



## Effects of thinning intensities on tree water use, growth, and resultant water use efficiency of 50-year-old *Pinus koraiensis* forest over four years



Juhan Park<sup>a</sup>, Taekyu Kim<sup>b</sup>, Minkyu Moon<sup>c</sup>, Sungsik Cho<sup>d</sup>, Daun Ryu<sup>a</sup>, Hyun Seok Kim<sup>a,d,e,f,\*</sup>

<sup>a</sup> Department of Forest Sciences, Seoul National University, Seoul, Republic of Korea

<sup>b</sup> National Institute of Environmental Research, Incheon, Republic of Korea

<sup>c</sup> Department of Earth and Environment, Boston University, Boston, MA, United States

<sup>d</sup> Interdisciplinary Program in Agricultural and Forest Meteorology, Seoul National University, Republic of Korea

<sup>e</sup> National Center for Agro Meteorology, Seoul, Republic of Korea

<sup>f</sup> Research Institute for Agriculture and Life Sciences, Seoul National University, Seoul, Republic of Korea

### ARTICLE INFO

#### Keywords:

Thinning intensity  
Water use efficiency  
Sap flux density  
Aboveground biomass increment  
Size-growth relationship

### ABSTRACT

This study investigated the effects of thinning intensities on tree water use and growth of 50-year-old Korean pine forests for four years. Thinning was conducted with two intensities (light thinning, heavy thinning, and control) in March 2012. Tree water use was estimated from sap flux density using Granier-type thermal dissipation sensors on 84 of total 103 trees. Tree diameter growth was measured in 97 trees with a dendrometer and converted to aboveground biomass increment using an allometric equation. Sap flux density increased initially in both thinning groups, but the effects of light thinning decreased over time. In the heavy thinning plot, sap flux density was stimulated for the entire study period. While light-thinning affected little on tree growth, tree diameter growth significantly increased from second year and this enhancement increased with time in the heavy-thinning plot. The tree diameter and growth rate were positively correlated in the light-thinning plot and negatively correlated in the heavy-thinning plot. The enhancement of sap flux density and diameter growth caused higher tree water use and tree level aboveground net primary productivity in heavy-thinning plot. Due to higher water use in the heavy thinning plot, increase in tree-level water use efficiency was observed in the high growth year only. Our results indicate that physiological responses of trees differed depending on thinning intensity and heavy thinning is an appropriate management practice for mature pine plantations.

### 1. Introduction

Forests affect the local weather conditions by changing the atmospheric composition through photosynthesis and respiration (Bonan, 2008). They also change the land surface albedo and affect energy partitioning into latent and sensible heat fluxes. These roles of forests in regulating regional or global weather are sensitive to changes in the physical and physiological characteristics of forest cover. The characteristics of forest cover are closely related to stand density, stand age, and species composition and are altered by natural disturbances or anthropogenic interference, such as forest management practices. Among various forest management practices, thinning or removal of some trees from the forest is widely conducted to produce more valuable and large-diameter timber. It reduces competition among the remaining trees, lowers the risk of natural fire, and helps to maintain a healthy forest (Kerr and Haufe, 2011).

Structural changes in the forest canopy due to thinning alter the

microclimatic conditions within the forest. For example, light distribution within the forest canopy is largely affected by leaf area index, crown structure, and canopy openness. Thinning increases canopy openness and reduces the fraction of absorbed light within the canopy (Hale, 2003). It also augments soil water availability by reducing the intercepted water loss (Breda et al., 1995; Aussenac, 2000; Ganatsios et al., 2010) and causes the groundwater levels to rise (Jutras et al., 2006). These microclimatic changes could improve growth conditions for the remaining trees and understory species. Thus, thinning enhances growth (Aussenac and Granier, 1988; McDowell et al., 2003; Anning and McCarthy, 2013) and photosynthetic efficiency (Gauthier and Jacobs, 2009) in the remaining trees. However, a short-term decline in the growth of remaining trees, which is called “thinning shock,” has also been widely reported (Harrington and Reukema, 1983; Dore et al., 2012).

Owing to the recent increase in drought duration and intensity due to changes in precipitation patterns (Trenberth, 2011), attention should

\* Corresponding author at: Department of Forest Sciences, Seoul National University, Seoul, Republic of Korea.  
E-mail address: [cameroncrazies@snu.ac.kr](mailto:cameroncrazies@snu.ac.kr) (H. Seok Kim).

be paid to thinning as a drought mitigation procedure. Thinning enhances drought resistance by reducing water stress due to decrement of interception loss and stand transpiration (Gebhardt et al., 2014). Trees in thinned stands show sustained growth under drought conditions and high resilience to severe drought (Kohler et al., 2010). However, this enhancement under drought conditions reduces with stand age; in fact, older stands that are thinned become more prone to drought (D'Amato et al., 2013). In *Pinus* species, thinning promotes not only basal area increment and water use efficiency, but also increased light interception and nutrient availability (Warren et al., 2001). Similar to other species, thinning improved drought resistance and recovery in *Pinus* species, but these were short-term effects (Sohn et al., 2016). These positive effects could be offset by high vulnerability to insect damage and mortality which might be caused by trunk or root damage during thinning procedure (Zhang et al., 2016).

In conclusion, thinning effects can differ depending on the site water availability and capacity of tree species to adjust to sudden changes in environmental conditions. In addition, the magnitude of thinning effects depends on but is not always proportional to the degree of thinning intensity. Several studies have reported that light thinning stimulates individual tree growth, while heavy thinning hampers growth (Harrington and Reukema, 1983; Laurent et al., 2003; Jimenez et al., 2011). Other studies have reported that the thinning effects increased positively with thinning intensity (Makinen and Isomaki, 2004b; Zhang et al., 2006). However, the enhancement of growth with increase in thinning intensity appeared only in young stands, and this trend was reversed in old stands (Juodvalkis et al., 2005). In addition, the impact of thinning intensities is affected by site location, and it is more intense at windward sites than at leeward sites (Pérez-de-Lis et al., 2011).

Thus, the objective of the present study was to quantify the effect of thinning intensities on water use and growth of individual trees, which could help providing guidelines for the appropriate thinning intensity in mature Korean pine plantations.

## 2. Materials and methods

### 2.1. Study site

The study was conducted at Mt. Taehwa in central Korea (37.18N, 127.18E, 190 m a.s.l.). The majority of forest is composed of *Quercus* species (58.8%), with Korean pine (*Pinus koraiensis*) occupying 20.1% (165 ha) of the area. Our 0.5 ha study plot was established within a 16 ha portion of a 50-year-old Korean pine plantation. The soil is loam and the mother rock is granite mixed with gneiss. The area is undulating, with a 9–10 m difference in elevation, and two streams, in which water flows only after heavy rainfall events, are located in the northern and southern parts of the experimental plot. The 30-year mean annual temperature at the nearest weather station is  $11.4 \pm 0.6$  °C, and the mean annual precipitation is  $1355.8 \pm 300.2$  mm.

The stand is composed of single overstorey species, Korean pine, and some understorey species such as *Toxicodendron trichocarpum* (Miq.) O. Kuntze, *Rhododendron yedoense*, *Magnolia kobus* DC., and *Zanthoxylum schinifolium* Siebold et Zucc. These understorey species occupied less than 10% of the total basal area (BA) and were not included in the stand transpiration calculation.

