Moreno-Gutiérrez et al. 2011, 2012). As soon as growth conditions improved later during the growing season, the dual isotope approach suggests that HT trees increased both g and A (no change in $\Delta^{13}C$ and significant decrease in $\delta^{18}O$ relative to control) compared to values of the previous year. Thus, despite a possibly short period of more restricted gas exchange during early summer including the formation of false year rings, the recent heavy thinning (i.e. two years ago) allowed for enhanced stomatal aperture once water availability improved during late summer. In turn, assimilate availability apparently increased in support of growth as compared to control trees. In addition, the favorable climatic conditions in the two years after thinning and before the drought in 1976, may have replenished soil water stores in the thinned stands, and hence mitigated growth reductions during the drought (Hartmann et al., 2008). Our results support findings of Moreno-Gutiérrez et al. (2011) who attributed increases in g and A along with growth during the first year following heavy thinning in a *Pinus halepensis* stand in semiarid Spain to reduced competition for limited water.

At Göggingen, the generally modest growth reductions in 1976 are likely to have caused the similar resistance across treatments as opposed to the increased resistance of HT trees at Freising. The limited drought period at the Göggingen site during early summer led to the formation of false tree rings that were least distinct in HT trees. Isotopic composition of tree rings during the drought remained largely unaffected by the thinning treatments, reflecting comparable growth response in thinned and unthinned stands. Comparing both experiments, the high drought resistance of HT trees was found at the site with higher soil water holding capacity (i.e. Freising), confirming findings by Laurent et al. (2003) for recently thinned stands of Norway spruce in the Belgian Ardennes.

In addition to their higher drought resistance, HT trees from Freising recovered faster after the drought in 1976 compared to trees in denser stands, confirming our second hypothesis. The faster growth recovery of HT trees was probably facilitated by the humid conditions during the post-drought period. Considering the high water holding capacity of the soil at lower stand density, HT trees should have high soil water availability. The positive growth trend of HT trees throughout the whole post-thinning period indicates an ongoing positive thinning effect. Even during the drought, radial growth was similar to the two pre-drought years. Following the drought, isotopes indicate a larger range for g and A in HT compared to control trees (stable $\Delta^{13}C$ and several significant deviations of latewood $\delta^{18}O$ relative to control), which may suggest a higher potential to take advantage of favorable growth conditions when soil water availability was high (cf. McDowell et al., 2006).

Conversely at Göggingen, heavy thinning led to a significantly slower growth recovery, in the three years after the 1976 drought compared to trees in denser stands. The reason for the slower recovery of HT trees remains obscure, in particular as isotopic signatures suggest similar photosynthetic responses of trees irrespective of the thinning treatment.

Growth response to drought in 2003

The 2003 drought occurred about 30 years after the initial and 7–10 years after the last thinning intervention. Meanwhile trees grown at thinned plots developed both larger leaf area and fine root mass per tree compared to controls (Sohn et al., 2012). The 2003 drought led to a stronger decline in radial growth (40–60% less than in 2002) compared to 1976, at both sites and regardless of the thinning treatment. This agrees well with the more severe and longer-lasting drought in 2003 than in 1976 (Figs. 2-6g, h and 2-7g, h). Overall, growth resistance was lower in heavily thinned trees compared to moderately thinned and control trees. This confirms our first hypothesis that for severe drought events the related decline of radial growth is not mitigated by thinning. At Freising, in correspondence with the stronger decline in radial growth, isotopes in latewood suggested a similar drop in g along with a larger decline in A of HT compared to control trees (i.e. smaller reduction in $\Delta^{13}C$ at similar increase of $\delta^{18}O$). Likewise at Göggingen, HT trees displayed a smaller growth resistance compared to control trees. As indicated by stable isotopes, the smaller resistance was accompanied by a decrease of g at a smaller A (increase in $\delta^{18}O$ relative to control at a similar decrease in $\Delta^{13}C$) at this site. Hence, the corresponding decline in growth rate of HT compared to control trees at both sites may be related to a higher transpirational demand owing to a larger total leaf area per tree

(McDowell et al., 2006) and/or decreased boundary layer due to increased air flow in the canopy.
At both sites, radial growth of HT trees recovered faster than in trees growing in denser stands, confirming our second hypothesis. Nevertheless, full recovery was only achieved two year after the drought event in both growth and stable isotopes.

At Freising, in contrast to the better growth recovery of HT trees, isotopes implied a decreased g and A relative to the control (i.e. increased $\delta^{18}O$ relative to controls and similarly constant $\Delta^{13}C$) and all treatments had a temporal delayed recovery in isotopes, implying minor water shortage in 2004. The reason for the diverging results of radial growth and isotopic compositions could not be clarified completely, but the combination of higher fine root surface and leaf area of HT trees (Sohn et al., 2012) should greatly increase whole-tree C gain and hence provide the basis for a better growth recovery (c.f. McDowell et al., 2006).

In contrast, at Göggingen C and O isotopic composition suggest that the faster growth recovery was paralleled by a recovery of photosynthetic C gain. Trees of the heavily thinned stands significantly increased g (i.e. decreased $\delta^{18}O$) relative to controls in the post-drought years. At the same time, $\Delta^{13}C$ in latewood stayed rather constant after the drought, suggesting more effective CO_2 fixation at higher g.

Conclusion

The mitigating effect of thinning during the drought depends on the time span between thinning and drought. In recently thinned stands, increased water availability likely allows trees to maintain higher stomatal aperture and growth rates during droughts compared to control stands. This advantage is reduced over time by the increased water demand of the remaining trees caused by an increasing leaf area and fine root biomass. This confirms findings of McDowell et al. (2006) that tree structures have to be considered when interpreting growth patterns using stable isotopes in tree rings – in particular if the thinning treatment was conducted more than one decade ago. As a consequence, 30 years after the initial and 7–10 years after the last thinning the growth decline of HT trees during the 2003 drought was larger than in control stands.

The growth recovery of trees immediately after the drought was improved through thinning irrespective of the time span between thinning and drought. This resulted from a likely increase in soil water availability in recently thinned stands. In the medium to long term and after several thinnings, the more rapid post-drought recovery of stem growth may be attributed to a structural adaptations of large trees, i.e. high foliage area and fine root biomass, that allow them to take advantage of improving conditions. Overall, we conclude that repeated thinning improves drought response of Norway spruce and should be considered as a management strategy for immature Norway spruce stands.

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Chapter 3

The more, the better? Water relations of Norway spruce stands after progressive thinning[1]

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The more, the better? Water relations of Norway spruce stands after progressive thinning

Agricultural and Forest Meteorology 197 (2014) 235–243

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Abstract

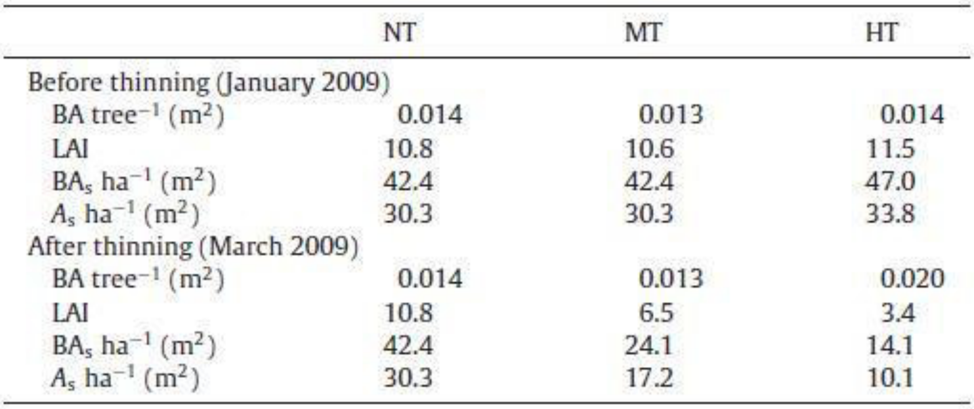
Predicted intense and prolonged drought events challenge forest management. Thinning is debated as a silvicultural measure for reducing drought risk in densely established forest stands. We report on a thinning experiment in a 26-year-old Norway spruce stand (Picea abies), comprising of two thinning intensities and one unthinnned control. The removal of 43% (moderate thinning, MT) and 67% (heavy thinning, HT) of the initial basal area led to increased water availability during the entire three-year observation period. Stand-level transpiration (E_S) was decreased by about 25% upon moderate, and by about 50% upon heavy thinning during the first year after the interventions had been carried out. However, differences in E_S across the treatments decreased within three years after thinning mainly due to increased single-tree transpiration and additional understory evapotranspiration at HT. Nevertheless, due to lower interception and transpiration on the thinned plots three years after treatment MT and HT still showed a substantial surplus in extractable soil water. The results showed that the main determinants concerning the extent of the mitigation effect with increasing thinning intensity were the available soil water storage capacity and the emerging understory vegetation. We conclude that repeated moderate thinning, through enhancing the water availability to the remaining trees, can mitigate drought risk in young spruce standsand thus, represent a viable silvicultural measure in anticipating possible water limitations due to climate change

Introduction

The expected increase in air temperature during growing sea-sons in combination with severe and extended periods of drought (Meehl and Tebaldi, 2004) challenge forest management all over the world: decreasing primary productivity or whole-stand decline caused by pest may threaten forestry (Ciais et al., 2005; Bréda et al., 2006; Rouault et al., 2006). Present forest management strategies for counteracting the consequences of climate change in Central Europe are to diversify tree species composition and to convert mono-specific stands of drought sensitive species into mixed-species stands (Bolte et al., 2009). Norway spruce (Picea abies [L.] Karst.), a drought sensitive tree species, may be severely affected by climate change (Ammer et al., 2008; Kölling et al., 2009; Temperli et al., 2012). However, in Germany, Norway spruce occupies more than 3.3 million ha (c.30% of total forest area) 32.7% of the Norway spruce stands are still even-aged and mono-specific (BMELV, 2008). In Bavaria (Southern Germany), even 43% of the forests consist of pure Norway spruce, which is by far the economically most important tree species in Germany. However, on sites where its future cultivation in mono-cultures is questioned, spruce stands older than 60 years may be replaced by another more drought tolerant species or they may be converted into mixed stands by under-plantings with a different tree species (for review see Ammer et al., 2008). This is no option for the Norway spruce stands <40 years of age growing on more than 1.0 million hectares in Germany (BMELV, 2008). Therefore, the question arises whether silvicultural interventions may help to mitigate the risk of drought on young Norway spruce stands. One frequently discussed option is thinning (Bolte et al., 2009). Experimental evidence from different studies covering a variety of species suggests that thinnings may help to substantially reduce climatic stress by augmenting water supply (Lagergren et al., 2008; Magruder et al., 2013; Hawthorne et al., 2013; Giuggiola et al., 2013). Moreover, retrospective tree ring analyses revealed trees of thinned stands to be favoured in recovery after exception-ally dry years (Kohler et al., 2010; Sohn et al., 2013). D’Amato et al. (2013) confirmed these findings but only for young stands. Reversal effects were found for old stands. However, dendro-chronological studies cannot fully disentangle thinning effects from such of cli-mate on growth (Laurent et al., 2003). Common silvicultural thinning practice in immature Norways pruce stands is promoting the future crop trees in growth and stability by reducing light competition through successively removing competitors (Röhrig et al., 2006). Although effects of thinning intensity and frequency have been repeatedly studied on single tree performance and stand growth, structural development and wood properties (Misson et al., 2003; Mäkinen and Isomäki,2004; Jaakkola et al., 2005a, b; Slodicak et al., 2005; Cao et al.,2008; Wallentin and Nilsson, 2011), much less is known on the effect on tree water consumption and stand water balance. As for light (Binkley et al., 2013) the response of single trees to improved soil water conditions may be completely different from the response of the entire stand. Thus, thinning may increase single-tree transpiration due to increase in light, air flow in the crown and water availability but reduce stand water consumption on a short-term scale (Morikawa et al., 1986; Aussenac and Granier, 1988; Hager, 1988; McJannet and Vertessy, 2001; Simonin et al., 2006, 2007). Water interception is decreased while the water status of the remaining trees is improved due to rising soil moisture (Donner and Running, 1986) Conversely, in some studies the thinned stands showed increasing transpiration, already after the second year (Stogsdill et al., 1992; Bréda et al., 1995; Lagergren et al., 2008). The differing results may partly be explained by thinning intensity. As Aussenac and Granier (1988) reduced total basal area of a Douglas fir stand (Pseudotsuga menziesii var. menziesii) down to 50%, which resulted in increased soil water reserves during at least the three subsequent years, Bréda et al. (1995) and Lagergren et al. (2008) performed less intense thinnings (basal area removed 35%and 25% respectively). Although Stogsdill et al. (1992) reduced basal area down to 50% and 75%, improved water availability occurred only during humid years, due to increased throughfall. However, the water status of an entire stand is controlled by both the residual trees after thinning and the understory vegetation which may establish shortly after the silvicultural intervention. To our knowledge understory effects on ecosystem-level water consumption after thinning have been considered only by Simonin et al. (2007). They showed that in dry years the contribution of understory evapotranspiration compensated the lower overstory evapotranspiration. In summary, it can be concluded that the reliability of thinning for mitigating drought risk is not yet clear. Overall, knowledge and mechanistic understanding of graduated thinning affecting stand-level water relations and productivity, taking water consumption by trees and understory vegetation into account, is scarce. In this study, we report on an experiment in a mono-specific Norway spruce stand where two thinning intensities were carried out and compared with an un thinned control. The aim of our study was to clarify to which extent increasing thinning intensity may promote water availability of the remaining trees in parallel to reducing the stand-level water consumption. Both the water demand of tree and understory vegetation were taken into account.

It was hypothesized (i) that increasing thinning intensity decreases stand-level transpiration while increasing soil water content, (ii) that such effects decline over time due to increases in tree and understory transpiration and understory interception, and (iii) that the water use efficiency of target trees released from competition is lower than that of control trees.

Table 3-1 Stand characteristics: mean basal area per tree (BA tree^{-1}), leaf area index of the stand (LAI), stand basal area (BA ha^{-1}) and stand sapwood area (A_s ha^{-1}) of the unthinned control plots (NT), moderately thinned plots (MT) and heavily thinned plots (HT) before and upon thinning in 2009^{-1}.



	NT	MT	HT
Before thinning (January 2009)			
BA tree^{-1} (m^2)	0.014	0.013	0.014
LAI	10.8	10.6	11.5
BA_s ha^{-1} (m^2)	42.4	42.4	47.0
A_s ha^{-1} (m^2)	30.3	30.3	33.8
After thinning (March 2009)			
BA tree^{-1} (m^2)	0.014	0.013	0.020
LAI	10.8	6.5	3.4
BA_s ha^{-1} (m^2)	42.4	24.1	14.1
A_s ha^{-1} (m^2)	30.3	17.2	10.1

Materials and methods

Experimental stand and site

The study was conducted near Landshut (48°38´20´´N, 11°57´49´´E, Bavaria, Germany) in a monoculture of Norway Spruce (Picea abies [L.] Karst.). The mean annual precipitation in the region reaches 778 mm and the mean annual temperature was 7.9°C(DWD). The stand was planted in 1982 on luvisol (loess over tertiary) with approx. 3700 seedlings ha^{-1}. Available soil water storage capacity (ASWSC) reached about 160 l m^{-2}(per ground area down to 60 cm soil depth). The experiment was initiated in 2008 and has continuously been monitored since that time. The research area (75 m × 50 m) was subdivided into 6 plots of 25 m × 25 m each. In January 2008, the stem diameter at breast height (1.30 m, DBH) of all trees was measured and their co-ordinates were mapped. Prior to initiation, about 430 future crop trees (target tree) per hectare were selected. Target trees were defined as dominating vital trees (in most cases the trees with the highest diameter). DBH increments of all trees were recorded after each growing season and up-scaled to stand level. In February 2009 four out of six randomly selected plots were thinned, while two plots remained unchanged as control (NT = not thinned). Two plots each were moderately (MT) or heavily thinned (HT; Table 3-1; Fig. 3-1). MT represented the stand treatment commonly carried out in Germany, i.e. thinning from above by removing two competitors per target tree on average. MT reduced stand basal area by c. 43.0%. On HT all trees but the target trees were removed, resulting in BA reduction of c. 67.0%. Thinning was performed by a harvester.

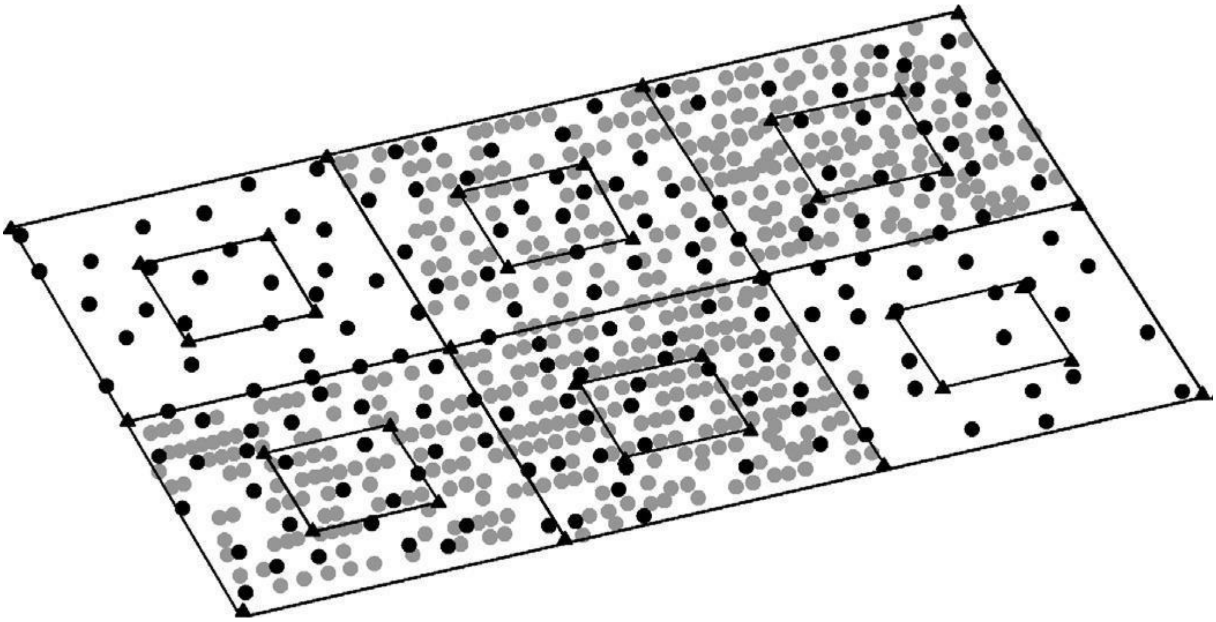


Figure 3-1 The research area (75 m × 50 m), subdivided in 6 plots of 25 m × 25 m with an inner intensive measurement area 10 m × 10 m each (triangle). Each circle represents one tree. About 430 future crop trees (target trees) per ha (black circles) were selected prior to thinning. Four out of the six randomly selected plots were thinned, while two plots remained unchanged as control (NT = not thinned). Two plots each were moderately (MT) or heavily thinned (HT).

Motor-manual felling were done inside the centre of the plots in order to maintain the integrity of prior instrumental installations which were placed on a central 10 m × 10 m subplot on each plot. Leaf area index (LAI) of the plots was calculated by the allometric relationship between basal area (BA, cross sectional area at breast height) and projected leaf area (LA) of the trees. For LAI determination 12 trees were harvested covering the entire range of DBH.

After assessing crown projected area the trees were cut and all first order branches were counted and their diameters were measured. For a subsample of c. 10% of the branches from sun-exposed and shaded crown parts, the total length of all lateral branches was assessed. Subsequent with another subsample consisting c. 10% of the total length of all lateral branches, the projected LA per branch was determined in the laboratory. Using the correlation of projected LA to branch diameter whole tree projected LA was calculated and scaled to stand level (LA = 2592.4 × BA − 5.2525; R^2= 0.9269). LAI was calculated using the corresponding crown projection area.