### 2.2. Experimental design

In 2011, coordinates were assigned to all trees with a diameter at breast height (DBH) > 2 cm throughout the plot, and their diameters were measured. The coordinates and DBH were used to compute the competition indices (Hegyi, 1974). Thinning was conducted in March 2012. The two thinning intensities were selected on the basis of target stand densities, which were 400, 320, and 240 trees per hectare in the control (0.125 ha), light-thinning (LT, 0.188 ha), and heavy-thinning

**Table 1**

Stand characteristics of control (Con), light-thinning (LT) and heavy-thinning (HT) plots before and after thinning. Stand density (SD) and basal area (BA) are expressed per hectare, diameter at breast height (DBH) and competition index (CI) are stand arithmetic means. Leaf area index (LAI) is sum of individual tree's leaf area estimated by allometric equation and specific leaf area within each plot.

|           | SD (trees<br>ha <sup>-1</sup> ) | BA (m <sup>2</sup><br>ha <sup>-1</sup> ) | DBH (cm)   | LAI (m <sup>2</sup><br>m <sup>-2</sup> ) | CI        |
|-----------|---------------------------------|--|------------|--|-----------|
| Con       | 400                             | 27.4                                     | 29.1 ± 5.1 | 4.15                                     | 2.0 ± 0.5 |
| LT Before | 458                             | 30.2                                     | 28.4 ± 5.8 | 3.76                                     | 2.0 ± 0.6 |
| After     | 333                             | 25.1                                     | 30.9 ± 4.2 | 2.95                                     | 1.6 ± 0.5 |
| HT Before | 408                             | 28.6                                     | 29.4 ± 5.0 | 3.47                                     | 1.8 ± 0.6 |
| After     | 258                             | 20.0                                     | 31.2 ± 3.9 | 2.30                                     | 1.2 ± 0.4 |

(HT, 0.188 ha) plots, respectively. To minimize the interference due to thinning treatments, we maintained a 5 m buffer zone between the treatments. The trees were cut using chainsaws and removed by hand to minimize disturbances such as soil compaction and physical damage to the remaining trees. Trees were selected for thinning based on three criteria: small DBH, short distance to neighboring trees, and previous treatment history (e.g., pruning). Thinning resulted in an increase in mean DBH of a stand. It removed ca. 27 and 37% of the stand density and ca. 17 and 30% of the basal area from LT and HT plot, respectively (Table 1).

### 2.3. Data collection

Sap flux density ( $J_s$ ) was measured by the Granier's type heat-dissipation probe method (Granier, 1987). This method employs an upper heated probe that is supplied constant power (0.2 W) and a lower reference probe. These two probes were installed at breast height vertically, 10–15 cm apart to avoid thermal interference. Each probe consisted of a needle 20 mm long with a diameter of 1.6 mm, and the temperature was measured at the middle of the needle by a T-type thermocouple. The temperature difference between the two probes was measured at 30-s intervals, and the average value over 30 min was recorded by a data logger (CR-1000, Campbell Scientific, USA).

The sensors were installed on 22 of 32 trees in control plot, 36 of 40 trees in LT plot, and 26 of 31 trees in HT plot in March 2012. The trees were chosen to avoid edge effects, and the probes were installed on the outer part (0–20 mm) of the sapwood on the north side of each tree. To measure the radial and circumferential variation in  $J_s$ , additional probes were installed on the middle (20–40 mm) and inner parts (40–60 mm) of the sapwood of five trees, and at six directions (0, 60, 120, 180, 240, and 300°) on another three trees. The mid- and inner parts of the sapwood area transport 13.7 and 6.9% of the total sap, and sap flow across sapwood area deeper than 60 mm was assumed to be negligible.  $J_s$  of the northern side showed little difference with azimuth-averaged  $J_s$  (Moon et al., 2015; Moon et al., 2016); therefore, circumferential variation in  $J_s$  was not considered. The trees were considered to have the same radial variations. Tree water use (TWU) was scaled up by multiplying the measured  $J_s$  and relevant sapwood area (Eq. (2)), as follows:

$$TWU(\text{kg d}^{-1}) = \sum_{i=1}^3 J_{si} A_{Si} \quad (1)$$

where  $J_{si}$  = the daily mean sap flux density of outer ( $i = 1$ ), mid ( $i = 2$ ), or inner ( $i = 3$ ) sapwood ( $\text{kg m}^{-2} \text{d}^{-1}$ ) and  $A_{Si}$  = relevant sapwood area ( $\text{m}^2$ ).

Meteorological data were measured from a 25-m high walk-up tower located 100 m from the treatment plots. Photosynthetic active radiation ( $Q$ ) was measured by quantum sensor (LI-190, LI-Cor). Air temperature ( $T_a$ ) and relative humidity (RH) were measured by HMP-45C (Campbell Scientific), and precipitation was measured by rain gauge (03319-00, Cole-Parmer) at the top of the tower. Vapor pressure

deficit ( $D$ ) was calculated from  $T_a$  and RH. Data gap due to sensor damage or power failure in meteorological data was filled using data from a 50-m flux tower that is 50 m from the walk-up tower. Volumetric soil water content ( $\theta$ ) of upper 30 cm of soil layer was measured by TDR sensors (CS-616, Campbell Scientific, USA) placed at three positions on each treatment plot in January 2012 and additional 16 sensors installed in May 2014. All the environmental variables were measured at 30 s intervals, and the average values over 30 min of data were stored in a data logger (CR-1000, Campbell Scientific, USA).

Diameter growth was measured with a hand-made dendrometer band on nearly all the trees on every plot. The recording was manually conducted 7–13 times per year. Annual relative growth rate (RGR) of each tree was calculated by following equation:

$$\text{RGR}_i = \frac{\text{diameter growth}_i}{\text{DBH}_i} \quad (2)$$

where  $\text{DBH}_i$  = diameter at breast height of tree  $i$ .

These diameter growth values were used to calculate the single tree biomass gain by using the allometric equation (Ryu et al., 2014), which showed consistency with other reported allometric equations on same species (Son et al., 2001; Li et al., 2011).

$$\text{Above ground biomass (kg)} = 0.2849\text{DBH}^{2.0553} \quad (3)$$

The annual aboveground net primary productivity of each tree ( $\text{ANPP}_{\text{Tree}}$ ) was calculated by difference in biomass at the beginning and end of each year. Tree water use efficiency ( $\text{WUE}_{\text{Tree}}$ ) is the ratio between annual  $\text{ANPP}_{\text{Tree}}$  and TWU.

#### 2.4. Gap filling

Major data gaps occurred from June 2012 to July 2012 because of a power failure after a typhoon. At other times during the study period, minor gaps occurred due to sensor damage. Data gaps from individual trees in  $J_s$  were filled using the linear relationship with other trees in the same plot. Data from 10 days before and 10 days after the gap were used, and trees that showed the highest correlation with the data-gap tree were selected as reference trees. The average correlation coefficient was 0.98 and the minimum coefficient was 0.91. Major gaps for which no reference sap flux data were available were filled using the linear relationship between  $J_s$  and combination of environmental variables like  $Q$ ,  $T_a$ , and  $D$ . Similar to gap filling of a single-tree gap, an empirical correlation was induced using data from 10 days before and 10 days after the data gaps. The average correlation coefficient was 0.78 and the minimum coefficient was 0.64. These gap-filled data were not used in the  $J_s$  comparison, but only in total tree water use estimation.

#### 2.5. Environmental variables

Environmental conditions varied considerably over the 4-year study period.  $T_a$  was similar during the study period; however, seasonal trends differed between the first two years (2012, 2013) and last two years (2014, 2015).  $T_a$  was higher during summer in the first two years than in the last two years, and it was higher in the winter during the last two years than in the first two years (Fig. 1a). Annual mean  $Q$  followed the annual rainfall frequency pattern and was highest in 2012 and lowest in 2014 (Fig. 1b). Notably, the mean growing season  $D$  (March–October) was similar between wet years, but showed a dramatic difference between dry years (Fig. 1c). In 2014, it was 14.0% lower than the 4-year-mean  $D$ , while in 2015, it was 16.0% higher.