Meteorological parameters

Air temperature (T_{air}) and P_g (gross- precipitation) were measured at an open field climate station on a meadow at a distance of about 100 m from the experimental forest site (Table 2). Due to technical failure temperature was sporadically missing. In these cases mean daily T_{air} data were interpolated by linear regression (R2> 0.90) using T_{air} measured at the climate station Feistenach (Bavarian Institute for Agriculture, LfL) which was located in 30 km distance to the experimental site. To account for missing data of the cumulated P_g per growing season in 2010 and 2011, a correction factor was calculated between cumulated P_g per growing season at the study site and the climate station of Feistenach in 2009. To account for P_s (throughfall) a 10 m long rain gorge with a collecting area of 1.0 m^2 was installed permanently on each central 100 m^2 subplot. Ensuring representativeness, gorges were split into one 6 m and one 4 m section each, arranged by an angle of 110° to each other. Both sections of each gorge discharged into one tip-ping bucket. The interception of the overstory (I_o) was therefore assessed by

$$I_o = P_g – P \qquad (1)$$

where is the overstory interception, P_g the gross–precipitation (open field precipitation) and Ps the throughfall.

Soil water content and fine root biomass

For measuring volumetric soil water content (θ) TDR – sensors (Time Domain Reflectometry, Soil moisture Equipment Corp., Santa Barbara, California) combined with MiniTrase 6050X3 (Soilmoisture Equipment Corp., Santa Barbara, California) were installed at three locations on a diagonal transect across each subplot. At each location waveguides were installed horizontally in the upper three soil horizons and one sensor per subplot plot was positioned at about 1 m depth into the deepest quarter (C- horizon). Measurements were recorded every 20 min for each sensor throughout the study period. In total 60 sensors (6 subplots × 3 locations × 3 sensors + 1 in the deepest horizon) provided data on θ.

Undisturbed soil samples per horizon were taken during sensor installation to measure soil water retention curves of each soil horizon in the lab-oratory (3–4). Plant extractable soil water content (We) down to 60 cm depth (comprising more than 90% of total fine-root biomass) was calculated and accumulated for each location by the measured extractable storage capacity (range between field capacity and permanent wilting point) and the thickness of each soil horizon. Each year upon thinning, fine-root biomass was measured at the end of the growing season in soil core samples taken with a cylindrical soil corer (0.08 m × 1 m; 10 samples down to 1 m depth per year and plot). The samples were randomly selected, using a 1 m × 1 m grid omitting positions of previous samplings.

Stand transpiration

Sap flux density per unit sapwood area A_s (*u*) was assessed by the heat dissipation method (Granier, 1985, 1987). On each central subplot two sensors were installed opposite to each other on five target trees at breast height. u was measured (condensed to 10-min means) in the outer part of the xylem (0–20 mm), while the radial u profile was assessed with additional sensors in one further tree on each plot, inserted 20–40 mm and 40–60 mm deep into the trunks and averaged including all plots. The attenuation factor of u towards heartwood was calculated for the 20–60 mm depth (n = 6), extrapolated for 60–80 mm and employed in determining whole-tree transpiration. Radial sapwood depths of individual trees were derived from increment cores taken with a Suunto increment borer (5 mm in diameter), covering the range of stem diameters of the trees (N = 13) present at the site. A_s and BA per tree were then correlated to calculate total stand A_s (A_s= 0.7537* BA − 0.0012; R^2= 0.9853). With the corrected *u* and the total stand A_s the total daily overstory transpiration (E_o) was calculated and expressed per unit ground area (kg m^{-2} d^{-1}). On NT and MT with negligible under-story vegetation during the entire observation period, E_o is assumed to represent whole stand transpiration (E_s). In contrast to NT and MT, on HT understory vegetation emerged by the second year after thinning. Therefore, for calculating E_s on HT evapotranspiration of the understory vegetation (E_u, see below) was taken into account. Due to high annual radial growth of the trees all sensors had to be re-installed on the same trees every year before the growing season

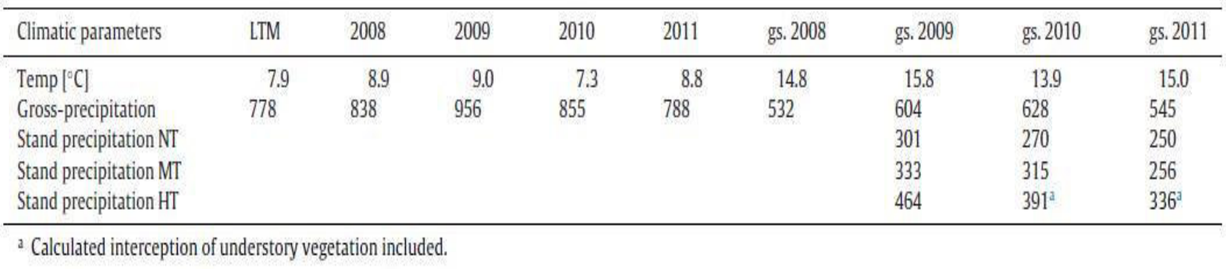
Understory vegetation

Composition and dominance (% of ground area) of understory vegetation was monitored during the growing seasons of 2009,2010 and 2011 according to standard protocols (Dierschke, 1994). On NT and MT plots understory vegetation reached dominance between 0 and 4% and was putatively negligible in water balance calculations. On HT plots more than 60% of the understory vegetation was composed of *Rubus idaeus* and *Rubus fruticosus* covering c. 52% in 2010 and 75% in 2011. E_u was assessed with a closed chamber approach (vol. 0.32 m^3) in combination with a HOBO-logger (Onset Computer Corporation, Bourne, MA, USA) in July 2010 at the peak of leaf area development of the R*ubus* plants (Müller and Bolte, 2002). After preceding measurements of air temperature and air humidity within the understory vegetation (c. 50 cm height) the chamber was positioned. Subsequently the increase in air humidity yielded the evapotranspiration rate (kg s^{-1}) inside the chamber. To prevent bias due to stomata closure (darkness) and temperature-related changes of transpiration rate and air humidity the derivation of evapotranspiration rate was confined to the linear time dependence of the increase in air humidity (R^2> 0.97, max. 300 s). In order to calculate E_u per foliage area and therefore to scale up to stand basis, foliage area per ground area was assessed. For that purpose total foliage was harvested on 6 m × 0.25 m subplots and the projected LA scanned in the laboratory. With the scanned projected LA and the dominance of the understory vegetation at each HT-plot total projected LA of the HT plots was calculated. Total E_u was up-scaled to the stand level per ground area (kg $m^{-2}d^{-1}$) and related to the overstory transpiration (E_o) during the corresponding time interval. Subsequently to calculating daily total E_s of the HT plots, the additional daily E_u in respect to E_o was added to E_o on a daily basis. The interception of the understory vegetation (I_u) was assessed by

$$I_u = P_s - (\Delta W_e + E_o + E_u + R_g) \qquad (2)$$

where P_s is the throughfall, ΔW_e the difference in extractable water before and after the rain events, E_o the overstory transpiration, E_u the understory evapotranspiration and R_g the groundwater runoff during the rainy period. To calculate mean I_u and eliminate R_g only months without W_e saturation were taken into account (2 months in 2010 and 4 in 2011). Due to the dependency of I_u on the intensity of rain events (kg $m^{-2}d^{-1}$) I_u was calculated both as monthly mean (N = 6) and for rain events with $P_s > 5$ mm d^{-1}(N = 11). Subsequently mean I_u (%) was assessed including the weighting factor as based on the percentage of the sum of Ps > 5 mm d−1to total P_s during the respective months.

Table 3-2 Climatic parameters; long- term mean (LTM; provided by “Deutscher Wetterdienst” DWD), mean daily air temperature and cumulated gross precipitation (mm) of the years 2008 through 2011 and for the growing seasons (gs, i.e. April through October each). Cumulated stand precipitation on the unthinned (NT), moderately (MT), and heavily thinned (HT) plots for the growing seasons 2009 through 2011.



Climatic parameters	LTM	2008	2009	2010	2011	gs. 2008	gs. 2009	gs. 2010	gs. 2011
Temp [°C]	7.9	8.9	9.0	7.3	8.8	14.8	15.8	13.9	15.0
Gross-precipitation	778	838	956	855	788	532	604	628	545
Stand precipitation NT							301	270	250
Stand precipitation MT							333	315	256
Stand precipitation HT							464	391[a]	336[a]

[a] Calculated interception of understory vegetation included.

Water balance

The periods under observation covered the growing seasons and therefore the difference in We before and after the growing season was included in the following water balance

$$P_g + \Delta W_e = I_o + I_u + E_o + E_u + R_g \qquad (3)$$

where P_g is the measured gross- precipitation (open field precipitation), ΔW_e is the difference in measured extractable soil water at the beginning and at the end of the growing season, I_o the calculated interception of the overstory, I_u the calculated interception of the understory,

E_o the measured overstory transpiration, E_u the measured understory transpiration, R_g the ground water runoff.

Water-use efficiency

Water use efficiency is the ratio of assimilated carbon per transpired water. Here, to assess the effect of thinning on the water-use efficiency of the target trees (WUE_t) and the whole stand (WUE_s) basal area increment (BAI) per growing season was used to represent assimilated carbon. Therefore the water- use efficiency for the target trees was assessed by

$$WUE_t = BAI_t / E_t \quad (4)$$

where BAI_t is the basal area increment of the target tree per growing season and E_t the transpiration of the target tree accumulated over the respective growing season. For the whole stand the water-use efficiency was assessed by

$$WUE_s = BAI_s / E_s \quad (5)$$

where BAI_s is the stand basal area increment per growing season and E_s the total stand transpiration.

Statistical analysis

Statistical tests were conducted using IBM SPSS Statistics 21(Release Version 21.0.0; IBM SPSS Inc.). Data from both plots were pooled for calculating differences between thinning intensities. Differences between treatments and between years within the same treatment were tested via one-way ANOVA.

Results

Growth

Stand basal area (BA_s), and leaf area index (LAI) were reduced by the thinning treatments down to 57% (MT) and 33% (HT) of the corresponding value on the control (NT) (Table 3-1). However, although BA_s was still highest at NT (48.2 m^2 ha^{-1}) in 2011, the stands on the thinned treatments had already reached 69% (MT) and 47.7% (HT) of this value. In 2008, before thinning, no differences had existed in relative basal area increment (rBAI, basal area increment divided by the initial basal area) of the target trees (Fig. 3-2). After thinning, rBAI of the target trees on the thinned plots was significantly increased ($p < 0.0005$) compared to NT. rBAI was increased by 98% (MT) and 145.0% (HT) relative to NT (Fig. 3-2) during the first year after thinning. rBAI of target trees on the thinned plots did not differ significantly from one another and between years.

Fine root biomass

Following thinning in February 2009 total fine root biomass down to 60 cm soil depth was significantly reduced by 57.2 (MT)and 60% (HT) relative to NT (Fig. 3-3a). Contrasting to the results of total fine root biomass, fine root biomass related to foliage area of the individual trees did not differ between treatments and years after thinning (exception MT in 2009) (Fig. 3-3b).

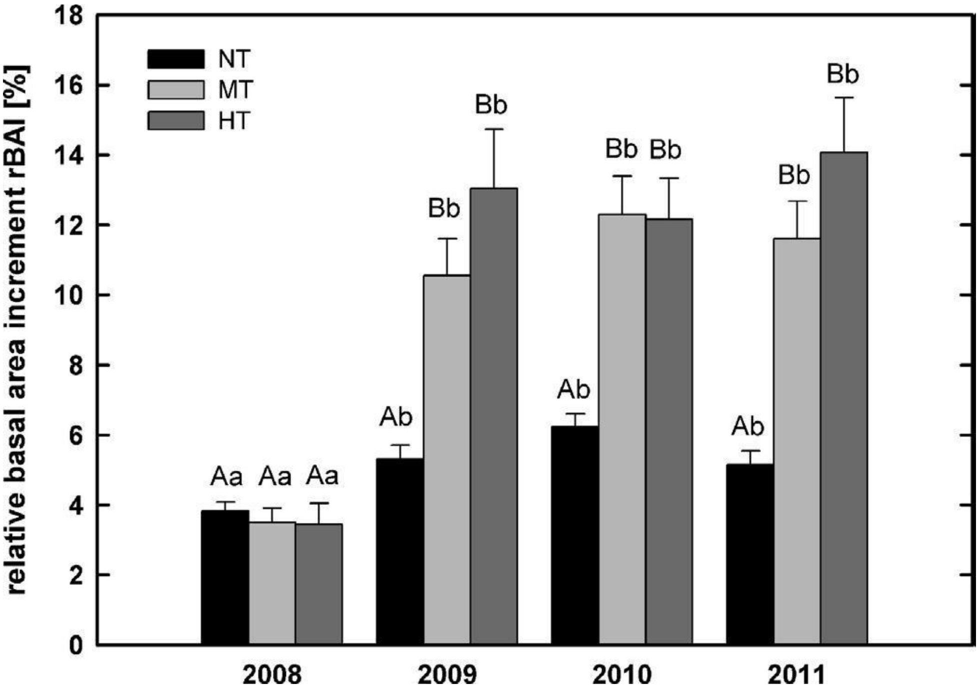


Figure 3-2 relative basal area increment (rBAI) of target trees in the unthinned (NT), moderately (MT), and heavily thinned (HT) plots before (2008) and after thinning in 2009, 2010 and 2011 (N = 10). The capital letter represents significant differences ($p < 0.05$) between thinning treatments, and the lower-case one between years within the same treatment.

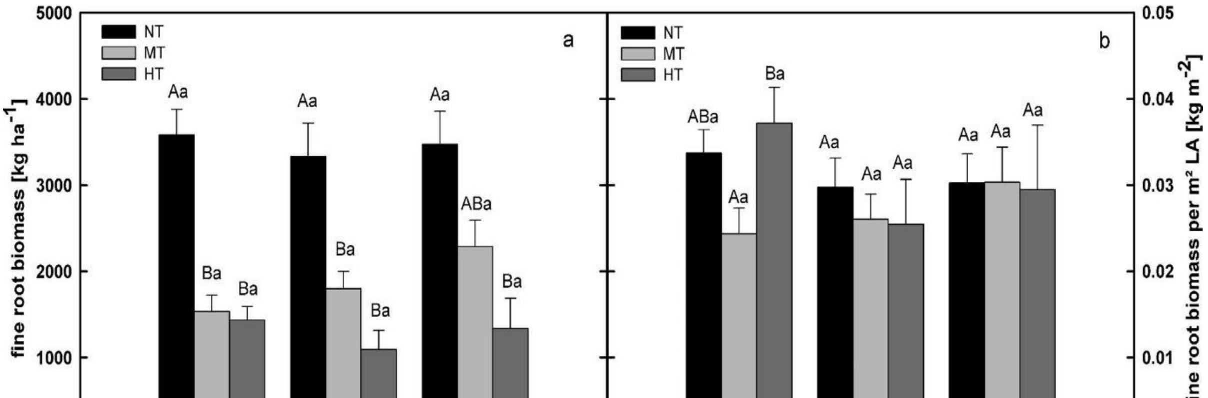


Figure 3-3 Total fine root biomass down to 60 cm soil depth (a; N = 20) and fine root biomass per projected leaf area (b) in unthinned (NT), moderately thinned (MT) and heavily thinned (HT) plots one (2009) two (2010) and three (2011) years after thinning (N = 20). The capital letters represents significant differences ($p < 0.05$) between thinning treatments, and the lower-case one between years within the same treatment.

Transpiration

On the thinned plots E_s was reduced by 113.8, 72.2 and 40.3 kg m^{-2}(MT) and by 200.7, 93.4 and 51.0 kg m^{-2}(HT) in 2009, 2010 and 2011, respectively (Fig. 3-4). In two out of the three years significant differences in E_s occurred. Nevertheless, E_s was levelled during the three years. At HT, evapotranspiration of the understory vegetation (E_u) was 35.3% of tree transpiration E_o. Consequently, in2010 and 2011 the transpiration of the ground vegetation increased E_s at HT by additional 56.2 and 66.2 kg m^{-2}, respectively. E_s as derived from sap flux accounted for about 100% (±2%) of water loss calculated by the stand precipitation and soil water depletion ($E_s= P_s+ \Delta W_e$) on NT during the monitored growing seasons. On MT E_s accounted for c. 76%, 79% and 91% and on HT for c. 42%, 52%and 71% in 2009, 2010 and 2011, respectively. On a single-tree basis, thinning led to increased daily u of the target trees. Mean daily sapflux density increased by 28.7, 31.0 and 36.6% (MT), and by 54.0, 45.5 and 60.6% (HT) during the growing seasons of 2009, 2010 and2011, respectively (Fig. 3-5).

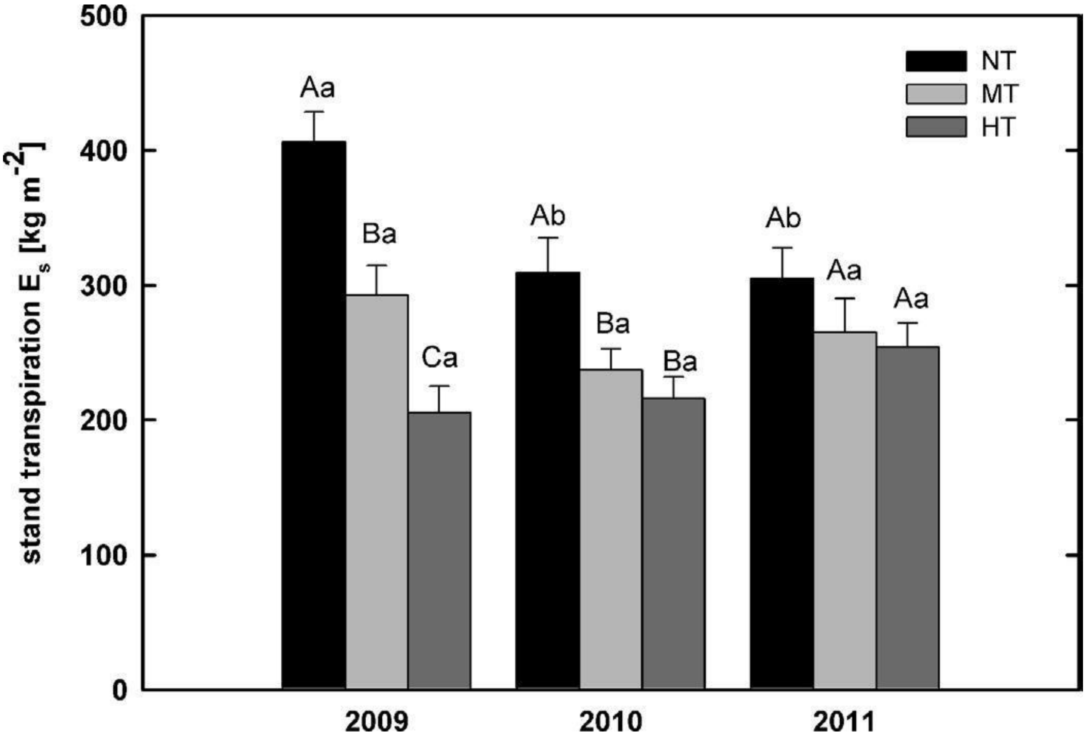


Figure 3-4 cumulated stand transpiration E_s (kg m^{-2} ground area) of the unthinned (NT), moderately (MT) and heavily thinned (HT) plots for growing seasons (April to September) of 2009, 2010 and 2011. In 2010 and 2011, transpiration of the under-story vegetation and soil evaporation was included into the HT values. The capital letter represents significant differences ($p < 0.05$) between thinning treatments, and lower-case one between years within the same treatment.

Precipitation

Rainfall during the growing seasons 2009–2011 was by 95–178 mm higher than the long-term mean at the study site (Table 3-2). Canopy throughfall increased with thinning intensity, being enhanced on MT plots during growing seasons by 31.8, 44.8and 6.5 mm in 2009, 2010 and 2011, respectively, and on HT plots by 163.0, 179.8 and 137.2 mm, respectively, compared to NT plots. Canopy interception (I_c), being c. 53.8% of precipitation on NT plots, was reduced to 49.2% (MT), and 26.9% (HT) on the thinned plots. The weighted interception mean I_u of understory vegetation accounted for an additional loss in water input of about 13.0% at HT during the second and third year after thinning. In total, interception at HT was 39.9% of the precipitation during the years 2010 and 2011.

Extractable soil water

In 2008, before thinning, no differences ($p > 0.05$) in soil water content existed between plots. Reduced interception and stand transpiration after thinning led to a significant ($p < 0.005$) increase in mean daily W_e (Fig. 3-6). At MT, the mean daily We was increased by 21.0, 19.0 and 29.5 kg m^{-2}, and at HT by 42.9, 38.1 and 50.2 kg m^{-2} compared to NT during the growing seasons of 2009, 2010 and2011, respectively. Three years after treatment, the thinned plots showed still substantial surplus in extractable soil water compared to NT.

Water use efficiency

Stand-level WUE_s was increased on the thinned plots MT and HT throughout the three years by thinning up to 217% (MT, 2011) compared to NT. Throughout the three years upon thinning WUE on stand level was lower than WUE_t in all treatments. Reductions were 30.2, 40.6 and 55.6% at NT, 24.9, 38.4 and 32.0 at MT during 2009, 2010 and 2011, respectively. On HT the additional transpirational loss by the ground vegetation reduced the WUE_s by 44.7and 42.1% in 2010 and 2011, respectively. Also on the single tree basis, thinning induced increased WUE_t throughout the three years after treatment. Increases relative to NT were 87.7, 82.4 and 62.1%at MT and 88.4, 66.5 and 65.3% at HT during 2009, 2010 and 2011, respectively (Fig. 3-7).

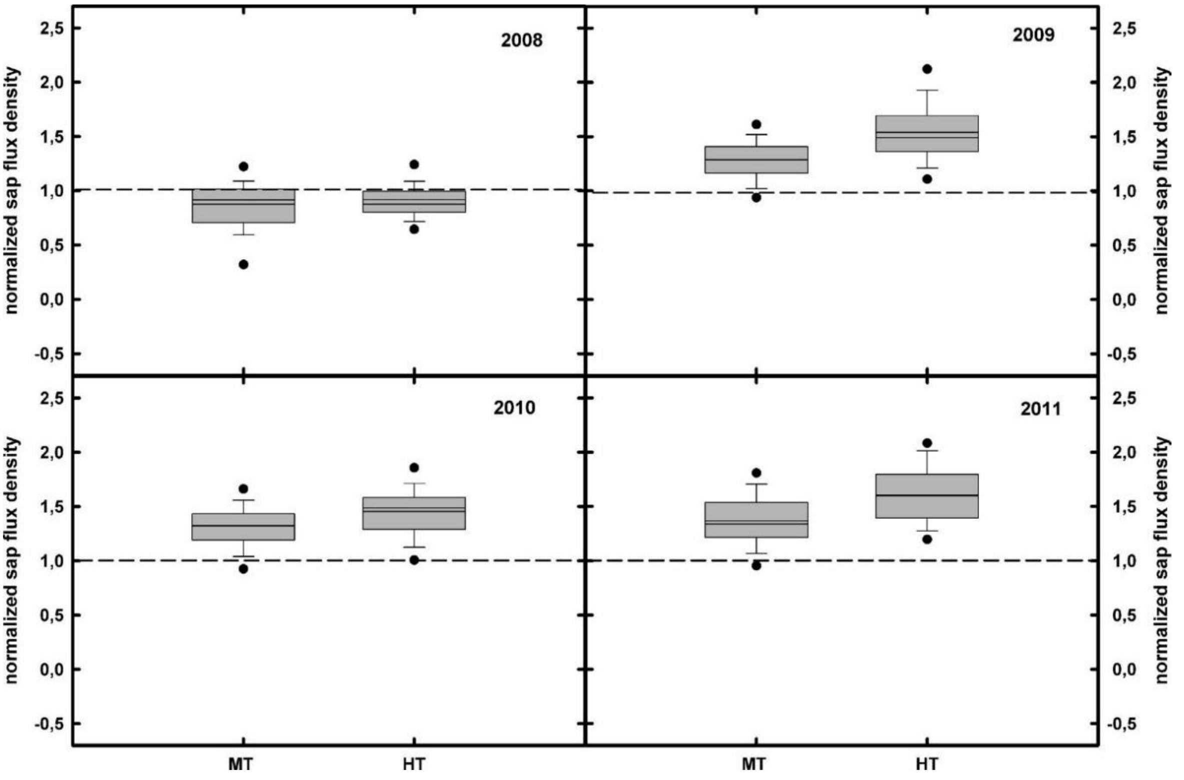


Figure 3-5 Mean daily xylem sap flux density (u) of the target trees in moderately (MT) and heavily (HT) thinned plots, related for normalization to the unthinned treatment (NT, dashed line) during growing seasons of 2009 through 2011 (April-September each; in 2008, mid-July–October).

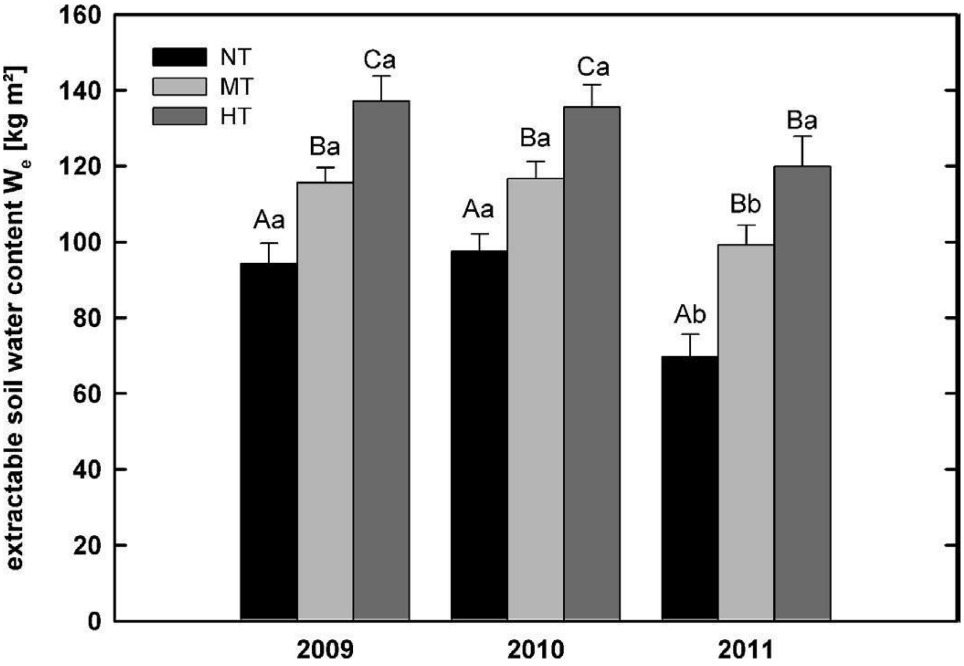


Figure 3-6 Mean daily extractable soil water content in kg m^{-2}(ground area) down to60 cm depth in unthinned (NT), moderately (MT) and heavily thinned (HT) plots during growing seasons (April–September each) 2009–2011 upon thinning (N = 6each). The capital letter represents significant differences ($p < 0.05$) between thinning treatments, and the lower-case one between years within the same treatment.

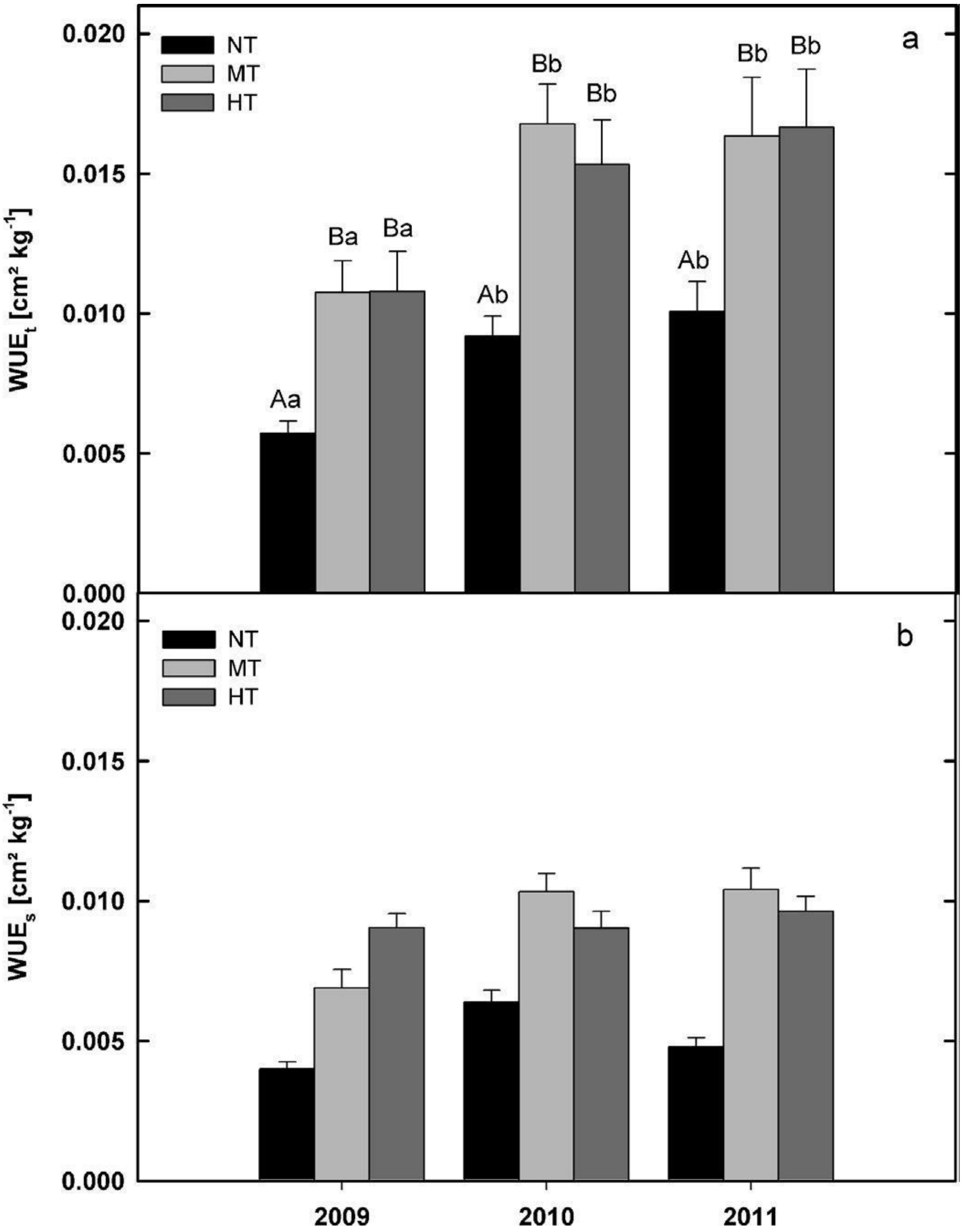


Figure 3-7 Water-use efficiency of the target trees (WUE$_t$; N = 10 each)) and up-scaled to stand (WUE$_s$; N = 2) for the growing seasons 2009, 2010 and 2011. The capital letter represents significant differences ($p < 0.05$) between thinning treatments, and the lower-case one between years within the same treatment.

Discussion

Water consumption

Increased thinning intensity led to reduced total stand transpiration and increased soil water content. Thus, our first hypothesis can be accepted. The thinnings removed around 40 to 70% of the initial BA. This led to decreased stand-level transpiration (E_S) of 25.4 (MT) and 49.7% (HT) during the first year after thinning. Thus, the reduction in E_S was lower than the reduction in stand density. This finding is in line with other thinning experiments. Bréda et al. (1995) reported on a removal of 35% of BA in sessile oak which corresponded to a reduction in E_S by about 25%. Morikawa et al. (1986) found the transpiration rate of *a Chamaecyparis obtusa* stand to decrease by 17% after reduction of foliage mass by 22%. In our study the disproportional decrease in E_S compared to BA and LA reduction was related to the significant increase of mean daily sap flux density by 28.7 (MT) and 54% (HT) of the target trees due to increased sun-light exposure and reduced leaf boundary layer caused by Increased air flow within the crown. Conversely, Lagergren et al. (2008) found initial over-proportional decrease of E_S by 40% after the removal of 24% of BA in a mixed Norway spruce-Scots pine forest. They assumed the remarkable effect to be caused by a light shock of the previously shaded leaves and/or root injury by the thinning operation. Nevertheless, the variability of sap flux density and rBAI of the target trees increased with progressive thinning intensity as in our study indicating different crown proportions amongst target trees exposed to direct sunlight by thinning with differential transpiring effects. Courses of E_S during 2009 and 2011 confirmed also our second hypothesis which stated declining differences of stand transpiration across treatments during the years after thinning. Differences in E_S successively vanished from 2009 through 2011 due to increased stand transpiration on the thinned plots, but in 2011also partly due to reduced transpiration on NT caused by water limitation. The difference on HT would have been larger if the ground vegetation had not responded so quickly to the increased light and water availability after thinning. Hence, E_u diminished the differences in E_S to NT by 26%. This is in line with the estimated E_u contribution of 26% to total E_S as reported by Granier et al. (1996). Lüttschwager et al. (1999) found that the proportion of the understory vegetation (dominated by *Calamagrostis epigeios* and *Deschampsia flexuosa*) in stand-level transpiration was even up to 50% in three stands of Scots pine. However, *Calamagrostis epigeios* is known to have a higher transpiration rate per leaf area than *Rubusidaeus* (Müller and Bolte, 2002), which was, beside *Rubus fruticosus*, the dominant species on our plots. Our results showed that under-storey vegetation has to be taken into account when calculating mitigation effects of thinnings.

Water balance

The reduction of LAI by 40% at MT led to a slight increase of cumulative throughfall during growing seasons. Water loss due to interception varied highly between plots and treatments through-out the study period. Canopy interception is highly influenced by climatic factors including differences in wind velocity, temperature, relative air humidity and global radiation during rain events and primarily by the intensity of the rain events. Under rain of low intensity high water adherence of the canopy can be expected (Aussenac and Granier, 1988; Frischbier, 2012). Therefore, the decrease of cumulative differences in P_s between NT and MT during the years 2010 and 2011 are assumed to be mainly a result of differences in total amount of rain and rain intensity during the growing seasons. W_e was improved over the whole study period on the MT and HT plots. Moreover, W_e clearly increased with increasing thinning intensity, even though increased single tree transpiration of the thinned stands and additional E_u and I_u on the HT plots partly compensated for the positive progressive thinning effect on water availability in 2011. While the differences between treatments in E_s were successively reduced, the differences in mean daily W_e of the thinned plots increased on the MT and HT plots compared to the control plots, during the years after thinning. However, higher throughfall (P_s) and reduced stand transpiration (E_s) on the thinned plots led to W_e close to available soil water storage capacity (ASWSC) during the first growing seasons after thinning. Consequently ground water runoff (R_g) based on the water balance accounted for up to c. 30% on MT and up to 57% on HT of total water loss of the thinned plots. In contrast on NT the water loss due to R_g was negligible. Therefore, the differences between the thinning treatments and NT on potential available soil water content also declined during the years after thinning, but were restricted by ASWSC. In conclusion, besides the emerging understory vegetation, ASWSC was the second major factor influencing the extent of the mitigation effect of progressive thinning. In our study the loss of water due to transpiration and interception of the up-coming understory vegetation in the second and third year on HT was considered when calculating E_s and the water balance. In contrast, evaporation from the litter and soil was not taken into account which may have led to a slightly overestimation of R_g on MT and for the first year on HT. Beside LAI, evaporation from the forest floor is mainly determined by the wettability of the understory vegetation and water storage capacity of the litter and highly decreases with decreasing water content of these components (Wilson et al., 2000; Kelliher et al., 1993; Köstner et al., 2001; Barbour et al., 2005; Staudt et al., 2011; Ringgaard et al., 2012). In our case on MT and in the first year on HT emerging understory vegetation was negligible and therefore stored and evaporated water in the litter may mainly have led to a slight over-estimation of ground water runoff R_g. Furthermore, litter decreases soil evaporation acting as a diffusion barrier and reducing light and temperature penetration to the deeper soil layers. Therefore, we assumed that soil evaporation was negligible. However, evapotranspiration by the vegetation on the forest floor was taken into account and contributed substantially to stand water loss.

Water use efficiency

Thinning led to an increase of sap flux density in the target trees by about 30% and 50% in relation to increases in rBAI by 107 and 137% at MT and HT, respectively. Therefore, thinning of increasing intensity enhanced the productivity-related water-use efficiency(WUE) in target trees by up to 90%. Thus, our third hypothesis stating that WUE of target trees released from competition is lower than that of control trees is clearly rejected. The over proportional increase of BA compared to the increase of transpiration of the tar-get trees indicates that light was the limiting resource on NT during the observation periods. Gspaltl et al. (2013) recently found that light-use efficiency of wood production of Norway spruce trees increased along with tree size. Apparently, the efficiency of resource use (e.g. light or water) of single trees and forest stands can positively correlate with rates of resource capture (Binkley et al., 2004). This view is supported in our study by the observation that WUE_t of target trees was higher than stand-level WUEs, irrespective of treatment and study year. This is in line with a study on *Eucalyptus nitens* where the largest 200 trees per ha showed a 23% greater transpiration and 21% higher WUE three years after thinning compared to 200 control trees of an unthinned stand (Forrester et al., 2012). Therefore, subdominant trees seem not only to capture less resources but also are less efficient in resource use when compared to the dominant target trees (Binkley et al., 2002). In an extensive review Forrester (2013) could not find a single study reporting on significant declines in light use efficiency (LUE) or WUE with increasing tree size.

Conclusions

Thinning can enhance the stand-level capacity for plant-available water at sites stocked with Norway spruce. Such an effect persisted in the present study throughout, at least, three years after thinning. However, heavy thinnings such as HT are not likely to be accepted by forests practice. Although they might be a reasonable option in terms of economics (Knoke, 1998), if wooden biomass production is to be maximized they are not the best option. From a silvicultural point of view the extensively spread ground vegetation at the HT sites are unwanted. First, it competes with the trees for water. Second it occupies belowground space by fine roots which may become crucial for the trees under severe drought. Third, at later stages it may hinder natural regeneration. The extent of risk mitigation by the two thinning intensities applied in our experiment still needs to be verified under prolonged and severe summer drought episodes. At the current stage however, repeated moderate thinnings seem to be a reasonable option to reduce the risk of drought stress of young Norway spruce stands.

Acknowledgements

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Kapitel 4

Chapter 4

Medium-term potential of drought avoidance in Norway spruce (*Picea abies*) stands by increasing thinning intensity

(to be submitted)

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[1] The candidate made substantial contribution to the conception and design of the study, conducted the data collection, the analysis and interpretation of data and was lead author of the article draft. Karl-Heinz Häberle contributed to the interpretation of the data and the draft of the article. Christian Ammer and Rainer Matyssek made substantial contributions to the conception and the design and assisted the article draft.