The first two years were generally wet and the last two years were dry. The total annual precipitation was 1685.6 mm in 2012, 1366.9 mm in 2013, 791.5 mm in 2014, and 939.4 mm in 2015 (Fig. 1d). In addition, the precipitation distribution pattern was different for wet years (2012, 2013). The rainfall frequency was lowest in 2012 and rainfall was mainly due to two events (summer monsoon and typhoon). There was severe soil drying in spring 2012. The rainfall frequency was

highest in 2013. The two dry years (2014, 2015) showed similar precipitation patterns with high rainfall frequency during the growing season, but the spring drought lasted longer in 2014 than in 2015.

These conditions resulted in a distinct combination of environmental variables during the measurement years. In general, 2012 was a wet year with a strong spring drought, 2013 was a wet year with low light, 2014 was a dry year with a humid atmospheric condition, and 2015 was a dry year with a dry atmospheric condition (Fig. 1a–d).

#### 2.6. Statistical analysis

To evaluate the statistical difference in  $J_s$  among plots of different thinning intensities, average daily  $J_s$  was used. Diameter growth, RGR,  $\text{ANPP}_{\text{Tree}}$ , and  $\text{WUE}_{\text{Tree}}$  of each year were also compared using ANOVA. The normality of  $J_s$  and diameter growth data of each plot was assessed by Shapiro-Wilks test. The slope coefficients of linear regression between  $J_s$  of control and thinned plots were compared. The sensitivity of environmental variables on  $J_s$  and growth was also tested. The difference between thinning treatments during the entire measurement period was statistically evaluated by repeated measures ANOVA with Tukey's LSD post-hoc test. All analyses were conducted in R (R Core Team, 2016).

### 3. Results

#### 3.1. Effects of thinning intensities on sap flux density and tree water use

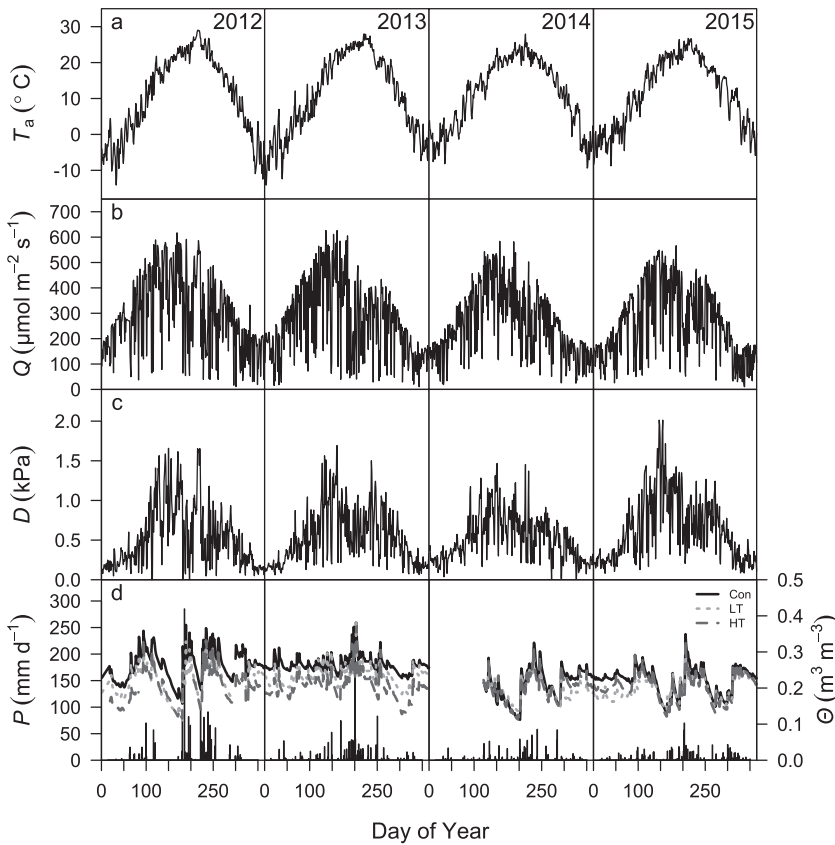
The mean  $J_s$  of thinned plot significantly increased soon after the thinning practice in March 2012; however, the duration of thinning effects on  $J_s$  differed according to thinning intensity (Fig. 2). The increment in  $J_s$  was continuously enhanced or sustained in the HT plot (+8.0% in 2012, +20.2% in 2013, 40.1% in 2014, and 17.8% in 2015, maximum  $p < .001$ ) but weakened with time in the LT plot (+11.1% in 2012, +8.9% in 2013, +9.5% in 2014, and -1.3% in 2015, maximum  $p < .001$ ).

Although the mean plot  $J_s$  increased significantly, TWU was not significantly increased in the first two years owing to large tree-to-tree variations (Fig. 3 and Table 2). In 2012, mean TWU was  $10.8 \pm 0.5$ ,  $12.0 \pm 0.5$ , and  $12.1 \pm 0.5$  kg in control, LT, and HT plots, respectively. TWU in 2013 was similar to that in 2012, but tree-to-tree variations within the same treatment were slightly increased. The mean TWU was  $10.6 \pm 0.6$ ,  $11.7 \pm 0.6$ , and  $12.4 \pm 0.7$  kg in the control, LT, and HT plots, respectively. In 2014, when the total precipitation was lowest, trees in the HT plot ( $16.5 \pm 1.6$  kg, maximum  $p < .01$ ) used more water than those in the control ( $10.1 \pm 1.0$  kg) and LT ( $11.7 \pm 0.8$  kg) plots. This increase in TWU persisted in 2015 also, and TWU in HT plot ( $18.6 \pm 0.8$  kg, maximum  $p < .05$ ) was higher than that in the control ( $15.3 \pm 0.8$  kg) and LT ( $14.4 \pm 0.7$  kg) plots.

The interannual variations in TWU reflected the variations in environmental conditions, but they differed according to thinning intensity. TWU in the control and LT plots showed similar interannual variations, while the HT plot showed a continuous increase in TWU for 4 years. Although precipitation declined by 19% between 2012 and 2013, annual TWU did not reduce in all treatment plots. Despite the huge decrease in annual precipitation, TWU decreased in the control and LT plots in 2014 compared to that in the previous year. In contrast, TWU in the HT plot increased compare to that in the previous year (33.1%). TWU in all plots increased in 2015 compared to that in 2014, reflecting the increase in annual precipitation and atmospheric dryness.

#### 3.2. Effects of thinning intensities on diameter growth

Heavy thinning stimulated individual tree diameter growth and RGR, and this growth enhancement was apparent from the second year after thinning (Fig. 4 and Table 2). The thinning-induced growth enhancement in the HT plot intensified with time ( $+27.3 \pm 65.0\%$  in



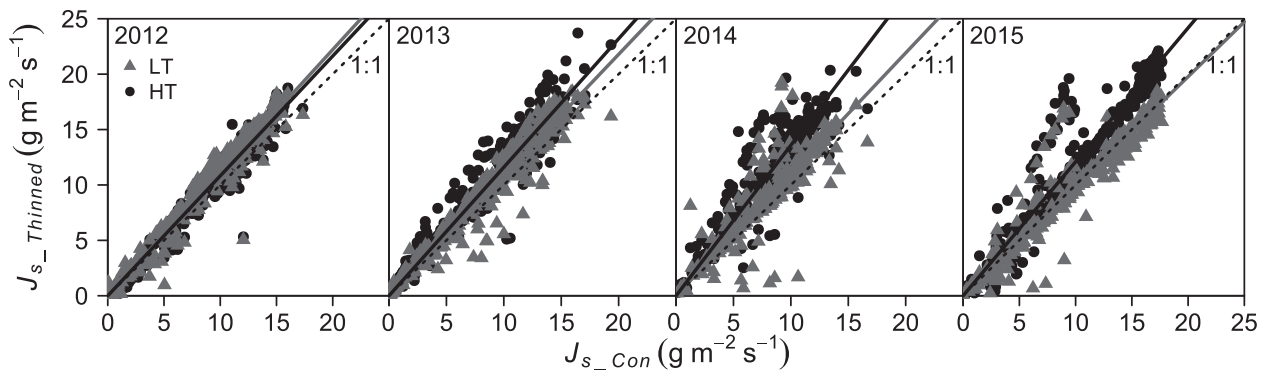
**Fig. 1.** Meteorological conditions from 2012 to 2015. (a) Daily mean air temperature ( $T_a$ ), (b) daily mean photosynthetically active radiation ( $Q$ ), (c) daily mean vapor pressure deficit ( $D$ ), and (d) daily mean volumetric soil water content ( $\theta$ ) at 0–30 cm in the control (black), light-thinning (light-grey), and heavy-thinning (dark-grey) plots, along with daily total precipitation ( $P$ ). The soil water content was measured at three points per plot until April 2014, after which soil water content was measured at six points in the control plot and at nine points in each thinned plot.