Medium-term potential of drought avoidance in Norway spruce (*Picea abies*) stands by increasing thinning intensity

(to be submitted)

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Key words: *climate change, Norway spruce, relative extractable soil water content, resistance, growth*

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Abstract

Mitigation of adverse climate change effects on forest stands, like declining precipitation and increased temperatures during summer, becomes increasingly important in silvicultural management. Therefore, thinning as a silvicultural measure to mitigate drought on the short to medium-term in young forest stands are frequently discussed. In the present study we report on a thinning trial, with increasing thinning intensity in a young Norway spruce (*Picea abies*) stand and hypothesized, that the potential of increasing thinning intensity to reduce the time span below critical relative soil water content (REW_{crit}) on the medium-term will be diminished. The benefits on the REW between the moderate thinning (MT, stand basal area reduction of 43%) and the heavy thinning (HT, and stand basal area reduction 67%) was diminished within 2 years which was attributed to emerging ground vegetation on HT. Furthermore, the belowground competition of the ground vegetation suppressed the fine root recovery on the heavy thinning plots, at least for 5 years following thinning. Both thinning intervention reduced the time below (REW_{crit}) between 5 and 7 years compared to the un-thinned stand (stand basal area $42m^2$ ha^{-1}) leading to a similar intensity of the soil water deficit during the dry spells in 2013 and 2015. Hence, leading to a decline in relative basal area increment during the drought years irrespective of the treatment 5 and 7 years following the thinning intervention and to a similar recovery in radial growth increment during 2014. We concluded, that frequent thinning interventions by avoiding the establishment of a vital ground vegetation should be considered as a silvicutural measure to increase the potential of drought avoidance in young Norway spruce stands.

Introduction

Sustainability of forest stands is mainly determined by silviculture in view of climate prediction. Mitigation of adverse climate change effects on forest stands becomes increasingly important in silvicultural management (Ammer, 2016; Bolte et al., 2009). Limitations are expected through declining precipitation and increased temperatures during summer, projected for Central Europe as prolonged and intense drought periods (IPCC, 2013, 2007).

Most strategies for adapting forest ecosystems to climate change follow long-term aims, such as tree species diversification or introduction of drought-tolerant species (Ammer et al., 2008;

Knoke et al., 2008). However, short to medium- term approaches for adapting young stands to drought are scarce. For example, thinning has been discussed as an adaptive measure for mitigating drought impacts (Martín-Benito et al., 2010; Misson et al., 2003; Sohn et al., 2013), as immediate effects reduce stand transpiration and interception (del Campo et al., 2014; Gebhardt et al., 2014) and, therefore, increase soil water availability.

However, water loss via stand transpiration could equalize or even outperform within a few years between the thinned and the un-thinned stands by the increased transpiration of the remaining trees (Bréda et al., 1995b; Lagergren et al., 2008). Additionally, increasing within-stand insolation may foster ground vegetation growth in heavy thinned stands, which additionally increase the evapotranspiration on stand-level (Gebhardt et al., 2014; Simonin et al., 2007).

In previous studies, the relative growth decline during the drought year of remaining trees in thinned compared to un-thinned stands was found to be similar (Kohler et al., 2010) or depend on the time-lag between thinning and the drought event (Sohn et al., 2013).

Besides the intensity, the duration of the drought is of particular importance (McDowell et al., 2008). With increasing time-lag between the thinning intervention and the drought event, stand-level evapotranspiration may be enhanced upon thinning, thus leading to an increased time span of the remaining trees below critical soil water content, exacerbating drought stress in remaining trees. Thus, additionally rendering tree species like Norway spruce (*Picea abies*) susceptible to secondary pests. Wind-throw, drought and subsequent bark beetle attacks have been ranked as the major risks for decay and break-down of forest (Anderegg et al., 2012; Christiansen et al., 1987; Dobbertin et al., 2007; Levanič et al., 2008; Weslien and Schroeder, 1999).

Relative extractable soil water content (REW) with values lower than 0.4 (REW_{crit}) was found to be a viable threshold explaining soil water deficit induced stomatal regulation for different tree species under various soil types (Bréda et al., 1995b; Granier, 1987; Granier et al., 2007, 1999; Grossiord et al., 2014). Two variables are important for the potential of thinning to reduce the time span below REW_{crit}, the initial REW at the beginning of the drought event and the decline rate during the drought. Both depending on the stand transpiration and interception.

In this study, we report on a thinning experiment with three thinning intensities in a mono-specific Norway spruce stand. The aim of our study was to clarify to what extent increasing thinning intensities improve the relative soil water content during the growing seasons. Furthermore, to what extent the initial REW at the beginning of the drought and the decline rate may change with increasing time-lag after thinning between the thinned and the un-thinned stands. Therefore, possibly extending the time span below REW_{crit} soil water deficit for the remaining trees of the thinned stand and contributing to a increased growth decline compared to trees in the un-thinned stand.

We hypothesized that

1. Thinning increases the relative extractable soil water content during the growing seasons, but not necessarily with increasing thinning intensity

2. The potential of increasing thinning intensity to reduce the time span below critical soil water content will be diminished over time

3. The relative higher decline in radial growth during drought years of target trees in the thinned compared to un-thinned on the medium-term can be related to an increased time span below critical soil water

Material and methods

Experimental site and meteorological parameters

The experimental site and design have been described in Gebhardt et al. (2014). Briefly, the study was conducted 2008 in a 26-year-old monoculture of Norway Spruce (*Picea abies* [L.] Karst.) near Landshut (48° 38´20“N, 11° 57´49“E, Bavaria, Germany). The stand was planted on luvisol (loess over Tertiary) with a mean annual precipitation and air temperature in the region of 778 mm and 7.9 °C, respectively (DWD).

The research area (75 x 50 m) was subdivided into 6 plots of 25 x 25 m each. Prior to initiation, about 430 future crop trees (target tree) per hectare were selected. Target trees were defined as dominating vigorous trees (trees with the highest diameter). The initial stem diameter at breast height (1.30m DBH) of the trees within the plots were measured before the thinning intervention in February 2009 and the increments were recorded within and after each growing season.

In February 2009 four out of six randomly selected plots were thinned, while two plots remained unchanged as control (NT=not-thinned). Two plots each were moderately (MT) thinned with a reduction of stand basal area (BA) by ca. 43 % and heavily thinned with a BA reduction of ca. 67 % compared to the basal area of 42.4 m² on the NT- plots. The moderate thinning was carried out via thinning from above by removing 1-2 competitors of the target trees and for the heavy thinning all trees, besides the target trees were removed. Open field gross- precipitation (P_g) and air temperature (T_{air}) were measured at a climate station on a meadow with about 100 m distance from the experimental site. Occasional data failure in mean daily T_{air} was interpolated by linear regression ($R^2 > 0.90$) using T_{air} measured at the climate station Feistenaich (Bavarian Institute for Agriculture, LfL). Regarding data gaps of seasonal P_g, a correction factor was calculated correlating to P_g at the climate station of Feistenaich. For further details on the experimental design see Gebhardt et al. (2014).

Relative extractable soil water content and fine root biomass

As described in Gebhardt et al. (2014) volumetric soil water content (θ) was measured with TDR- sensors (Time Domain Reflectometry, Soilmoisture Equipment Corp., Santa Barbara, California) combined with MiniTrase 6050X3 (Soilmoisture Equipment Corp., Santa Barbara, California). The waveguides were installed horizontally in the upper three soil horizons and one sensor per subplot was positioned at about 1 m depth into the C horizon at three locations on a diagonal transect across each subplot. In total 60 sensors (6 subplots x 3 locations x 3 sensors + 1 in the deepest horizon) provided data on θ every 20 minutes throughout the study period.

To calculate maximum plant available soil water content, the minimum θ during the 8 years' period (mean of 2 weeks during the drought 2015) for each soil layer was identified and defined as the lower margin of soil water content (high transpirational demand but no changes in θ). Regarding the relative extractable soil water (REW_{60}), for each location the daily extractable soil water content down to 60 cm (comprising > 90% of the fine root biomass) was related accordingly to the maximum extractable soil water content within the 8 years (mean of 2 weeks) of each location.

Regarding the potential to extend the time to reach critical REW_{60} or complete soil water depletion with increasing thinning intensity, the initial REW_{60} (dependent on stand transpiration and stand precipitation prior to the dry spell), and the depletion rate (dependent on stand transpiration) of NT and MT was calculated at the beginning and during the dry spells, respectively. The differences of initial REW_{60} and the decline on NT and MT compared to HT (Fig. 3, 4, 7 and 8), was calculated during dry spells of at least 9 to 11 days without an increase of soil moisture during the growing season and considered as the beginning of a drought period. At each instant, initial REW_{60} of NT and MT was related to HT and the decline was calculated via linear regression and related to the decline of REW_{60} on HT to analyze the extended desiccation time of HT compared to NT and MT.

Four times upon thinning (2009, 2010, 2011, 2013), fine-root biomass was sampled at the end of the growing season by cylindrical soil cores down to 1m (10 samples per year and plot). The samples were randomly selected, using a 1 m × 1 m grid while omitting positions of previous samplings.

Basal area increment

The basal area increment of each year and target tree was recorded via permanent measure tapes installed in 2008.

The relative basal area increment of each year (rBAI) was calculated by

$$\text{rBAI (\%)} = \frac{BA_t - BA_{t-1}}{BA_t} * 100 \quad (1)$$

where BA_t represents the basal area of the target tree at the end of the growing season and BA_{t-1} the basal area at the end of the previous year.

The relative basal area increment until July of each year was calculated by

$$\mathrm{rBAI}_{\mathrm{July}}\,(\%) = \frac{BAI_{July}}{BAI} * 100 \tag{2}$$

were $\mathrm{rBAI}_{\mathrm{July}}$ represents the basal area increment amounted by July of the growing season and BAI the basal area increment of the whole growing season.

Resistance and recovery

The resistance to and the recovery from the drought events was calculated similar to the indices suggested by Lloret et al. (2011) by

Resistance 1 = rBAI DY/ rBAI PreDy 3

Resistance 2 = rBAI DY/ mean rBAI 4-6 PreDY 4

Recovery 1 = rBAI PostDY/ rBAI DY 5

where DY is the drought year, PreDY is DY-1, PostDY is DY+1, Mean 4 or 6 PreDYs are the mean rBAI of the 4 post drought years for 2013 and the mean rBAI of the 6 post drought years for 2015

Results

Relative extractable soil water content

After thinning in February 2009, the REW_{60} of MT and HT was enhanced throughout the first post-thinning summer. REW_{60} of NT decreased during spring to 40% and c. 30% in June. In contrast, on MT and HT REW_{60} decreased only to 60% and 70 %, respectively, due to reduced transpirational depletion and increased replenishment (Fig. 4-2). High precipitation at the end of June and during July (Fig. 4-1) increased REW_{60} to saturation on MT and HT and to c. 80% on NT. After the rain event the steep decline combined with lower P_g on NT compared to MT and HT (Fig 4-1.) led to desiccation of REW_{60} to below 40% within 2 weeks and to a minimum of c. 10% by the end of September. On MT and HT, minimum REW_{60} during the growing season 2009 was distinctly higher (37 % and 60 %, respectively). During the following post-thinning years (2010- 2012) decreased depletion and increased replenishment on MT and HT led to an overall enhanced REW_{60} compared to NT. During this period REW_{60} in NT was below the threshold of 40% during 39%, 30 %, 80%, 89% of the days during growing seasons in 2009, 2010, 2011 and 2012 respectively. In contrast the REW_{60} on HT did not decrease below 40% REW during this period. On MT, the REW_{60} was substantially below 40% in the fourth year after the treatment (2012) with 46% of the days during growing seasons.

In 2013 (five years upon thinning), REW_{60} of both MT and HT did not differ from NT during the growing season (Fig 4-5). In addition, high P_G (200 mm) during June saturated REW_{60} across treatments, whereas the hot-dry conditions later-on generally lowered REW_{60} towards 10% (Fig 4-5). Therefore, the remaining trees of MT and HT in addition with the emerging ground vegetation (upon HT only) compensated the thinning effect on stand transpiration, so that decline rates were similar across treatments during spring through summer (Fig. 4-6).

In the following year 2014 P_g was more scattered over the whole growing season (Fig 4-4.) which led to an increased replenishment on the thinned plots compared to the un- thinned plot and therefore REW_{60} was enhanced with increasing thinning intensity, despite similar depletion rates (Fig 4-5). Nevertheless, REW_{60} of all treatments decreased below the threshold of 40 % during summer.

Also, the second drought year 2015 (7 years upon thinning) differed by rain events which were evenly distributed until the end of July at similar moisture depletion rate in NT, MT and HT compared to the growing season 2013. Nevertheless, the exceptionally hot-dry weather conditions (Fig 4-4.) decreased REW_{60} across treatments by September (Fig 4-5.).

However, during late summer REW_{60} of NT consistently was below 40%, contrasting with HT at below 40 % during 2013 through 2015 (i.e. 5-7 years upon thinning).

With the same initial REW_{60} at the beginning of the first growing season 2009, the thinning on MT and HT led to a c. 50 % slower depletion of REW during spring compared to NT (Fig.4-2, Fig. 4-3). During the growing season the additional stand throughfall on the thinned plots and the decreased depletion rate added up to an increased initial REW_{60} in mid and late-summer of 2009. Therefore, the 40% lower initial REW_{60} in summer 2009 of NT relative to HT in combination with the significant higher depletion rate on NT relative to HT could extend the time to reach critical soil water deficit by about 80% on HT compared to NT (Fig. 4-3). As mentioned above during late summer of 2009, the REW_{60} of NT was below the threshold of 40%, thus the difference in depletion rate relative to HT was reduced (Fig. 4-3). Nevertheless, the difference in initial REW_{60} during late summer was up to 70 % between NT and HT.

In 2010, the initial REW_{60} in spring and summer due to the high Pg did not differ between the treatments at the end of May and June (Fig. 4-3). The depletion rate on NT relativ to HT was higher during spring compared to summer and therefore the extend in time of HT compared to NT was about 60 % and 40 % during spring and summer respectively. The emerged ground vegetation during increased the stand transpiration during the summer on HT (Gebhardt et al. 2014) and therefore reduced the difference to NT.

Depletion rates and initial REW_{60} of MT resembled those of HT during the growing seasons except a slightly reduced initial REW_{60} late summer of 2009 and 2015 (data not shown).

In 2013 the above mentioned high P_g and similar depletion rates during spring and early summer led to similar initial REW_{60} at the beginning of the drought period in July irrespective of the treatment. Furthermore, the increased stand transpiration 5 years after the thinning treatment on HT (and MT) led to a similar depletion rate compared to NT (Fig. 4-6) and therefore no benefit on HT in relation to extended desiccation time was found. Therefore, the duration under soil water deficit ($REW_{60} < 40\%$) during the summer drought in 2013 was similar for all treatments.

Nevertheless, permanently increased throughfall at HT and MT in 2015 (the second year with a summer drought period and 7 years after the thinning intervention) added up to a significant difference of the initial REW_{60}. Hence initial REW_{60} of HT was increased compared to NT by 20%, 30% and 40% during spring, summer and late summer, respectively (Fig.4-6). The differences at the beginning of the summer drought reduced the duration under soil water deficit ($REW_{60} < 40\%$) on HT. (Fig. 4-6)

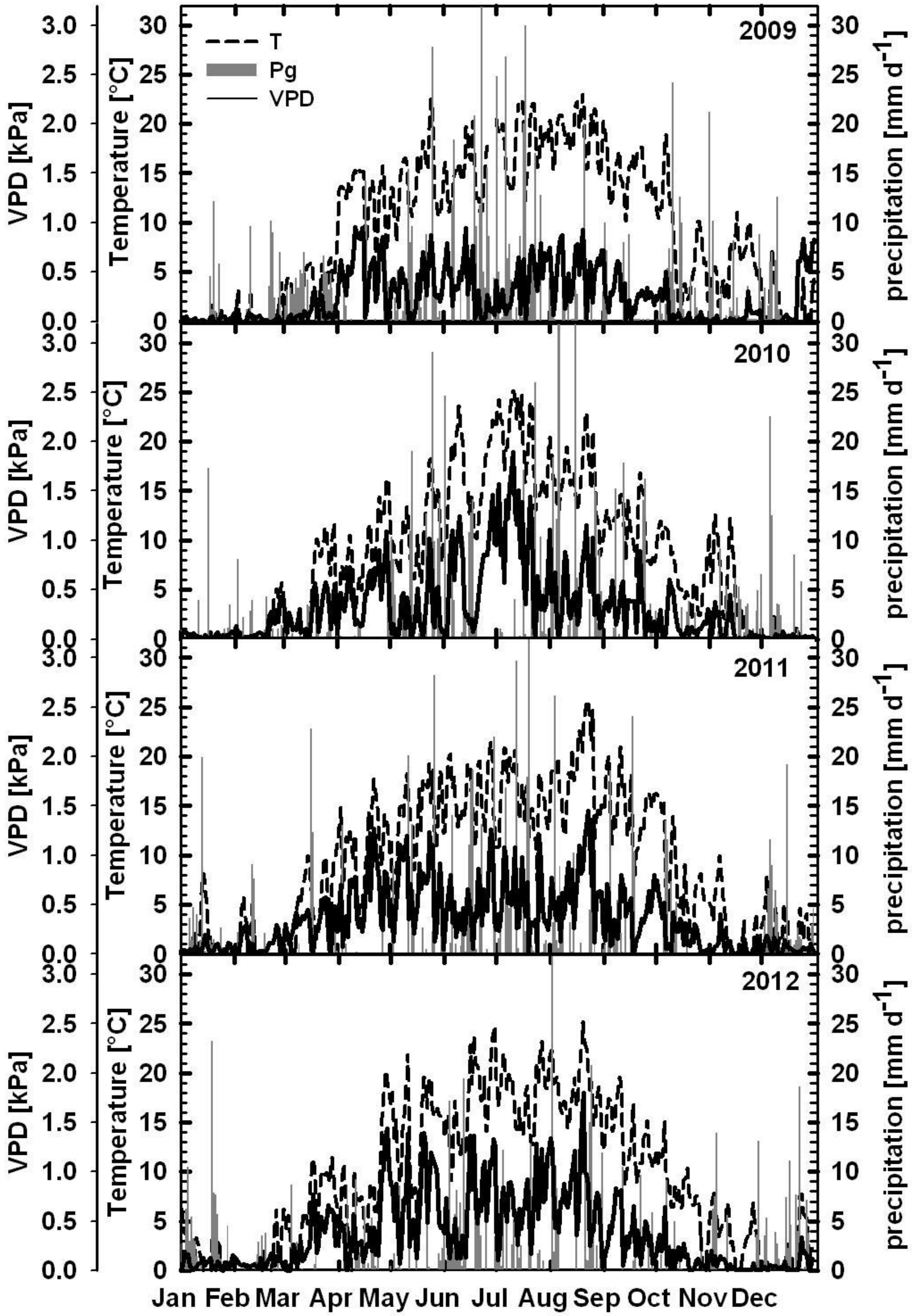


Figure 4-1 mean daily air temperature (°C) and VPD (kPa) and daily precipitation (P_g mm d^{-1}) during the post-thinning years 2009 – 2012