2012,  $+48.7 \pm 46.3\%$  in 2013,  $+51.0 \pm 43.9\%$  in 2014, and  $+61.4 \pm 46.5\%$  in 2015). Tree growth in LT plot was not significantly different from that in the control plot for the entire study period ( $+15.8 \pm 55.6\%$  in 2012,  $+14.3 \pm 54.0\%$  in 2013,  $+11.6 \pm 53.8\%$  in 2014, and  $+13.5 \pm 50.4\%$  in 2015). In 2012, the seasonal growth pattern differed among the plots. While trees in the control and LT plots showed a similar growth pattern, trees in the HT plot showed delayed growth initiation and rapid catch-up after growth initiation. The differences in growth pattern disappeared in 2013, and the HT plot showed a consistently higher growth rate throughout the growing season.

The interannual variations in growth were similar regardless of the difference in thinning intensity; however, the magnitude of variation was highest in the HT plot. This interannual variation in growth was caused by differences in environmental conditions, especially in water

availability during the growth onset period. During the years with low annual growth (2012 and 2014), there was severe drought in the spring. In addition, a similar overall growth rate was observed in the control and LT plots despite the huge differences in total annual precipitation and  $Q$ . Meanwhile, trees in the HT plot showed a higher growth rate in 2014 than in 2012. There was no spring drought or only a short one during the years with high growth rate (2013 and 2015). As in the low-growth years, trees in the control and LT plot showed similar growth rates in 2013 and 2015 and trees in the HT plot showed higher growth in 2015 than in 2013 (Fig. 4).

These growth increment caused the higher  $ANPP_{Tree}$  in HT plot from the second year after thinning (Fig. 5). The trees in LT plot showed consistently statically same but slightly higher  $ANPP_{Tree}$  than the control plot for the entire study period (minimum  $p = .247$ ). The thinning effects in tree growth sustained during the entire study periods, and



**Fig. 2.** Relationship between daily mean sap flux density ( $J_s$ ) at 0–2 cm of sapwood area in the control plot, light-thinning (LT; grey triangle), and heavy-thinning (HT; black circle) plots from 2012 to 2015. Colored line indicates linear regression line of control and thinned plots, fit with a zero intercept. (LT,  $y = 1.111x$ ,  $r^2 = 0.99$ ,  $P < .001$  in 2012,  $y = 1.089x$ ,  $r^2 = 0.98$ ,  $P < .001$  in 2013,  $y = 1.095x$ ,  $r^2 = 0.96$ ,  $P < .001$  in 2014,  $y = 0.987x$ ,  $r^2 = 0.98$ ,  $P < .001$  in 2015 and HT,  $y = 1.080x$ ,  $r^2 = 0.99$ ,  $P < .001$  in 2012,  $y = 1.202x$ ,  $r^2 = 0.98$ ,  $P < .001$  in 2013,  $y = 1.406x$ ,  $r^2 = 0.97$ ,  $P < .001$  in 2014,  $y = 1.213x$ ,  $r^2 = 0.99$ ,  $P < .001$  in 2015).

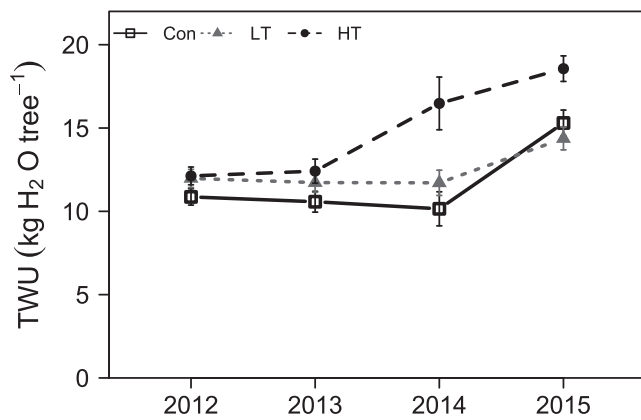


Fig. 3. Mean daily tree water use of control (Con; open square), light-thinning (LT; closed grey triangle), and heavy-thinning (HT; closed circle) plots from 2012 to 2015. The vertical bars represent the standard error (SE).

Table 2

Yearly mean ± 1 SE of sap flux density ( $J_s$ ), Tree water use (TWU), diameter growth, Tree level aboveground net primary productivity ( $ANPP_{Tree}$ ), and tree-level water use efficiency ( $WUE_{Tree}$ ) for control (Con), light-thinning (LT) and heavy-thinning (HT) plots.

| Variable  | Year  | Con                      | LT                       | HT                       |
|---|-------|--------------------------|--------------------------|--------------------------|
| $J_s$ (g m <sup>-2</sup> s <sup>-1</sup> )            | 2012  | 8.4 ± 0.4 <sup>a</sup>   | 9.5 ± 0.4 <sup>a</sup>   | 9.3 ± 0.4 <sup>a</sup>   |
|   | 2013  | 8.5 ± 0.5 <sup>a</sup>   | 9.5 ± 0.5 <sup>a</sup>   | 9.9 ± 0.6 <sup>a</sup>   |
|   | 2014  | 8.3 ± 0.8 <sup>a</sup>   | 9.6 ± 0.6 <sup>a</sup>   | 13.4 ± 1.3 <sup>b</sup>  |
|   | 2015  | 11.4 ± 0.6 <sup>a</sup>  | 10.7 ± 0.5 <sup>a</sup>  | 13.7 ± 0.6 <sup>b</sup>  |
|   | Whole | 9.3 ± 0.4 <sup>a</sup>   | 9.9 ± 0.3 <sup>a</sup>   | 11.6 ± 0.4 <sup>b</sup>  |
| TWU (kg d <sup>-1</sup> Tree <sup>-1</sup> )          | 2012  | 10.8 ± 0.5 <sup>a</sup>  | 12.0 ± 0.5 <sup>a</sup>  | 12.1 ± 0.5 <sup>a</sup>  |
|   | 2013  | 10.6 ± 0.6 <sup>a</sup>  | 11.7 ± 0.6 <sup>a</sup>  | 12.4 ± 0.7 <sup>a</sup>  |
|   | 2014  | 10.1 ± 1.0 <sup>a</sup>  | 11.7 ± 0.8 <sup>a</sup>  | 16.5 ± 1.6 <sup>b</sup>  |
|   | 2015  | 15.3 ± 0.8 <sup>a</sup>  | 14.4 ± 0.7 <sup>a</sup>  | 18.6 ± 0.8 <sup>b</sup>  |
|   | Whole | 11.8 ± 0.5 <sup>a</sup>  | 12.5 ± 0.4 <sup>a</sup>  | 14.9 ± 0.5 <sup>b</sup>  |
| Diameter Growth (mm y <sup>-1</sup> )                 | 2012  | 2.8 ± 0.2 <sup>a</sup>   | 3.2 ± 0.3 <sup>a</sup>   | 3.6 ± 0.3 <sup>a</sup>   |
|   | 2013  | 3.6 ± 0.3 <sup>a</sup>   | 4.1 ± 0.3 <sup>a</sup>   | 5.4 ± 0.3 <sup>b</sup>   |
|   | 2014  | 2.9 ± 0.2 <sup>a</sup>   | 3.2 ± 0.2 <sup>a</sup>   | 4.3 ± 0.2 <sup>b</sup>   |
|   | 2015  | 3.7 ± 0.3 <sup>a</sup>   | 4.2 ± 0.3 <sup>a</sup>   | 5.9 ± 0.3 <sup>b</sup>   |
|   | Whole | 3.2 ± 0.3 <sup>a</sup>   | 3.7 ± 0.2 <sup>a</sup>   | 4.8 ± 0.3 <sup>b</sup>   |
| $ANPP_{Tree}$ (kg C Tree <sup>-1</sup> )              | 2012  | 3.0 ± 0.3 <sup>a</sup>   | 3.7 ± 0.3 <sup>a</sup>   | 3.9 ± 0.4 <sup>a</sup>   |
|   | 2013  | 3.8 ± 0.4 <sup>a</sup>   | 4.7 ± 0.4 <sup>a</sup>   | 6.0 ± 0.3 <sup>b</sup>   |
|   | 2014  | 3.1 ± 0.3 <sup>a</sup>   | 3.7 ± 0.4 <sup>a</sup>   | 4.9 ± 0.2 <sup>b</sup>   |
|   | 2015  | 4.0 ± 0.4 <sup>a</sup>   | 4.9 ± 0.4 <sup>a</sup>   | 6.8 ± 0.3 <sup>b</sup>   |
|   | Whole | 3.5 ± 0.4 <sup>a</sup>   | 4.3 ± 0.3 <sup>a</sup>   | 5.4 ± 0.4 <sup>b</sup>   |
| $WUE_{Tree}$ (g C kg H <sub>2</sub> O <sup>-1</sup> ) | 2012  | 0.78 ± 0.08 <sup>a</sup> | 0.85 ± 0.05 <sup>a</sup> | 0.96 ± 0.09 <sup>a</sup> |
|   | 2013  | 1.06 ± 0.13 <sup>a</sup> | 1.13 ± 0.10 <sup>a</sup> | 1.49 ± 0.14 <sup>b</sup> |
|   | 2014  | 1.03 ± 0.14 <sup>a</sup> | 1.01 ± 0.12 <sup>a</sup> | 1.05 ± 0.12 <sup>a</sup> |
|   | 2015  | 0.72 ± 0.07 <sup>a</sup> | 1.04 ± 0.11 <sup>a</sup> | 1.08 ± 0.08 <sup>b</sup> |
|   | Whole | 0.89 ± 0.09 <sup>a</sup> | 1.00 ± 0.07 <sup>a</sup> | 1.13 ± 0.09 <sup>a</sup> |

Different letters next to numbers represent significantly different means ( $p < .05$ , Tukey's LSD post hoc tests). The difference in each year was tested by simple ANOVA, and the difference in whole periods was tested by repeated measure ANOVA.

caused a huge increment in  $ANPP_{Tree}$  from  $3.9 ± 0.4$  kg C in 2012 to  $6.8 ± 0.3$  kg C in 2015.

In addition, the relationship between DBH and annual growth rate showed a huge difference between the two thinning intensities (Fig. 6a). In the LT plot, large trees grew significantly more than small trees, but the opposite trend was seen in the HT plot. These size-growth relationships were observed during the entire 4-year study period. Meanwhile, trees in the control plot showed no significant relationship between tree size and growth rates. Competition intensity, which was estimated by distance and size differences between neighboring trees, was negatively correlated with tree growth rate in the LT plot, whereas there was a significant positive correlation in the HT plot and no significant correlation in the control plot (Fig. 6b). In the HT plot, reduction of competition intensity by thinning was positively correlated

with tree growth (Fig. 6c).

### 3.3. Effects of thinning intensities on tree water use efficiency (WUE)

Owing to the insignificant effects of LT as well as the synchronized changes in TWU and tree growth in HT,  $WUE_{Tree}$  was not affected by thinning (Table 2). The only significant difference appeared between control and HT plots in high growth years (2013 and 2015,  $p < .05$ ). In 2012,  $WUE_{Tree}$  values were  $0.78 ± 0.08$ ,  $0.85 ± 0.05$ , and  $0.96 ± 0.09$  g C kg H<sub>2</sub>O<sup>-1</sup> for the control, LT, and HT plots, respectively. In 2013, the  $WUE_{Tree}$  values were  $1.06 ± 0.13$ ,  $1.13 ± 0.10$ , and  $1.49 ± 0.14$  g C kg H<sub>2</sub>O<sup>-1</sup> for the control, LT, and HT plots, respectively. In all plots,  $WUE_{Tree}$  was higher than in the previous year (2012), and the HT plot showed a greater increase in  $WUE_{Tree}$  than the control and LT plots. In 2014,  $WUE_{Tree}$  was reduced in all plots owing to the drought. The  $WUE_{Tree}$  values were  $1.03 ± 0.14$ ,  $1.01 ± 0.12$ , and  $1.05 ± 0.12$  g C kg H<sub>2</sub>O<sup>-1</sup> for the control, LT, and HT plots, respectively. In 2015,  $WUE_{Tree}$  of the thinned plots recovered with increase in precipitation, whereas it was low in the control plot. The  $WUE_{Tree}$  values were  $0.72 ± 0.07$ ,  $1.04 ± 0.11$ , and  $1.08 ± 0.08$  g C kg H<sub>2</sub>O<sup>-1</sup> for the control, LT, and HT plots, respectively.  $WUE_{Tree}$  showed different interannual variations after thinning treatment. The control plot showed a decrease in  $WUE_{Tree}$  after drought, but  $WUE_{Tree}$  recovered in the thinned plots after the drought year. The magnitude of WUE was higher in the HT than in the LT plot (Fig. 7).

## 4. Discussion

A few studies have quantified the effects of thinning on sap flux density and growth productivity in mature forests (Breda and Granier, 1996; McJannet and Vertessy, 2001); however, studies focused on the effects of thinning intensities are scarce (Makinen and Isomaki, 2004b). In this study, we provide evidence that thinning treatment has considerable effects on water use and growth of trees in mature pine forest and these thinning effects are controlled by thinning intensity.

### 4.1. Effects of thinning intensities on tree water use

After thinning treatment,  $J_s$  initially increased in trees at both thinning intensities. The initial increment of  $J_s$  is largely due to changes in the light environment, because thinning has little effect on morphological or anatomical adaptations to the changed light environment in such a short period of time (Gebauer et al., 2013). Thinning created more gaps, allowing remaining trees to receive more light, especially on the lower and shaded leaves. This improved light environment induced more leaf-level transpiration as long as soil water was not limited. This initial increase in  $J_s$  was not shown in other studies that reported short-term post-thinning stress in transpiration (Reid et al., 2006; Jimenez et al., 2008; Lagergren et al., 2008). Stress induced by thinning might be caused by light stress on previously shaded leaves (Harrington and Reukema, 1983), mechanical damage to shoots or roots during the thinning procedure, or additional freezing damage early in the growing season due to greater exposure of the canopy to wind. In the present study, the average  $J_s$  increase of LT plot in the first year was higher (ca. 11.1%) than that of HT plot (ca. 8.0%). This finding might indicate that there was higher light stress in the HT plot than in the LT plot.