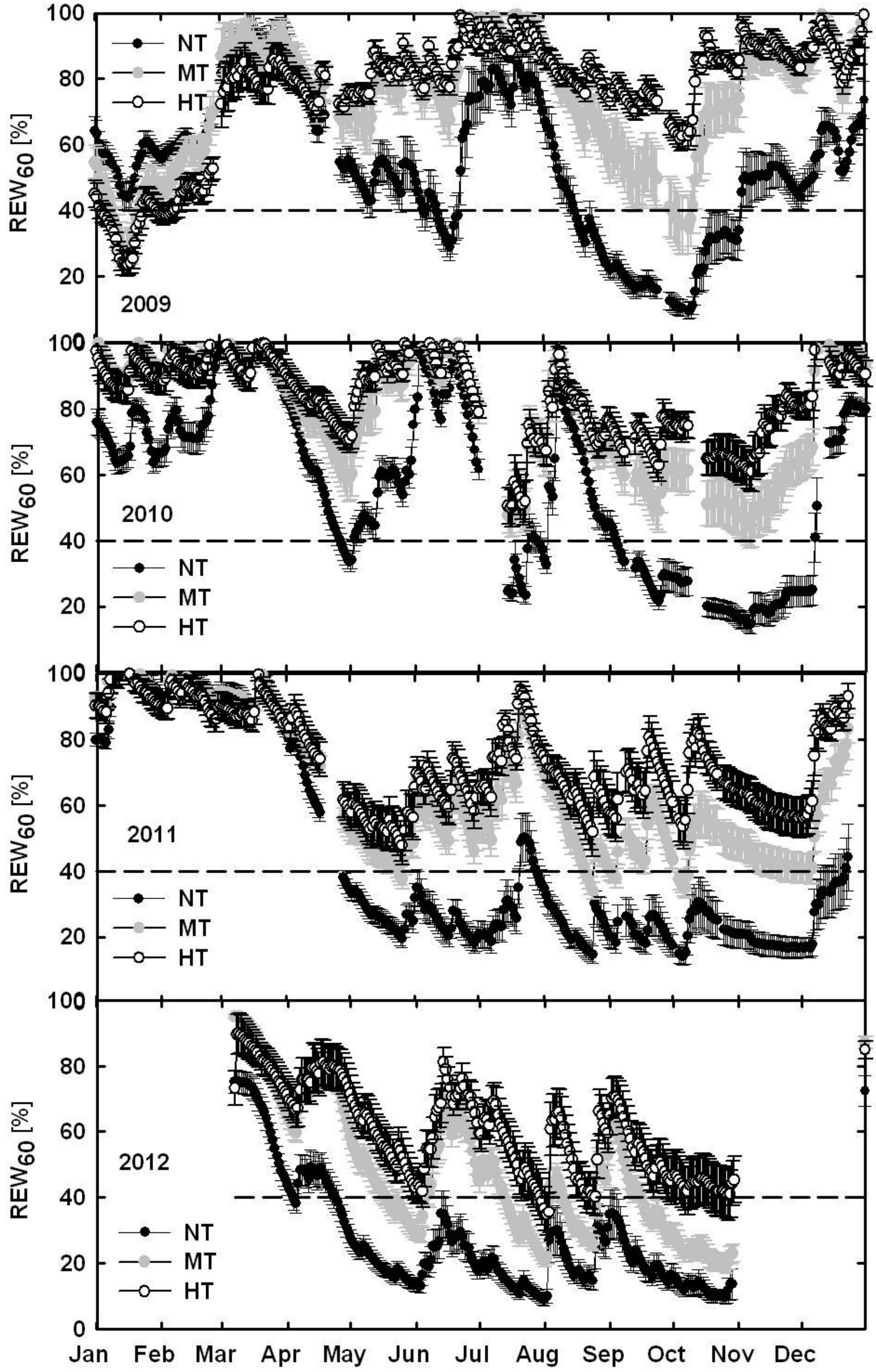
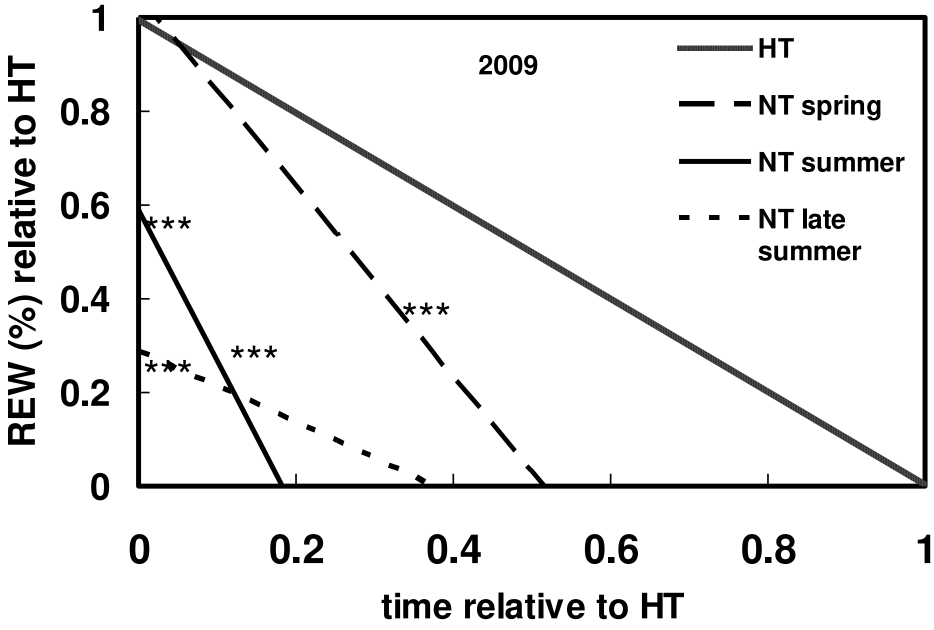


Figure 4-2 relative extractable soil water content down to 60 cm (REW $_{60}$) of NT (no thinning) MT (moderate thinning) and HT (heavy thinning) during the post-thinning years 2009 – 2012



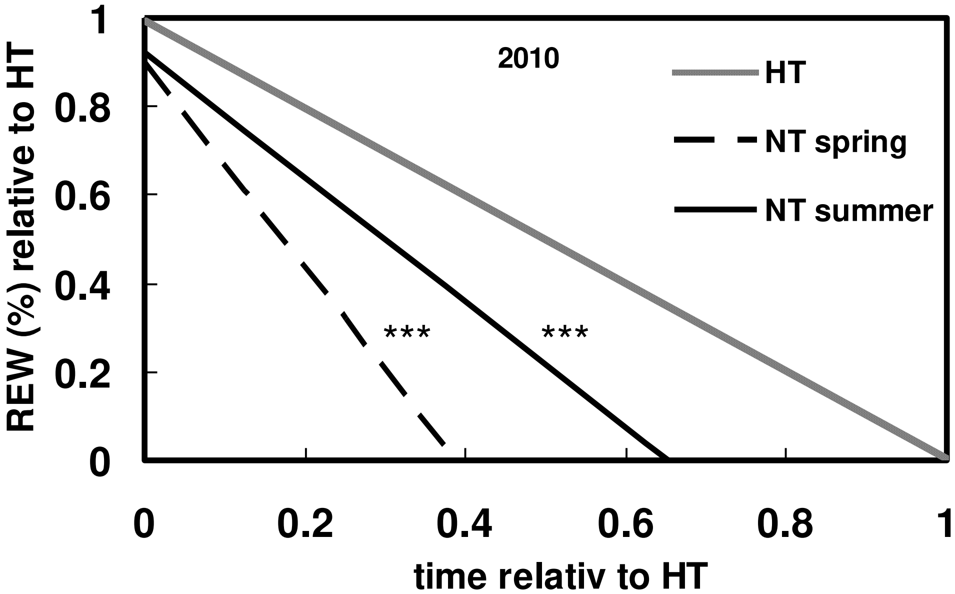


Figure 4-3 depletion rate of REW_{60} of NT relative to HT during the post-thinning years 2009 and 2010. In 2009 spring represents the time span between 4/7/2009 and 4/16/2009, summer 8/11/2009 and 8/19/2009 and late summer 9/6/2009 and 9/14/2009. In 2010 spring represents the time span between 4/3/2010 and 4/11/2010 and summer from 6/21/2010 to 6/29/2010. Stars at the y-axis indicate significant differences of the starting point ($p < 0.001$) and the stars at the lines indicate significant differences ($p < 0.001$) of the slope of NT compared to HT.

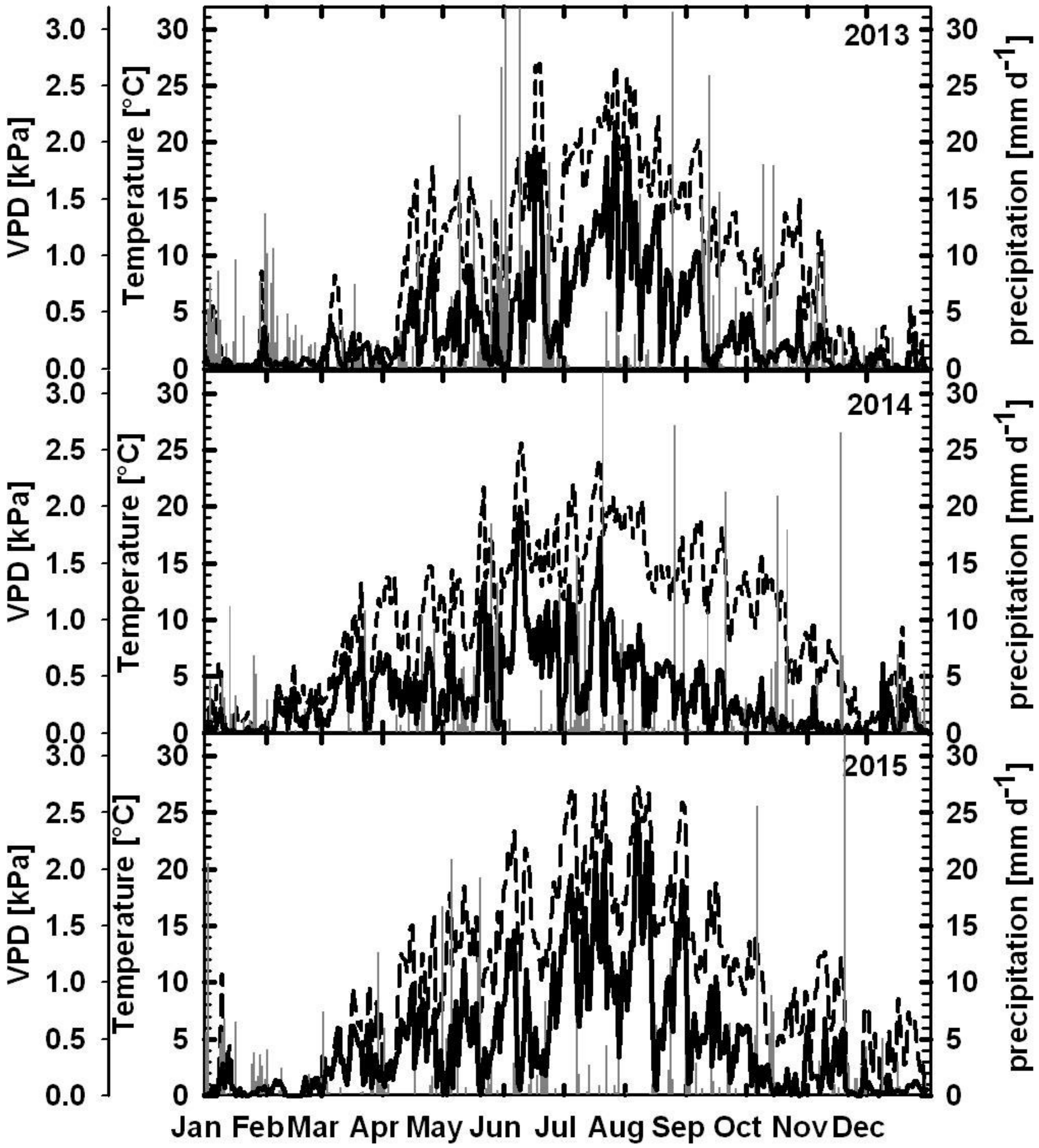


Figure 4-4 mean daily air temperature (°C) and VPD (kPa) and daily precipitation (P_g mm d^{-1}) during the post-thinning years 2013 – 2015

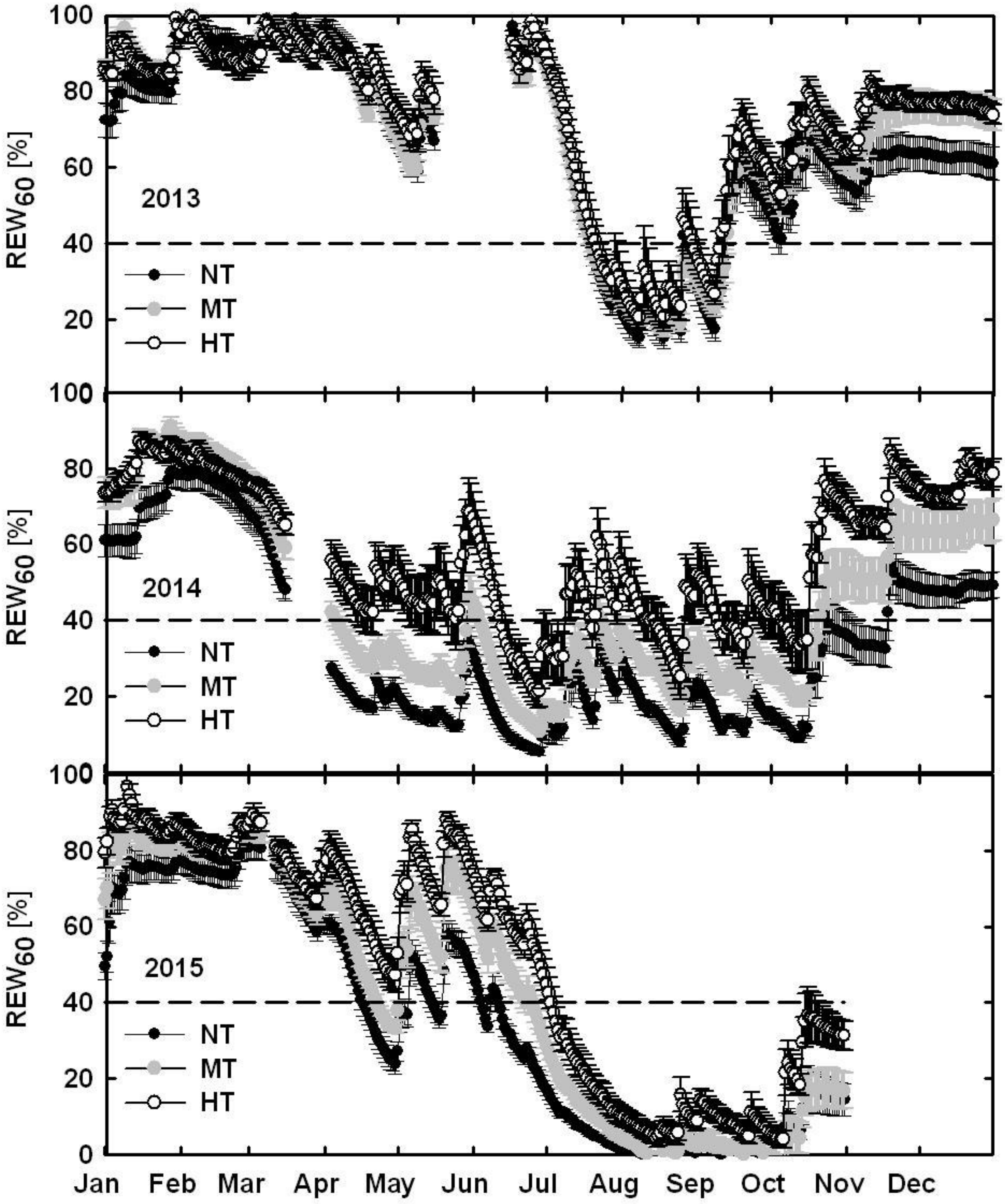
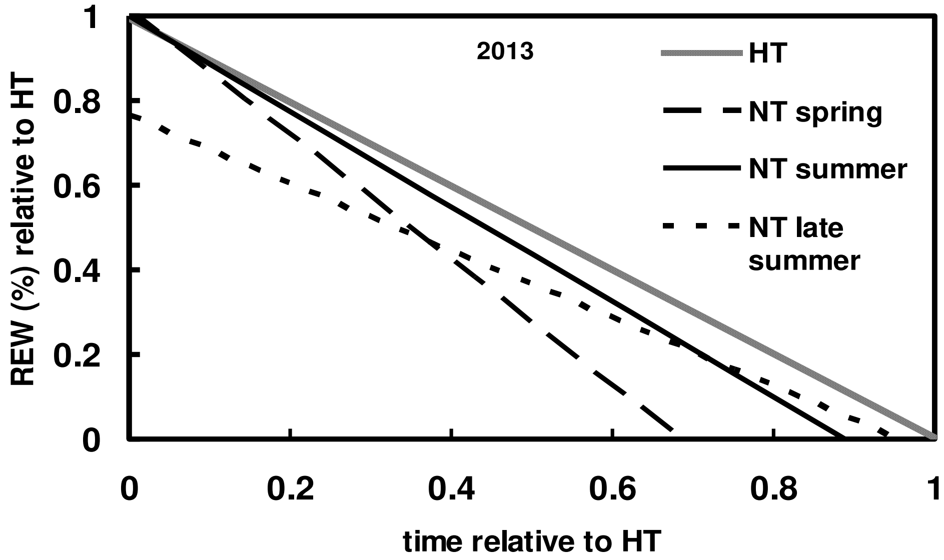


Figure 4-5 relative extractable soil water content down to 60 cm (REW $_{60}$) of NT (no thinning, control) MT (moderate thinning) and HT (heavy thinning) during the post thinning years 2013 – 2015



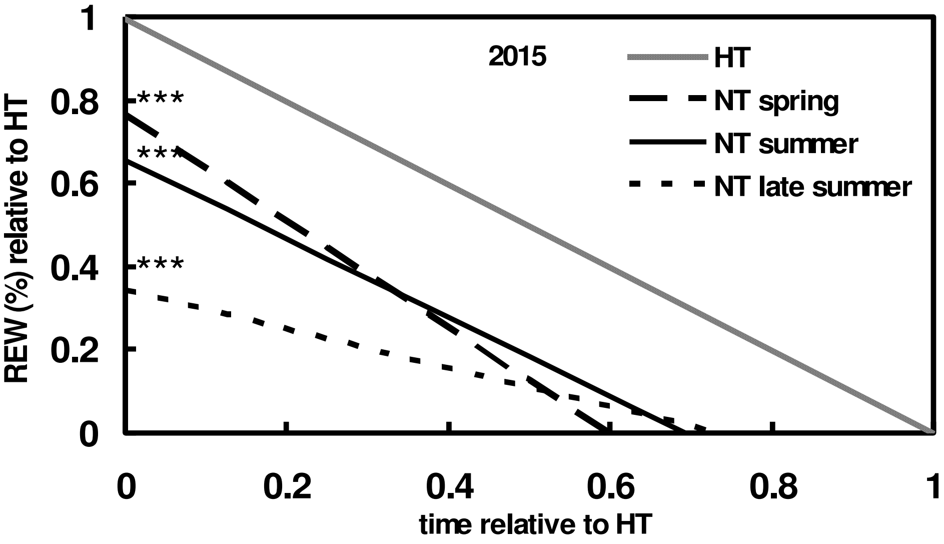


Figure 4-6 depletion of REW_{60} of NT relative to HT during the post thinning years 2013+2015. In 2013 spring represents the time span between 4/12/2013 and 4/19/2013, summer between 7/7/2013 and 7/15/2013 and late summer between 7/30/2013 and 8/7/2013. In 2015 spring represents 4/7/2015 until 4/17/2015 summer from 5/29/2015 until 6/6/2015 late summer 7/13/2015 until 7/21/2015. Stars at the y-axis indicate significant differences of the starting point ($p < 0.001$) and the stars at the lines indicate significant differences ($p < 0.001$) of the slope of NT compared to HT.