This initial increment of  $J_s$  increased consistently during the four years in the HT plot, whereas enhancement of  $J_s$  declined with time in the LT plot and showed no difference with the  $J_s$  in the control plot in 2015. The extent of these enhancements depends on thinning type and intensity, site-specific climatic conditions, species and age of remaining trees, and disturbance regime. Especially, it depends primarily on two factors (1) increased water flow through pre-existing sapwood area and (2) increased hydraulic conductivity of newly formed sapwood (Deckmyn et al., 2006). The increased water flow is promoted by the increased water demand of the new conditions such as excess light and

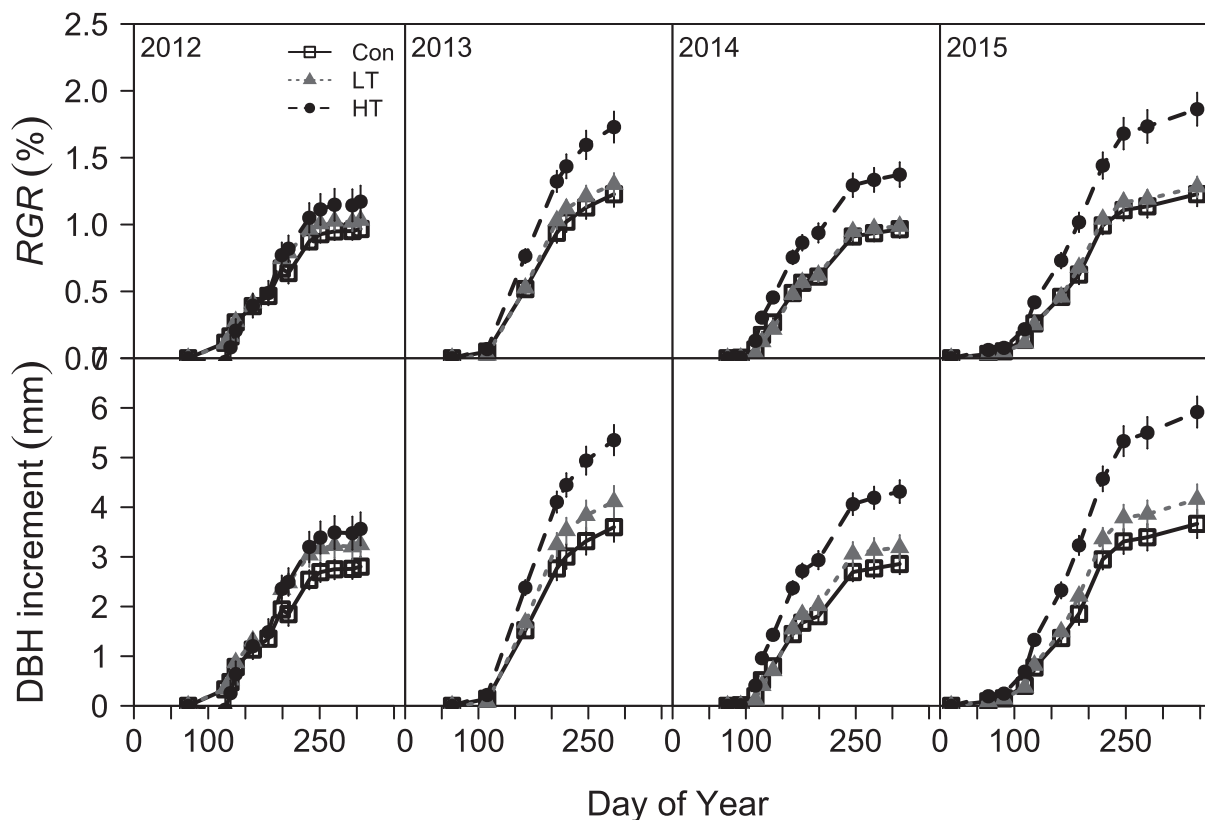


Fig. 4. Annual patterns of relative growth rate (RGR; top) and absolute diameter growth (bottom) in control (Con; open square), light-thinning (LT; grey triangle), and heavy-thinning (HT; closed circle) plots. The vertical bars represent the standard error (SE).

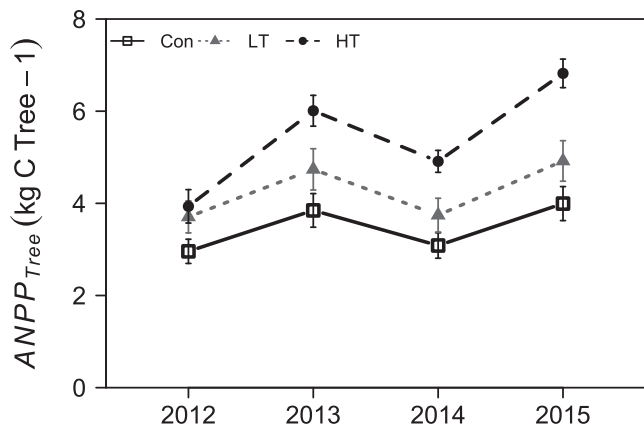


Fig. 5. Tree-level aboveground net primary production ( $ANPP_{Tree}$ ) of control (Con; open square), light-thinning (LT; grey triangle), and heavy-thinning (HT; closed circle) plots for 4 years. The vertical bars represent the standard error (SE).

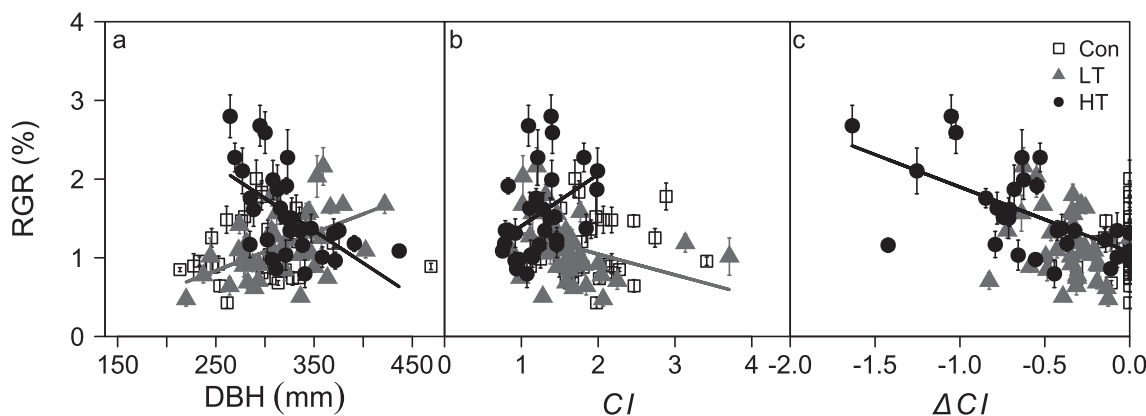
soil water, but is constrained by the limited water transport capacity of the existing sapwood. The increased hydraulic conductivity is enabled by the increased tracheid size (Gebauer et al., 2013), formation of new sapwood area (Nadezhkina et al., 2010), or a fertilization effect (Gough et al., 2004).

Although the thinned plots showed increased  $J_s$  soon after thinning, high tree-to-tree variation within the plots caused insignificant differences in TWU for the first two years. Owing to both sap flux density increment (Fig. 2) and diameter growth increment (Fig. 4), TWU increased significantly in HT plot in the third year after thinning (Fig. 3). Similar results have been reported in a wide range of tree species and locations (Medhurst et al., 2002; Gebhardt et al., 2014).

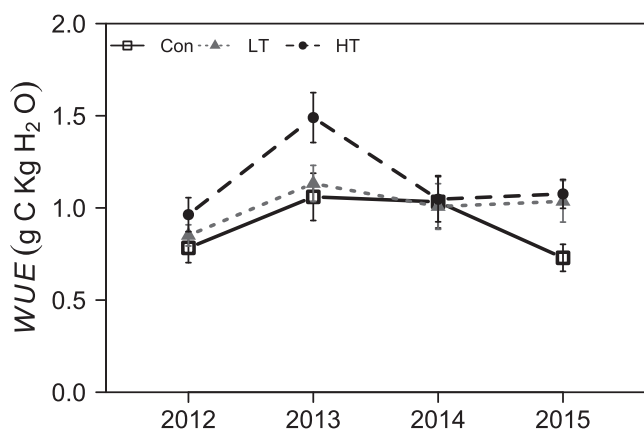
#### 4.2. Thinning-induced growth enhancement

In general, water and light are the major limiting factors of tree growth. Water stress is especially notable in the Asian monsoon climate, where most of the annual precipitation occurs during the summer season and there are periodic droughts in the spring and fall. Drought in the spring and fall might disturb phenological development (Borchert et al., 2002), with critical effects on productivity (Richardson et al., 2010). The diameter growth of *Pinus* species in particular is limited by spring drought (Oberhuber et al., 1998; Rigling et al., 2002). Our results showed that reduction of stand density by thinning enhanced the growth of the remaining trees in thinned plot by improving either or both of the limiting conditions (water and light; Fig. 4). Thinning promotes photosynthetic capacity by increasing the leaf water potential (Donner and Running, 1986; Gauthier and Jacobs, 2009).

The growth increment of the remaining trees was more pronounced in the HT plot (Fig. 4), in accordance with previous results from studies on various tree species (Makinen and Isomaki, 2004a, b; Martin-Benito et al., 2010). The insignificant growth increment in the LT plot might be due to the small removal of the basal area, which was not enough to cause considerable changes (Misson et al., 2005). In addition, the growth rate of trees may increase with tree size, because large trees can support more leaves, which increases the whole-tree photosynthetic rate (Enquist, 2002). However, growth rates are affected not only by tree size but also by competition for light and nutrients as well as environmental conditions. Competition for light is more important for small trees, whereas competition for nutrients affects all trees, regardless of their size (Coomes and Allen, 2007). In addition, sensitivity to competition shows a high correlation with site water availability (Gomez-Aparicio et al., 2011). In the LT plot, thinning did not increase the site water availability because TWU was similar to that in the control plot, and the reduced competition for light did not boost the growth of small trees. Meanwhile, in the HT plot, thinning improved



**Fig. 6.** Relationship between (a) diameter at breast height (DBH) and 4-year average relative growth rates (RGR), (b) competition index (*CI*) and RGR, and (c) changes in competition index ( $\Delta CI$ ) and RGR in control (Con; open square), light-thinning (LT; grey triangle), and heavy-thinning (HT; closed triangle) plots. Vertical and horizontal bars represent the standard error (SE), and colored lines indicate significant regression between RGR and (a) DBH (LT,  $y = 0.005x - 0.362, r^2 = 0.25, P < .001$  and HT,  $y = -0.008x + 4.222, r^2 = 0.29, P = .001$ ), (b) *CI* (LT,  $y = -0.264x + 1.573, r^2 = 0.12, P = .033$  and HT,  $y = 0.657x + 0.745, r^2 = 0.17, P = .024$ ), and (c)  $\Delta CI$  (HT,  $y = -0.8251x + 1.074, r^2 = 0.38, P < .001$ ).



**Fig. 7.** Tree water use efficiency ( $WUE_{Tree}$ ) of control (Con; open square), light-thinning (LT; grey triangle), and heavy-thinning (HT; closed circle) plots for 4 years. The vertical bars represent the standard error (SE).

the site water availability as indicated by the huge increment in TWU (Fig. 3), which diminished the sensitivity of the trees to competition intensity. Therefore, small trees were benefited the most by thinning and showed higher growth rates than large trees.

**4.3. Effects of thinning intensities on tree water use efficiency**

WUE, which is the ratio of the amount of biomass gain per unit water loss by transpiration, was not increased by thinning treatment except in high growth years (Fig. 7 and Table 2). As mentioned, thinning reduces competition for water, light, and nutrients. The relative improvement of water and light conditions caused by thinning determines the effects of thinning on WUE. In general, thinning enhances WUE in a light-limited environment (Martin-Benito et al., 2010; Brooks and Mitchell, 2011) rather than in a water-limited environment (Moreno-Gutierrez et al., 2011; Giuggiola et al., 2015). Thinning increases light interception by individual trees and concentration of nutrients in the foliage, resulting in efficient carbon assimilation. High density stands showed less WUE than the low-density stands especially in shade-intolerant pine forests (Warren et al., 2001).

WUE is controlled more by carbon gain than by water use in mesic areas (Yang et al., 2016). Although there were huge differences in annual precipitation among the study years, soil water status reached the field capacity during summer precipitation in all the years, and soil water content was maintained above 15% during most of the growing periods (Fig. 1). Thus, TWU was hardly affected by fluctuation in annual precipitation (Fig. 3). In the years with low stand WUE (2012 and

2014), severe spring droughts (Fig. 1) hampered tree growth (Huang and Zhang, 2007).

In 2014, a notable combination of environmental conditions was observed: humid atmosphere and drought-affected soil (Fig. 1c and d).  $WUE_{Tree}$  is controlled by both *D* and  $\theta$ , with *D* dominating (Yang et al., 2010; Novick et al., 2016).  $\theta$  and WUE may have an opposite relationship for low and high *D* conditions due to failure in stomatal optimization. Under low *D* conditions, tree water use could be decoupled from  $\theta$  owing to loose stomatal regulation. Unregulated stomata resulted in similarly low  $WUE_{Tree}$  in all plots. In addition, the leaves that developed during previous humid conditions may fail to adjust their physiological characteristics to dry conditions completely. The huge reduction of  $WUE_{Tree}$  in HT plot was mainly caused by the improved TWU (Fig. 3).

$WUE_{Tree}$  increment of thinned plot in 2015 could be explained partly by “memory effects,” which are effects of previous drought on current productivity and water use (Zhang et al., 2014; Yang et al., 2016). Under drought conditions, trees increased their belowground allocation to increase their water uptake capacity. Evergreen conifer trees in particular tend to allocate more biomass to the drought enduring organs (Markesteyn and Poorter, 2009). The combination of improved soil water condition, high *D*, and previous investment to adapt to drought conditions caused a significant increase in  $WUE_{Tree}$  in 2015. Meanwhile,  $WUE_{Tree}$  was reduced in the control plot. Although both TWU and  $ANPP_{Tree}$  increased over the previous year in the control plot, the increment of water use outweighed that of biomass gain. Owing to higher density in the control plot relative to thinned plot, TWU responded to *D* more sensitively.

**5. Conclusions**

Our study shows that thinning enhanced the sap flux density and diameter growth. These positive effects of thinning on tree level water use and growth were more apparent in HT plot than in the LT plot. The interannual variations in water use efficiency indicated that light conditions might be the main driver of positive thinning effects. Other approaches, such as stable isotope analysis in leaves or tree core analysis could be used to reveal the hidden mechanism of thinning effects.

Our results indicate that thinning by 40% removal of total trees is an appropriate management practice in mature pine forests compared to thinning by 20% removal, and this results in improved tree growth together without loss in water use efficiency.

**Acknowledgments**

This work was supported by both the Korea Forest Service

(S211315L020120, S111215L020110) and the Korea Meteorological Agency (KIMPA-2012-0001-2). We are also thankful for the support of the Mt. Teahwa Seoul National University Forest and its staff.