Basal area increment

Basal area increment (BAI) and the relative basal area increment (rBAI) did not differ between target trees before thinning in 2008 (Fig. 4-7, Fig. 4-8). Thinning significantly stimulated BAI and rBAI in HT and MT during the examined seven years upon thinning compared to NT (except BAI MT 2009 and 2015). During the post-thinning years 2011 through 2014, BAI of HT was significantly higher than that of MT, whereas rBAI stayed similar in these two thinning treatments.

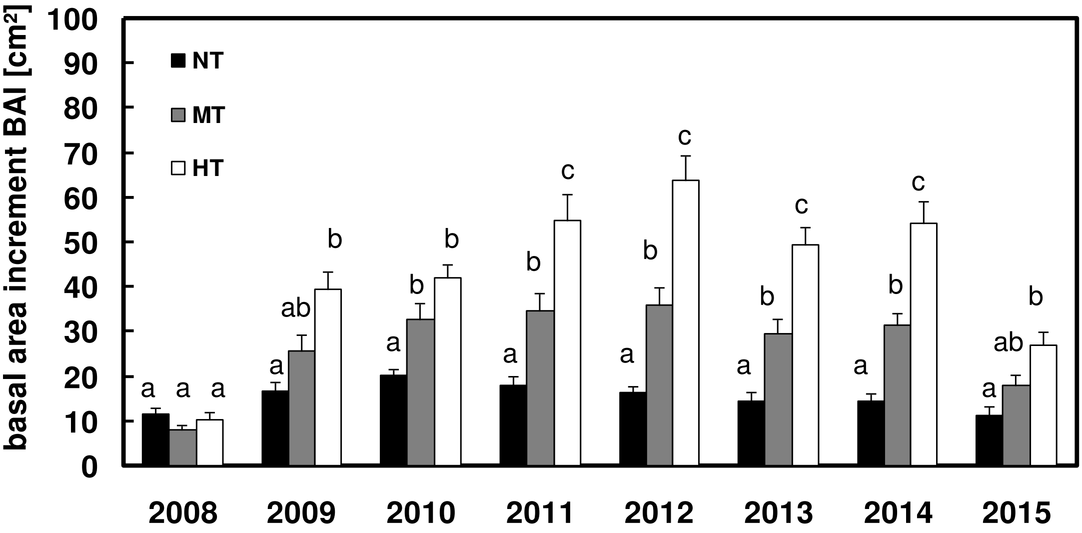


Figure 4-7 basal area increment of the target trees on NT (no thinning), MT (moderate thinning) and HT (heavy thinning) during 2008, the year before thinning and post-thinning years 2009 – 2015

During growing seasons 2013 and 2015 with hot-dry during late summer (see 3.1), the rBAI of the all treatments was significantly decreased relative to preceding humid year (s). During 2013, rBAI declined significantly by 15%, 25% and 31% compared to previous years each at NT, MT and HT, respectively (Resistance 1, table 4-1). Compared to the previous 4 years (Resistance 2, table 4-1), the rBAI declined by 22 %, 22%, 20 % on NT, MT and HT respectively.

During 2015 the rBAI declined by 26 %, 46 % and 54% on NT, MT and HT compared to the previous year (Resistance 1) and by 48%, 58% and 63 % on NT, MT and HT compared to the previous 6 years (Resistance 2).

Although there was no significant difference between Resistance 1 and Resistance 2 in 2013 and 2015 across treatments, target trees on HT tended to be reduced in growth resistance compared to the target trees on NT during dry-hot late summers. Furthermore there was no significant recovery from the drought year in all treatments, irrespective of thinning intensity.

Nevertheless, in absolute terms the BAI and rBAI of MT and HT were still higher compare to the NT during the drought years 2013 and 2015 (Fig. 4-8)

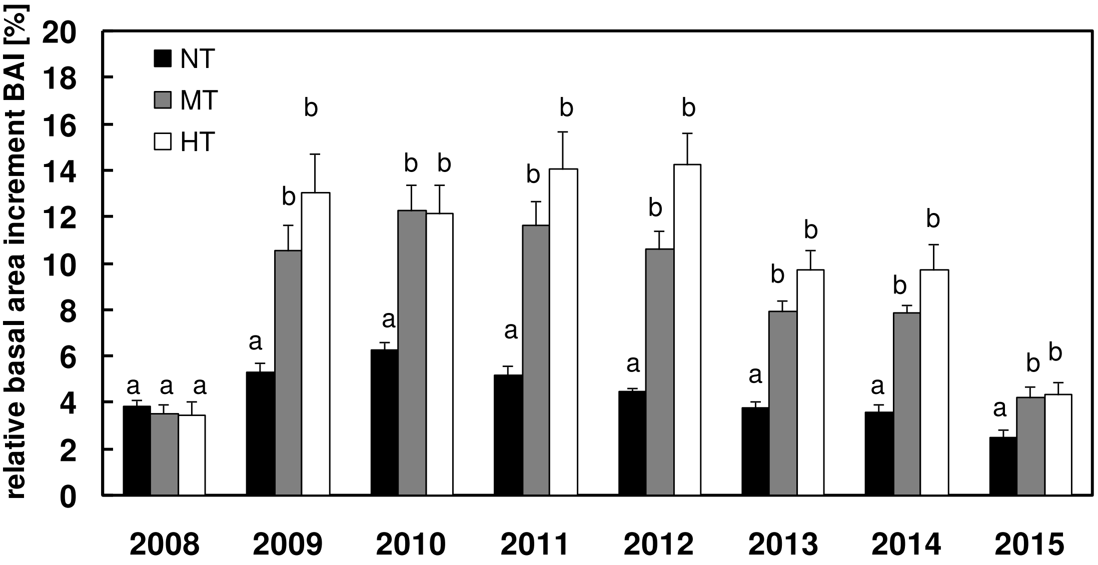


Figure 4-8 relative basal area increment (rBAI) of the target trees on NT (no thinning), MT (moderate thinning) and HT (heavy thinning) during 2008, the year before thinning and post-thinning years 2009–2015

Table 4-1 Resistance 1 and Resistance 2 in 2013 and 2015. Resistance relates the rBAI in the drought year to that of the previous year (resistance 1) or the previous 4 years (resistance 2) in 2013 and the previous 6 years in 2015 (resistance 2) and Recovery 1 2013 relates the rBAI after the drought year to that of the previous year. Bold letters indicate significant difference in the drought year. No differences of resistance occurred between the treatments

		NT	MT	HT
2013	Resistance 1	**0.85**	**0.75**	**0.69**
	Resistance 2	**0.78**	**0.78**	**0.80**
	Recovery 1	0.95	1.00	1.01
2015	Resistance 1	**0.73**	**0.54**	**0.46**
	Resistance 2	**0.52**	**0.42**	**0.37**

However, BAI of target trees on NT achieved by July, showed 70% completion already (Fig 4-9) when related to whole-year BAI (i.e. $rBAI_{July}$), regardless of the exceptional drought, attributed to soil water deficits on NT also in late summer with high Pg during the growing seasons (Fig. 4-1 +4-4). Springs were more dry in 2011 and 2014, when $rBAI_{July}$ stayed low. Thinning significantly reduced $rBAI_{July}$ in MT and HT compared to NT by c. 15% during years without dry spells, while absolute BAI achieved till July was increased. Furthermore, the absolute BAI from July to the end of each growing season of MT and HT was enhanced by thinning, also during the dry spell in 2013 (Fig. 4-11). This was not the case for 2015.

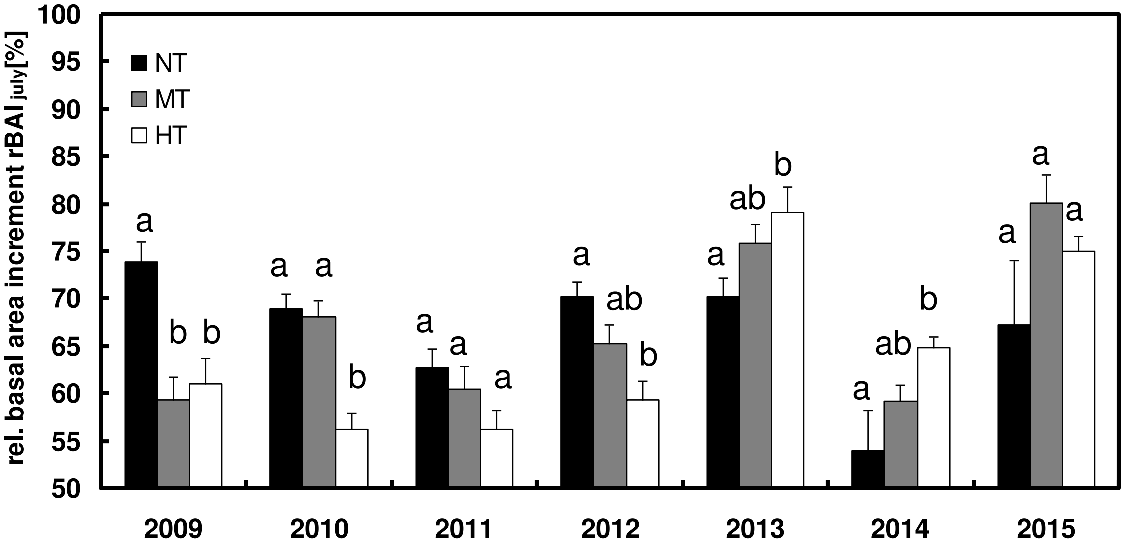


Figure 4-9 relative basal area increment of the target trees till July relative to the BAI of the same year ($rBAI_{July}$) during the post- thinning years 2009 – 2015. Letters indicate significant differences ($p<0.05$) between the treatments.

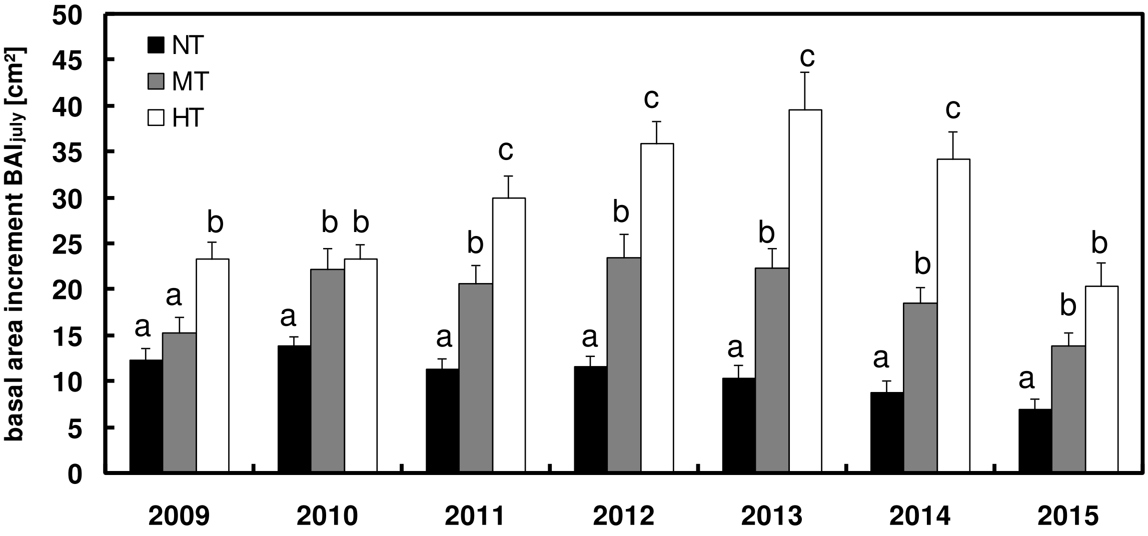


Figure 4-10 basal area increment of the target tress till July (BAI $_{\text{July}}$) during the post-thinning years 2009 – 2015. Letters indicate significant differences ($p<0.05$) between the treatments.

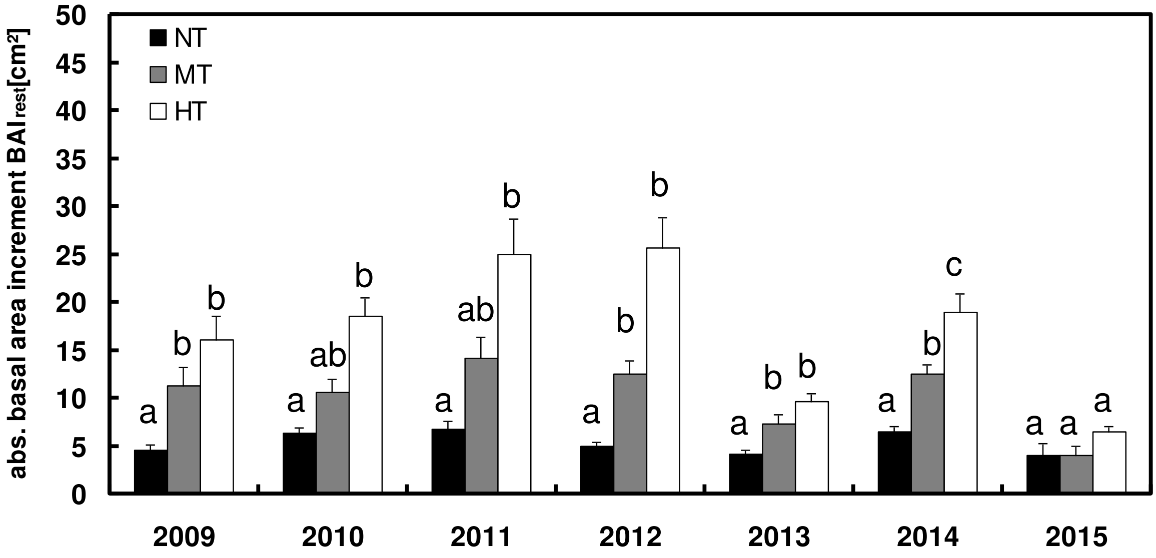


Figure 4-11 basal area increment of the target tress after July (BAI $_{\text{rest}}$) during the post-thinning years 2009 – 2015. Letters indicate significant differences ($p<0.05$) between the treatments

Fine root biomass

The fine root biomass (FRB_{60}) of the trees was initial reduced upon thinning by 57.2 % in MT and 60% in HT compared each to NT. Within the first 5 years after thinning the fine root biomass in MT increased significantly, whereas in HT the fine root biomass remained unchanged. Fine root biomass showed the accumulation maximum relative to NT within the upper soil of 40- 50 cm depth (Fig. 4-12). In HT, instead, increase of tree fine root biomass of the remaining trees stayed absent along the depth profile. Under consideration, however, of the understory fine root biomass, MT and HT did not differ (Fig. 4-13).

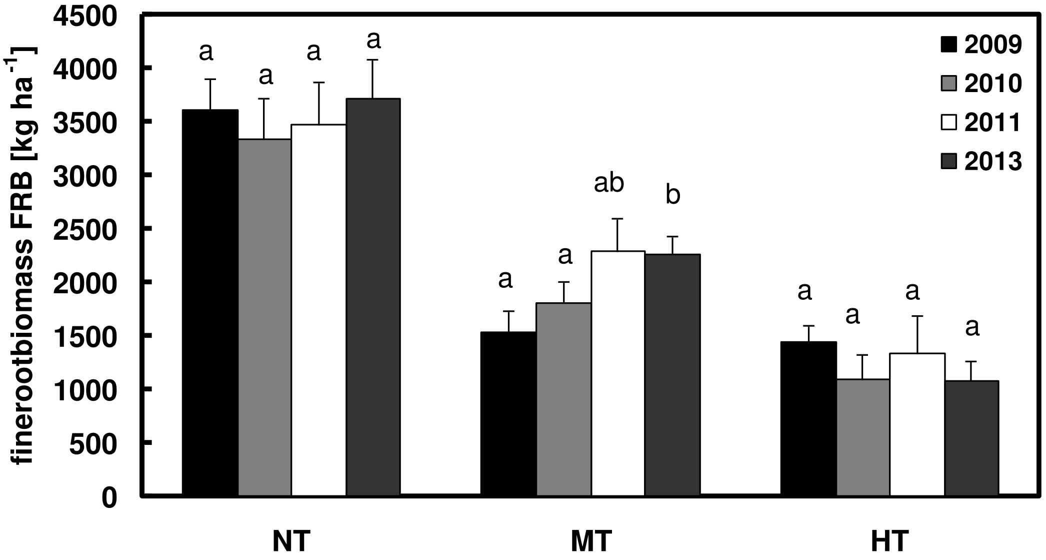


Figure 4-12 fine root biomass on NT (no thinning), MT (moderate thinning), HT (heavy thinning) in the post thinning years 2009 -2011 +2013. Letters indicate significant differences ($p<0.05$) within the same treatment

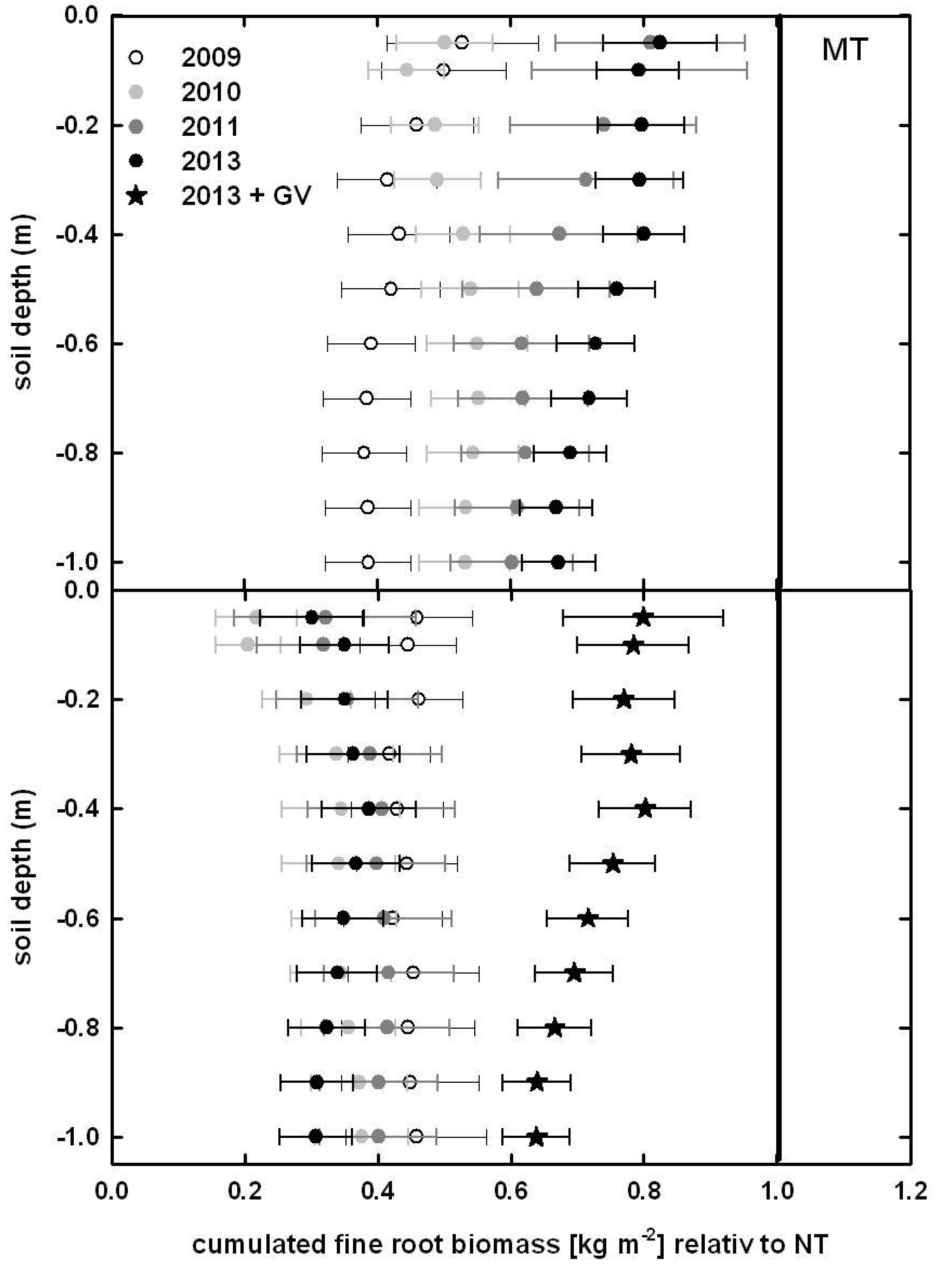


Figure 4-13 cumulated fine root biomass of the overstory on MT and HT relative [kg m²] to NT down to 1m soil depth in the post-thinning years 2009-2011 +2013. The stars represent the tree fine root biomass plus the fine root biomass of the ground vegetation.

Discussion

Relative extractable soil water content

Our first two hypotheses, that with increasing thinning intensity the relative soil water content is enhanced during the following growing seasons, but the potential to reduce the duration below critical soil water content diminishes, can be accepted. Thinning led to an increased relative soil water (REW) content on the moderate (MT) and the heavy thinning (HT) during the growing seasons following the intervention, but besides parts of first year the REW_{60} between MT and the heavy thinning HT did not differ. Furthermore, the benefit in REW_{60} of the thinned plots compared to the un-thinned plots was reduced over time.

While thinning can increase single-tree transpiration due to increased insolation, increasing air flow in the crown (Ma et al., 2010), the overall stand transpiration is reduced (del Campo et al., 2014; Gebhardt et al., 2014; Morikawa et al., 1986). Furthermore, the reduction in basal area and therefore leaf area leads to a decrease of intercepting surface, increasing stand precipitation and therefore enhanced soil water content (Donner and Running, 1986; Stogsdill et al., 1992).

The enhanced relative REW in the present study is in line with findings of a thinning experiment in 43-year-old *Quercus petraea* stand, in which Bréda et al. (1995) reported an increased relative extractable soil water in the thinned stand for the following 2 years. Likewise, del Campo et al. (2014) reported increased soil water content following thinning in a semiarid pine plantation. Moreover, Cotillas et al. (2009) reported an increase of soil moisture after thinning, but also reported a fast decline of the positive effects within three years, which was partly attributed to fast resprouting of the thinned stumps.

The fast equalization reported in the present study between MT and HT from the second year on, especially in the decline of REW, can be attributed to the additional evapotranspiration of emerging ground vegetation on HT on the study site (Gebhardt et al., 2014). The ground vegetation added an additional 26 % to the total stand transpiration and increased the interceptional loss by about 13 % over the growing seasons (Gebhardt et al., 2014). The contribution of ground vegetation to total stand evapotranspiration dependents primarily on the leaf area index of the overstory, the species, climatic conditions and soil water content

(Black and Kelliher, 1989; Granier et al., 1990; Simonin et al., 2007). The potential of thinning interventions to reduce the duration below REW_{crit} over time is primarily determined by the increase of stand transpiration and interception of the remaining stand during the years following the thinning intervention. Hence, regulating the initial REW at the beginning of a dry spell and the decline in REW during a dry spell. Stand transpiration of thinned stands compared to un-thinned stands has been shown to be equalized or even enhance within a few years following thinning (Lagergren et al., 2008; Stogsdill et al., 1992). After the initial increase on tree-level caused by increased insolation of former shaded leaves, changes in stand transpiration and interception primarily depend on the crown expansion and the increment of the LAI during the years following the thinning intervention. Both dependent on the tree (ground vegetation) species and the age of the stand. For example, Pokorný et al. (2008) reported a recovery of LAI within 2 years after a thinning related LAI reduction of about 18 % in a young mountain Norway spruce stand. In contrast, the leaf area index in a 43-year-old oak forest did not increase following thinning (Bréda et al., 1995b).

In the present study the potential of thinning to reduce the duration below REW_{crit} by reducing the decline in REW was absent in the 5th years. Therefore, increased stand transpiration and on the thinned compared to the un-thinned plots in the present study led to similar duration below REW_{crit} during the dry spell in late summer 2013. Nevertheless, minor differences in stand transpiration and interception during the growing season prior to the dry spell increased the initial REW at the beginning of the dry spell in late summer 2015 and therefore slightly reduced the duration below REW_{crit}.

Basal area increment

In contrary to our third hypothesis that the higher decline in radial growth during drought periods of target trees in heavy thinned stands can be related to an increased duration below critical relative extractable water (REW_{crit}), we found that the duration was similar or slightly reduced. The resistance (decline in relative basal area increment during the drought years compared to pre-drought years) of the target trees on HT tended to be lower (26% compared to NT) 7 years after the thinning treatment**.** This is in line with Sohn et al. (2013) who found lower resistance of the target trees during the summer drought of 2003 on heavily thinned plots 7-10 years after the thinning treatment. Furthermore, McDowell et al. (2006) reported for a thinning experiment in a *Pinus ponderosa* stand a higher sensitivity (i.e. greater relative decline) to drought for trees in low basal area treatments. On the target tree level thinning leads to an increased leaf area (Cregg et al., 1990; Guiterman et al., 2012), hence to an increased evaporative demand. Furthermore, in open stands canopy conductance primarily depends, besides radiation on the vapor pressure deficit (VPD) (Bréda et al., 2006). Under high radiation the canopy conductance sharply decreases with increasing VPD (Granier et al., 1996). This may have led to an enhanced reduction of the canopy conductance on the thinned compared to the un-thinned trees in 2015 relative to the pre-drought year (s).

Moreover, on HT an increase of fine root biomass by the remaining trees following thinning trees was non-existent for at least 5 years in contrast to the MT plots. The beginning of belowground recolonization of unoccupied soil compartments can be expected within the first few years (Ammer and Wagner, 2002; Aussenac and Granier, 1988; López et al., 2003). In the present study, the non-existent increase of fine root biomass on HT following thinning may be mainly attributed to belowground competition with the ground vegetation. In addition, increased water and nutrient supply after thinning may have caused changes in carbon allocation towards the aboveground biomass (i.e. leaf area and stem growth). Therefore, on the target tree level at HT increased aboveground water demand (leaf area, exposition) in combination with lower fine root biomass per leaf area (insufficient water supply) could have led to increased drought stress. In addition, during the year 2015 the drought was coincided with a heavy masting event causing an additional decline in the annual growth irrespective of the dry spell during late summer, which was also indicated by the reduced rBAI till July in all treatments.

Nevertheless, despite the tendency of higher sensitivity of the target trees on the thinned plots compared to the un-thinned, the BAI as well as the rBAI of the target trees was higher also during the drought years. This is in line with findings in the literature (Kohler et al., 2010; McDowell et al., 2003, 2006; Sohn et al., 2013). For example, Martínez-Vilalta et al. (2012) reported a greater drought impact on fast-growing *Pinus sylvestris* trees compared to slow-growing trees, but also higher absolute growth rates both during and after the drought. Furthermore, whereas the basal area increment on NT was already finished by more than 70% in July of each year, whatever the gross precipitation, the basal area increment untill July on MT and HT represented about 55% of the BAI of the whole growing season. This indicates recurring drought stress on NT during late summers of the pre-drought years whatever the gross precipitation and illustrates the avoidance of these drought events by thinning.

Furthermore, it is important to examine the recovery after the drought in 2015 which has been shown to be improved by heavy thinning interventions regardless of the time span between thinning and the drought event (Sohn et al. 2013) but which was non-existent in this study regardless of the thinning intensity and which may, besides the climatic conditions, be partly attributed to the ground vegetation on HT on the medium-term. The recovery on the medium to long-term may be attributed to increased leaf and fine root biomass per target tree and therefore structural changes rather than changes in the gas exchange (Fernández-de-Una et al., 2016; McDowell et al., 2006). Improved performance during the drought and enhanced recovery from the drought may be of particular importance for trees like Norway Spruce, highly susceptible to secondary pests.

Conclusion

Thinning as a silvicultural measure can improve the relative extractable soil water content and reduce the time span below critical soil water contents during the years following the intervention. Furthermore, thinning enhanced tree growth in absolute terms also during drought years. However, the benefits in water relations decrease with increasing time-lag between thinning and the drought event. Moreover, heavy thinning intensities may foster ground vegetation, hence diminishing the benefits in water availability and the potential to reduce the duration of soil water deficit compared to intense moderate thinning without ground vegetation. Furthermore, ground vegetation increased belowground competition for the target trees impeding fine rot biomass increment. In conclusion, repeated intense thinning from above which release the target trees from competition but avoid the establishment of competing ground vegetation in intervals of around 5 years (in the early stages) are suggested.

Acknowledgements

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Chapter 5

Synthesis

As described in the introduction the main aim of this study was to examine the potential of increasing thinning intensities as a forest management measure to mitigate drought stress in young Norway spruce stands. Furthermore, the underlying mechanisms and consequences of different thinning intensities for temporal changes of the stand water balance were disentangled.

To clarify the potential and the limits of increasing thinning intensities to mitigate drought stress and to provide recommendations for forest management a two-tier approach, i.e. retrospective analyses and continuous in-situ measurements, was conducted.

The radial growth is known to be highly related to climatic changes. Therefore, the consequences of two severe drought periods on the annual radial growth of future crop trees within increasing thinning intensities were examined retrospectively, at two different stands in the first part of the study (see chapter 2). Short-term, the drought resistance of radial growth increment (growth levels during the drought year compared to those before the drought year) was higher with increasing thinning intensity (i.e. 2 years after thinning) but lower with increasing thinning intensity on the mid- to long-term (i.e. ca. 30 years after first and 7-10 years after last thinning). These findings were confirmed by the results at the experimental site (see chapter 4) with the lowest resistance in radial growth by trend of future crop trees on the heavy thinning treatment during summer drought in 2015 (i.e. 7 years after the thinning intervention). Nevertheless, the recovery (growth levels after the drought year compared to those during the drought year) from the drought years 1976 and 2003 was higher for the target trees on the heavy-thinned compared to the un-thinned stands on the short-term as well as on the medium to long-term (chapter 2). This was not the case on the experimental site following the summer dry spell in 2013 (i.e. 5 years after the initial thinning intervention) (chapter 3). Nevertheless, the annual basal area increments of the future crop trees in absolute terms on the thinned plots were higher also during the drought years (chapter 2, 3, 4). The results of the stable isotope analysis indicated that the potential of thinning to mitigate drought stress during the drought years may mainly depend on the benefits of thinning on the water balance, whereas the recovery from the drought seems to depend additionally on structural changes of the future crop trees (i.e. increased fine root biomass and leaf area).

Effects of increasing thinning intensity on the water balance

The experimental study showed, that the benefits on the water balance on stand-level of both thinning intensities decreased over time and lasted 5-7 years. The benefits between the moderate and heavy thinning intensity were diminished for the most part within the first 3 years. The water balance was altered by the different stand densities regarding water input (via throughfall) and water consumption (via evapotranspiration) and therefore the available soil water content.

Thinning leads to a reduction of the leaf area index (LAI) and therefore reducing interception, hence leading to increased throughfall precipitation with increasing thinning intensity. Nevertheless the increase in throughfall was lower than the reduction in LAI (see chapter 2, (Aussenac and Granier, 1988; Teklehaimanot et al., 1991). Besides the reduction of the LAI, canopy interception is highly dependent on climatic variables like wind velocity, temperature and humidity during the rain event and most important the intensity of the rain event (Aussenac and Granier, 1988; Frischbier, 2012). Although not proportional to thinning intensity, increased throughfall has been shown as one of the most important variable of the water balance, altered by thinning, for increasing soil water availability and reducing drought stress on a tree level (chapter 4 (Molina and del Campo, 2012; Simonin et al., 2007; Stogsdill et al., 1992, 1989).

Furthermore, as a consequence of the reduced LAI, the reduced water loss via stand transpiration is the second component of the water balance altered by thinning in order to mitigate drought stress during drought years. With increasing thinning intensity, the water loss via transpiration on stand-level is reduced (chapter 3, (Aussenac and Granier, 1988; del Campo et al., 2014; Morikawa et al., 1986). Nevertheless, as for the interception, the decrease in stand transpiration was not proportional to thinning intensity and LAI reduction.

Accordingly, the reduction in stand transpiration during the first year after thinning was lower than the reduction in stand density, due to increased transpiration of the remaining trees on tree level (chapter 3). In the present study, the removal of 43% (moderate thinning, MT) and 67% (heavy thinning, HT) of the stand basal area reduced the stand-level transpiration by about 25% upon MT and 50% upon HT during the first year following thinning. This was attributed to increased insolation of former shaded leaves in the canopy of the remaining tree and the increase in available soil water content. Changes in the microclimate including increased insolation and additionally increased soil water availability leads to an increase of the transpiration on tree level (chapter 3, (Aussenac, 2000; del Campo et al., 2014). Measurements of microclimate changes in forest stands are very laborious and show high spatial variability. Existing studies reported significant changes of the microclimate within forest stands following thinning. For example, Ma et al. (2010) reported for an overstory thinning treatment in a mixed coniferous stand increasing air temperatures, decreased relative humidity, increased vapour pressure deficit and increased wind speed compared to the pre-thinning references. They also reported that the changes in microclimate variables corresponded with thinning intensity. Furthermore, overstory-thinning led to more extreme daily ranges and maxima of daily temperatures and vapour pressure deficit in a mixed-coniferous stand in Sierra Nevada (Rambo and North, 2009). Nevertheless, the present study and the literature showed an overall increase in growth related water use efficiency during the first years following thinning, which is in line with numerous findings in literature (see chapter 2, (Fernandes et al., 2016; Martín-Benito et al., 2010; McDowell et al., 2003, 2006).

However, the increase in transpiration of the remaining trees in thinned stands decreases the benefit of LAI reduction in relation to decreased stand transpiration and equalizes or even amplifies transpiration at stand level on the thinned compared to the un-thinned controls within the first years after thinning (Bréda et al., 1995; Lagergren et al., 2008; Stogsdill et al., 1992). Besides increasing water demand per unit leaf area and increased soil water availability, this may be attributed to leaf area increment of the remaining trees (Aussenac, 2000) and fertilization effect (Lagergren et al., 2008) (see chapter 3). Changes in stand transpiration and interception following thinning may mainly depend on the canopy expansion and therefore the increase of LAI during the years after thinning. Hence, leading to a similar water balance of the thinned plots compared to the un-thinned plots within a few years. The increase in leaf area following thinning depends on thinning intensity, tree species and stand age. For example, the leaf area index in a 43-year-old oak forest (*Quercus petraea* (Matt.) Liebl.) did not increase following thinning (Bréda et al., 1995) which was attributed to the slow growing oak trees. On the contrary, the leaf area index in a 10-year-old loblolly pine stand, with a basal area reduction of 50 and 75% , increased within one year following thinning by c. 9% and 20% respectively (Cregg et al., 1990). Likewise, in a 20-year-old Douglas-fir stand the water balance was recovered within the subsequent 3-5 years which was attributed to foliage and root biomass recovery (Aussenac and Granier, 1988). Furthermore, the LAI reduction by about 18% following thinning was recovered within two years in a 24-year-old Norway spruce stand (Pokorný et al., 2008).

In addition, thinning could lead to a rapidly invading herbaceous species dominated understory (Cregg et al., 1990; Thomas et al., 1999) which would contribute to stand water loss via additional evapotranspiration (Whitehead et al., 1994). This was the case on the heavy thinning plots on the experimental site in the second year following thinning (see chapter 2). The contribution of the ground vegetation to the stand transpiration was found to range from 6 to over 60%, depending on the overstory LAI, climatic variables, time of the year and species (see ref. in Black and Kelliher, 1989; Whitehead et al., 1994). For example, the understory transpiration was estimated to account for about 28 to 30 % of total stand transpiration in a *Pinus pinaster* stand during summer with 358 stems ha^{-1} and a LAI of 2.3 (Granier et al., 1990). This result is in line with the measured mean contribution of 26% to the total stand transpiration on the heavy thinning plots of the present study by the emerging ground vegetation with similar stand density and LAI (see chapter 3). As a result, the additional transpiration of the ground vegetation in the present study diminished the differences in stand transpiration between the moderate and the heavy thinning already in the second year after thinning (see chapter 2) as well as added an additional water loss via interception of around 13%.

Potential of increasing thinning intensity to mitigate drought

As mentioned above the retrospective approach showed a lower resistance in growth with increasing thinning intensity on the medium to long-term (i.e. 30 years after first and 7-9 years after last thinning). This was most likely attributed to increased stand transpiration of the thinned stands with ongoing time after the thinning and therefore similar or even more intensive soil water deficit (see chapter 2). The future crop trees at the experimental site showed a similar reduction in relative basal area increment during the summer drought seven years (2015) after the thinning treatment, with by trend a decreasing resistance with increasing thinning intensity (see chapter 4). Nevertheless, the annual basal area increments of the future crop trees in absolute terms on the thinned plots in general were higher also during the drought years (chapter 2, 3, 4).

The consequences of drought stress depend mainly on the duration and the intensity of the drought. Relative extractable water with values dropping below 40% have been shown as an index for soil water deficit induced stomatal regulation on forest trees (Granier et al., 2007, 1999; Grossiord et al., 2015; Rambal et al., 2003). Therefore, with increasing time span of the relative extractable soil water content below the threshold the drought stress on tree level increases. Consequently, the initial relative extractable water content at the beginning of the drought and the rate of reduction during the drought may be decisive to reduce the duration below critical soil water content and therefore mitigating drought stress. The experimental approach showed that the time span below the threshold of critical soil water content was reduced by thinning up to 5 and 7 years (see chapter 4). The combination of reoccurring short dry spells and rain events during the growing season can accumulate minor differences in throughfall and stand transpiration over the growing season. Hence leading to an increased REW on the thinned plots compared to the un-thinned plots at the beginning of the drought period (see chapter 4). Nevertheless, the intensity of the soil water deficit at the end of the growing season was similar on all treatments 5 and 7 years after the initial thinning.

The comparison of the resistance during drought events between different thinning intensities also depends on the radial growth during the pre-drought year(s). In the case, that tree growth in the un-thinned dense stands was limited by reduced soil water content also in the pre-drought summer months the decline during the actual summer drought will be less prominent for trees in the un-thinned compared to the thinned plots (see chapter 4). Moreover, the basal area increment of the future crop trees on the thinned stand was overall higher during post-thinning period, also during the drought years (see chapter 2,3). This is in line with numerous findings based on a range of tree species, tree ages, thinning intensities and climate zones (for example (Cotillas et al., 2009; D'Amato et al., 2013; McDowell et al., 2003; Misson et al., 2003;

White et al., 2009). Furthermore, Martínez-Vilalta et al. (2012) reported that fast-growing trees were proportionally more affected in growth by drought events, but performed better in absolute terms during as well as after the drought. The relative higher growth decline with increasing thinning intensity compared to the un-thinned future crop trees seven years after the intervention may partly represent a change in resource allocation to belowground biomass or from growth- to defence related metabolism due to current needs (see extended "Growth- Differentiation- Balance Theory" (Matyssek et al., 2005)). In contrast to the high density of the un-thinned stands, in which the trees may undergo a crucial trade-off associated to ensure competitiveness versus defence with resource loss (Matyssek et al., 2012), resources for defence may not to be limited for the remaining trees on the thinned plots. Indicated also by an overall higher absolute basal area increment also during the drought years. This may be important particularly for Norway spruce endangered by secondary pests like bark beetle attacks.

Nevertheless, stomatal regulation is not only depended on the available soil water content. With lower LAI in recently thinned stands, transpiration is directly coupled to changes in climatic parameters (Bréda et al., 1995). As mentioned above thinning leads to an increase in VPD and wind flow (reducing the boundary layer), which was reported to last up to one decade following thinning indicated by wood isotope analyses (Brooks and Mitchell, 2011; Martín-Benito et al., 2010). In combination with increased leaf area on tree level (Guiterman et al., 2012), this will lead to an increased evaporative demand on tree level. Under high radiation the canopy conductance decreases more sharply with increasing VPD (Granier et al., 1996). Leading to an intensified reduction of the canopy conductance on the heavy-thinned compared to the un-thinned trees during the drought event relative to the pre-drought year(s).

Furthermore, it is crucial that the benefit of increased soil water content and the increased demand can be supplied via belowground root biomass. There are only a few studies that measured belowground changes following thinning, but in general an increment in fine root biomass, but including a time delay, after thinning was reported. For example, in a boreal *Picea abies* forest no recovery of the tree root system was found in experimental gaps within 2–3 years (Taskinen et al., 2003). Furthermore, Aussenac and Granier (1988) attributed the reduced differences in radial growth between thinned and control stands in the fourth year after thinning to root recolonization and foliar mass increment. Likewise, López et al. (2003) reported an increase of fine root biomass in holm oak stands 4-5 years following thinning. Nevertheless, on stand-level, the total fine root biomass of overstory Norway spruce has been shown to be still lower in a stand four years after thinning (Petritan et al., 2011). This is in line with the experimental study, showing an increment in fine root biomass on the moderate thinning within the first 5 years (see chapter 4). On the long-term and after repeated thinnings on one of the sites (Göggingen) of the retrospective approach it has been shown that no differences in total fine root biomass were apparent between the thinning treatments (30 years after initial thinning) indicating an increased fine root biomass per tree (see chapter 2). The effective recolonization of unoccupied soil compartments and increased fine root biomass per tree is in line with model estimations for a 75-year-old Norway spruce stand including a gap formation 10 years earlier (Ammer and Wagner, 2002).

However, this was not the case on the heavy-thinned plots of the experimental site on the short to medium-term. The combination of two mechanisms may be responsible for the absence of fine root biomass increment on the heavy-thinned plots. According to the balanced-growth-hypothesis, an increase in water and nutrient availability may foster carbon allocation to the above ground biomass (Shipley and Meziane, 2002). For example, on a low productivity site, 36.4 % of total net primary production was used for fine root biomass production compared to 7.9 % on the high productivity site in a 40-year-old Douglas fir stand (Keyes and Grier, 1981). Additionally, the belowground competition with the emerged ground vegetation suppressed the recovery on the heavy-thinning plot compared to the moderate (see chapter 4).

The increased leaf area and evaporative demand on the heavy thinned plots, but relative reduced fine root biomass could lead to increased drought stress on tree level, on the heavy thinning. Simonin et al. (2007) reported on a thinned ponderosa pine stand, where the basal area was reduced by 82% and the leaf area index by 45% that the understory evapotranspiration compensated for the lower overstory transpiration during drought. Furhermore, the recovery on the medium to long-term may also partly be attributed to both, increased leaf and fine root biomass per target tree and therefore structural changes rather than changes in the gas exchange (see chapter 2,4) (Fernández-de-Una et al., 2016; McDowell et al., 2006).

Conclusion and forest management recommendation

In summary, it can be concluded from the presented results and the findings in the literature that thinnings have the potential to mitigate drought during the drought event and increase the recovery from such events. The mitigation of drought was attributed to a temporarily reduced soil water deficit by reducing transpiration and interception on the stand level in addition with fostering leaf area and root expansion. However, it has also been shown that thinning intensity and frequency seems to be crucial to increase available soil water, as well as leaf and root expansion for the remaining trees. On the one hand, if the thinning intensity is too low (by fostering not enough future crop trees) and therefore insufficient removal of basal area on stand level, the thinning intervention may increase the evaporative demand and insolation of the future crop tree without improving the water balance of the whole stand. On the other hand, if the thinning intensity is too heavy the emerging ground vegetation may diminish the benefit of increased thinning intensity on the water balance compared to a more moderate thinning intervention without ground vegetation. The competition with the ground vegetation for water and belowground expansion may exacerbate drought stress for future crop trees under severe and prolonged drought.

The intense moderate thinning on the experimental site (removal of about 40 % basal area, fostering ca. 400 target trees, by removing 1-2 competitors), but with a relative short thinning frequency for the first interventions of about 5 years seems to be a viable option to mitigate drought during and in combination with fostering leaf and fine root biomass increment of the target trees, to improve the recovery from drought.

Furthermore, thinnings are silvicultural measures which shall not only improve the water balance, but also increase productivity and stand stability. Very heavy thinning may lead to total stand productivity which does not reach a desired threshold. Particularly, high radial growth may also lead to reduced timber quality and trees which are temporally susceptible to windthrow. Thrown trees, however, attracts bark beetles.

Therefore, the present study suggests that frequent and intense thinning interventions while preventing the establishment of a vital ground vegetation seems to be the most promising forest measure to mitigate drought without increasing risks and without losing sight of economic needs.

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Summary

The predicted increase in frequency of intense and prolonged drought events challenges forest management. Centuries of forest management has led to Norway spruce (*Picea abies* [L.] Karst.) monocultures outside its natural range. In Germany, Norway spruce covers ca. 25% of the total forest area and represents the economically most import tree species. Thinning as a silvicultural measure has been discussed to reduce drought risk in young Norway spruce stands.

The aim of the present study is to investigate the potential and the limits of increasing thinning intensity to mitigate drought by reducing intraspecific competition and increasing the availability of soil water. A two-tier approach (i.e. retrospectively and in-situ measurements) was applied to examine differences in tree response to severe drought within increasing thinning intensities and the effects of such thinning intensities on the water balance.

To investigate tree response to severe drought events radial growth increments in combination with stable carbon and oxygen isotopes in the early- and latewood per year ring were measured retrospectively at two long-term thinning experiments in southern Germany. The initial thinning with increasing intensities was conducted in 1974 within a ca. 27-year-old Norway spruce stand. Annual radial growth and stable isotope analyses were used to unveil differences in physiological performance and radial growth between trees within increasing thinning intensities to the exceptional drought events 1976 and 2003.

To address changes in the stand water balance modified by increasing thinning intensity and therefore to investigate the potential to mitigate drought, a thinning experiment was established in 2008 in a 26-year-old un-thinned Norway spruce monoculture. Prior to the thinning treatment at the beginning of 2009 about 430 target trees per hectare were selected. On the experimental site 3 thinning intensities were conducted: A “not-thinned” control (NT) with a stand basal area of 42 $m^2\ ha^{-1}$, a moderate thinning (MT) with a reduction of the stand basal area by 43 % (thinning from above and fostering the target trees by removing 1- 2 competitors) and a heavy thinning (HT) with a reduction of 67% (removal of all trees except the target trees). Besides the variables of the water balance, like open field precipitation, throughfall, soil water content and stand transpiration, structural changes (i.e. fine root

biomass, ground vegetation) altered by the increasing thinning intensities were continuously assessed on the research plots.

The retrospective approach showed, that the drought induced decline in radial growth during drought years was reduced by intense thinning on the short-term but increased on the medium to long-term. The higher resistance in radial growth on the short-term was attributed to increased soil water availability, but this advantage is likely to be reduced over time. After the drought events, the recovery was increased on the heavy-thinned plots from a likely increase of available soil water content in recently thinned stands and additionally structural adaptions of the target trees fostered by repeated intense thinning interventions (i.e. higher foliage area and fine root biomass) on the medium to long-term.

The experimental approach showed, that the removal of basal area and therefore leaf area reduced transpiration on stand-level and an increased throughfall within the first years following the thinning intervention. But the thinning effect on stand transpiration and on Interception was not proportional to the reduction in basal area. The thinning led to an increased transpiration on tree-level of the remaining trees. Nevertheless, thinning increased the growth-related water use efficiency on tree- and stand level. Furthermore, over the whole study period the basal area increment was enhanced by thinning, also during the drought year. Furthermore, both thinning intensities allowed for a reduced time span below critical soil water content up to 5-7 years. However, with increasing time-lag after the thinning intervention the potential of thinning to reduce the time span decreased. Furthermore, the fast establishment of vital ground vegetation on the heavy-thinned plots added an additional water loss via evapotranspiration. The additional transpiration of the ground vegetation diminished the differences between MT and HT in stand transpiration within 2 years. Similar to the retrospective approach the radial growth decline in the target trees with increasing thinning intensity tended to be higher during the drought year in 2015 (7 years after initial thinning). This may partly be attributed to an intensified reduction of the canopy conductance compared to the pre-drought year(s) due to the open position of the target trees. Nevertheless, on HT the vital ground vegetation enhanced the competition for soil water. Moreover, the belowground competition of the ground vegetation also suppressed the recovery of fine root biomass on the heavy thinning plots compared to the more moderate thinning on the medium-term. The reduced fine root biomass compared to the increased leaf area on tree-level of HT and the competition for water may intensify drought stress for the target trees during the drought period and decrease the above mentioned favourable thinning effect on the recovery from the drought for HT on the medium-term.

In summary it can be concluded, that thinnings have the potential to mitigate drought during and to improve the recovery from drought. However, it has also been shown, that the benefits of a thinning intervention on the water balance are temporary and heavy thinnings may foster ground vegetation, enhancing competition for water and belowground fine root recovery. Furthermore, if the thinning intensity is too low (by fostering not enough future crop trees) and therefore insufficient removal of basal area on stand level, the thinning intervention may increase the evaporative demand and insolation of the future crop tree without improving the water balance of the whole stand. Nevertheless, if the thinning intensity is too heavy the emerging ground vegetation may diminish the benefit of increased thinning intensity on the water balance compared to a more moderate thinning intervention without ground vegetation. The intense moderate thinning on the experimental site (removal of about 40 % basal area, fostering ca. 400 target trees, by removing 1-2 competitors), but with a relative short thinning frequency for the first interventions of about 5 years seems to be a viable option to mitigate drought during and in combination with fostering leaf and fine root biomass increment of the target trees, to improve the recovery from drought. This may be particularly important for Norway spruce endangered by secondary pests.

Therefore, the present study suggests that frequent and intense thinning interventions while preventing the establishment of a vital ground vegetation seems to be the most promising forest measure to mitigate drought in young Norway spruce stands without increasing risks and without losing sight of economic needs.

Zusammenfassung

Die prognostizierte Zunahme der Häufigkeit von intensiven und langanhaltenden Trockenheitsereignissen stellt die Forstwirtschaft vor eine Herausforderung. Jahrzehntelange Forstwirtschaft führte zu einer monokulturartigen Struktur der Fichte (*Picea abies* [L.] Karst.) außerhalb ihres natürlichen Verbreitungsgebietes. In Deutschland stellt die Fichte, mit einem Flächenanteil von ca. 25% der gesamten Waldfläche, die ökonomisch wichtigste Baumart dar. Aus diesem Grund werden Durchforstungen als waldbauliches Mittel zur Abmilderung des Trockenstressrisikos in jungen Fichtenbeständen diskutiert.

Das Ziel der vorliegenden Arbeit ist es, das Potential und die Grenzen zunehmender Durchforstungsstärken im Hinblick auf die Abschwächung von Trockenheitsereignissen durch die Verringerung intraspezifischer Konkurrenz und erhöhter Wasserverfügbarkeit zu untersuchen. Um Unterschiede in der Reaktion der Bäume bei zunehmender Durchforstungsstärke auf strenge Trockenzeiten zu untersuchen und die Auswirkungen solcher Durchforstungsstärken auf den Wasserhaushalt festzustellen, wurde ein zweistufiger Ansatz mit retrospektiven Untersuchungen und in-situ Messungen gewählt.

Um die Reaktionen der Bäume auf strenge Trockenzeiten zu erfassen wurden retrospektiv auf zwei langfristigen Durchforstungsversuchen in Süddeutschland die Zuwachsreaktionen der Bäume in Verbindung mit den stabilen Kohlenstoff und Sauerstoff Isotopen im Früh- und Spätholz der Jahrringe aufgenommen. Die Erstdurchforstung mit ansteigender Durchforstungsstärke wurden 1974 in einem ca. 27-jährigen Fichtenbestand durchgeführt. Um mögliche Unterschiede in der physiologischen Reaktion und im Zuwachs zwischen den Bäumen auf den Flächen mit unterschiedlichen Durchforstungsstärken in den außergewöhnlichen Trockenjahren 1976 und 2003 aufzudecken, wurden die jährlichen Radialzuwächse sowie die Stabilisotopen-Analyse verwendet.

Um die Änderungen im Wasserhaushalt mit zunehmender Durchforstungsstärken und das Potenzial der Durchforstungseingriffe Trockenheit abzumildern, zu untersuchen, wurde 2008 in einer ca. 26-jährigen undurchforsteten Fichtenmonokultur ein Durchforstungsexperiment etabliert. Vor dem Durchforstungseingriff Anfang 2009 wurden ca. 430 Auslesebäume pro Hektar ausgewählt. Dabei wurden auf dem Standort 3 Durchforstungsstärken ausgeführt: eine undurchforstete Fläche (NT) mit einer Bestandesgrundfläche von ca. 42 m^2 ha^{-1}, eine

moderate Durchforstung (MT) mit einer Reduktion der Bestandesgrundfläche von 43% (Förderung der Auslesebäume durch die Entnahme der stärksten 1-2 Bedrängern) und eine starke Durchforstung (HT) mit einer Reduktion der Bestandesgrundfläche um 67% (Entnahme aller Bäume mit Ausnahme der Auslesebäume). Neben den Variablen des Wasserhaushaltes, wie Freilandniederschlag, Bestandesniederschlag, Bodenwassergehalt und Wasserverbrauch des Bestandes, wurden auch die strukturellen Änderungen (z.B. Feinwurzelbiomasse, Bodenvegetation) fortlaufend auf der Versuchsfläche aufgenommen.

Der retrospektive Ansatz zeigte, dass der trockenheitsbedingte Zuwachseinbruch kurzfristig nach dem Eingriff durch eine intensive Durchforstung verringert wurde, aber mittel- und langfristig erhöht war. Die kurzfristig erhöhte Resistenz im Zuwachs wurde auf eine zeitlich begrenzte erhöhte Wasserverfügbarkeit zurückgeführt. Nach beiden Trockenjahren, war die Erholung im Jahreszuwachs auf den stark durchforsteten Flächen verbessert. Sehr wahrscheinlich durch eine Verbesserung der Wasserverfügbarkeit in den kürzlich durchforsteten Beständen und längerfristig durch zusätzliche strukturelle Anpassungen (höhere Blattfläche und Feinwurzelbiomasse) der Auslesebäume durch wiederholte intensive Durchforstungseingriffe.

Der experimentelle Ansatz zeigte, dass die Entnahme der Grundfläche und dadurch der Blattfläche zu einer verringerten Transpiration und einem erhöhten Niederschlag auf Bestandesebene führte. Jedoch zeigte sich auch, dass die Auswirkungen auf die Bestandestranspiration und der Interzeption nicht proportional der Reduktion der Bestandesgrundfläche entsprachen. So führte die Durchforstung zu einer erhöhten Transpiration auf Einzelbaumebene der verbliebenen Bäume. Dennoch führte die Durchforstung zu einer erhöhten zuwachsbezogenen Wassernutzungseffizienz sowohl auf Baum- als auch auf Bestandesebene. Des weiteren, zeigten die Auslesebäume auf den durchforsteten Flächen über den gesamten Untersuchungszeitraum, auch während des Trockenjahres 2015, einen erhöhten Jahreszuwachs im Vergleich zu den Bäumen auf den undurchforsten Flächen. Bis zu 5-7 Jahre nach dem Durchforstungseingriff zeigten beide Durchforstungsstärken einen reduzierten Zeitraum unterhalb kritischer Bodenwassergehalte im Vergleich zu den undurchforsteten Flächen. Jedoch zeigte sich auch, dass mit zunehmendem zeitlichen Abstand nach der Durchforstung das Potenzial, den Zeitraum mit kritischen Bodenwassergehalten zu verringern, abnimmt. Des weiteren, führte die starke

Durchforstung zu einer raschen Entwicklung einer vitalen Bodenvegetation und dadurch zu einem zusätzlichen Wasserverbrauch durch Evapotranspiration. Die zusätzliche Transpiration der Bodenvegetation führte innerhalb von 2 Jahren zu einer Angleichung im Wasserverbrauch zwischen der moderaten und der starken Durchforstung.

In ähnlicher Weise, wie auch im retrospektiven Ansatz zeigte sich während des Trockenjahres 2015 (7 Jahre nach der Durchforstung), dass die Auslesebäume mit zunehmender Durchforstung während des Trockenjahres tendenziell stärker im Zuwachs eingebrochen sind. Dies könnte zum Teil auf eine verstärkte Reduktion der Kronenleitfähigkeit, aufgrund der Freistellung der Auslesebäume zurückzuführen sein. Dennoch, führte die Bodenvegetation auf der starken Durchforstung zu einer Verstärkung der Konkurrenz um das Bodenwasser. Des weiteren, führte die unterirdische Konkurrenz der Bodenvegetation in den Jahren nach dem Durchforstungseingriff zu einer Unterdrückung der Erholung der Feinwurzelbiomasse des Baumbestandes auf den starken Durchforstungen im Vergleich zu der moderaten Durchforstung. Die verringerte Feinwurzelbiomasse im Verhältnis zu der erhöhten Blattfläche auf Baumebene und die Konkurrenz um Wasser kann den Trockenstress für die Auslesebäume während der Trockenheit erhöhen und mittelfristig die oben beschriebene verbesserte Erholung von Trockenzeiten abschwächen.

Zusammenfassend konnte gefolgert werden, dass Durchforstungen das Potenzial besitzen Trockenstress abzumildern und die Erholung zu verbessern. Jedoch wurde auch gezeigt, dass die Vorteile eines Durchforstungseingriffes auf die Wasserbilanz zeitlich begrenzt sind und eine starke Durchforstung das Aufkommen einer Bodenvegetation fördern kann, welche die Konkurrenz um Wasser und um unterirdischen Feinwurzelzuwachses für die Auslesebäume erhöht. Bei einer zu schwach ausgeprägten Auslesedurchforstung (z.B. zu geringe Anzahl an geförderten Auslesebäumen) und dadurch eine nicht ausreichende Entnahme an Bestandesgrundfläche, wird die Nachfrage nach Wasser der Auslesebäume erhöht, ohne jedoch den Wasserhaushalt auf Bestandesebene zu verbessern. Eine zu starke Erstdurchforstung wiederum, kann zu einer aufkommenden Bodenvegetation führen, die die Vorteile auf den Wasserhaushalt der starken Durchforstung im Vergleich zu einer mehr moderaten Durchforstung verringert und möglicherweise das Trockenstressrisiko für die Auslesebäume erhöht. Die intensive moderate Durchforstung des Durchforstungsversuches (Entnahme von ca. 40% der Bestandesgrundfläche durch die Förderung von ca. 400

Auslesebäumen pro Hektar) - aber mit einer kurzen Zeitspanne zwischen den Durchforstungen von ca. 5 Jahren (für die ersten Durchforstungseingriffe) scheint eine praktikable Möglichkeit zu sein, um Trockenstress während einer Trockenheit abzumildern und in Kombination mit geförderten strukturellen Anpassungen der Auslesebäume die Erholung zu verbessern. Dies kann vor allem für die durch Sekundschädlinge gefährdete Fichte von besonderer Bedeutung sein.

Aus diesem Grund scheinen wiederholte intensive Durchforstungseingriffe, bei gleichzeitiger Vermeidung aufkommender Bodenvegetation, die erfolgversprechendste forstwirtschaftliche Maßnahme in jungen Fichtenbeständen zu sein, um Trockenzeiten abzumildern ohne das Risiko für die Auslesebäume zu erhöhen und ohne den Blick auf die ökonomischen Anforderungen zu verlieren.

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