## References

- Anning, A.K., McCarthy, B.C., 2013. Long-term effects of prescribed fire and thinning on residual tree growth in mixed-Oak forests of Southern Ohio. *Ecosystems* 16, 1473–1486.
- Aussenac, G., 2000. Interactions between forest stands and microclimate: ecophysiological aspects and consequences for silviculture. *Ann. For. Sci.* 57, 287–301.
- Aussenac, G., Granier, A., 1988. Effects of thinning on water stress and growth in Douglas-fir. *Can. J. For. Res.* 18, 100–105.
- Bonan, G.B., 2008. Forests and climate change: forcings, feedbacks, and the climate benefits of forests. *Science* 320, 1444–1449.
- Borchert, R., Rivera, G., Hagnauer, W., 2002. Modification of vegetative phenology in a tropical semi-deciduous forest by abnormal drought and rain 1. *Biotropica* 34, 27–39.
- Breda, N., Granier, A., 1996. Intra- and interannual variations of transpiration, leaf area index and radial growth of a sessile oak stand (*Quercus petraea*). *Ann. Sci. Forest* 53, 521–536.
- Breda, N., Granier, A., Aussenac, G., 1995. Effects of thinning on soil and tree water relations, transpiration and growth in an oak forest (*Quercus petraea* (Matt.) Liebl.). *Tree Physiol.* 15, 295–306.
- Brooks, J.R., Mitchell, A.K., 2011. Interpreting tree responses to thinning and fertilization using tree-ring stable isotopes. *New Phytologist* 190, 770–782.
- Coomes, D.A., Allen, R.B., 2007. Effects of size, competition and altitude on tree growth. *J. Ecol.* 95, 1084–1097.
- D'Amato, A.W., Bradford, J.B., Fraver, S., Palik, B.J., 2013. Effects of thinning on drought vulnerability and climate response in north temperate forest ecosystems. *Ecol. Appl.* 23, 1735–1742.
- Deckmyn, G., Evans, S.P., Randle, T.J., 2006. Refined pipe theory for mechanistic modeling of wood development. *Tree Physiol.* 26, 703–717.
- Donner, B.L., Running, S.W., 1986. Water stress response after thinning pinus contorta stands in Montana. *Forest Sci.* 32, 614–625.
- Dore, S., Montes-Helu, M., Hart, S.C., Hungate, B.A., Koch, G.W., Moon, J.B., Finkral, A.J., Kolb, T.E., 2012. Recovery of ponderosa pine ecosystem carbon and water fluxes from thinning and stand-replacing fire. *Glob. Chang. Biol.* 18, 3171–3185.
- Enquist, B.J., 2002. Universal scaling in tree and vascular plant allometry: toward a general quantitative theory linking plant form and function from cells to ecosystems. *Tree Physiol.* 22, 1045–1064.
- Ganatsios, H.P., Tsioras, P.A., Pavlidis, T., 2010. Water yield changes as a result of silvicultural treatments in an oak ecosystem. *For. Ecol. Manage.* 260, 1367–1374.
- Gauthier, M.M., Jacobs, D.F., 2009. Short-term physiological responses of black walnut (*Juglans nigra* L.) to plantation thinning. *Forest Sci.* 55, 221–229.
- Gebauer, R., Volařík, D., Urban, J., Børja, I., Nagy, N.E., Eldhuset, T.D., Krokene, P., 2013. Altered light conditions following thinning affect xylem structure and potential hydraulic conductivity of Norway spruce shoots. *Eur. J. Forest Res.* 133, 111–120.
- Gebhardt, T., Häberle, K.-H., Matyssek, R., Schulz, C., Ammer, C., 2014. The more, the better? Water relations of Norway spruce stands after progressive thinning. *Agric. For. Meteorol.* 197, 235–243.
- Giuggiola, A., Ogée, J., Rigling, A., Gessler, A., Bugmann, H., Treydte, K., 2015. Improvement of water and light availability after thinning at a xeric site: which matters more? A dual isotope approach. *New Phytologist*.
- Gomez-Aparicio, L., Garcia-Valdes, R., Ruiz-Benito, P., Zavala, M.A., 2011. Disentangling the relative importance of climate, size and competition on tree growth in Iberian forests: implications for forest management under global change. *Global Change Biol.* 17, 2400–2414.
- Gough, C., Seiler, J., Maier, C.A., 2004. Short-term effects of fertilization on loblolly pine (*Pinus taeda* L.) physiology. *Plant, Cell Environ.* 27, 876–886.
- Granier, A., 1987. Evaluation of transpiration in a Douglas-fir stand by means of sap flow measurements. *Tree Physiol.* 3, 309–320.
- Hale, S.E., 2003. The effect of thinning intensity on the below-canopy light environment in a Sitka spruce plantation. *For. Ecol. Manage.* 179, 341–349.
- Harrington, C.A., Reukema, D.L., 1983. Initial shock and long-term stand development following thinning in a Douglas-Fir plantation. *Forest Sci.* 29, 33–46.
- Hegyi, F., 1974. A simulation model for managing jack-pine stands. *Growth Models for Tree and Stand Simulation* 30, 74–90.
- Huang, J.G., Zhang, Q.B., 2007. Tree rings and climate for the last 680 years in Wulan area of northeastern Qinghai-Tibetan Plateau. *Clim. Change* 80, 369–377.
- Jimenez, E., Vega, J.A., Fernandez, C., Fonturbel, T., 2011. Is pre-commercial thinning compatible with carbon sequestration? A case study in a maritime pine stand in northwestern Spain. *Forestry* 84, 149–157.
- Jimenez, E., Vega, J.A., Perez-Gorostiaga, P., Cuinas, P., Fonturbel, T., Fernandez, C., Madrigal, J., Hernandez, C., Guijarro, M., 2008. Effects of pre-commercial thinning on transpiration in young post-fire maritime pine stands. *Forestry* 81, 543–557.
- Juodvalkis, A., Kairiukstis, L., Vasiliauskas, R., 2005. Effects of thinning on growth of six tree species in north-temperate forests of Lithuania. *Eur. J. Forest Res.* 124, 187–192.
- Jutras, S., Plamondon, A.P., Hokka, H., Begin, J., 2006. Water table changes following precommercial thinning on post-harvest drained wetlands. *For. Ecol. Manage.* 235, 252–259.
- Kerr, G., Haufe, J., 2011. *Thinning Practice: A Silvicultural Guide*. Forestry Commission, Edinburgh.
- Kohler, M., Sohn, J., Nägele, G., Bauhus, J., 2010. Can drought tolerance of Norway spruce (*Picea abies* (L.) Karst.) be increased through thinning? *Eur. J. Forest Res.* 129, 1109–1118.
- Lagergren, F., Lankreijer, H., Kucera, J., Cienciala, E., Molder, M., Lindroth, A., 2008. Thinning effects on pine-spruce forest transpiration in central Sweden. *For. Ecol. Manage.* 255, 2312–2323.
- Laurent, M., Antoine, N., Joel, G., 2003. Effects of different thinning intensities on drought response in Norway spruce (*Picea abies* (L.) Karst.). *For. Ecol. Manage.* 183, 47–60.
- Li, X., Yi, M.J., Son, Y., Park, P.S., Lee, K.H., Son, Y.M., Kim, R.H., Jeong, M.J., 2011. Biomass and carbon storage in an age-sequence of Korean pine (*Pinus koraiensis*) plantation forests in Central Korea. *J. Plant Biol.* 54, 33–42.
- Makinen, H., Isomaki, A., 2004a. Thinning intensity and growth of Norway spruce stands in Finland. *Forestry* 77, 349–364.
- Makinen, H., Isomaki, A., 2004b. Thinning intensity and growth of scots pine stands in Finland. *For. Ecol. Manage.* 201, 311–325.
- Marksteijn, L., Poorter, L., 2009. Seedling root morphology and biomass allocation of 62 tropical tree species in relation to drought- and shade-tolerance. *J. Ecol.* 97, 311–325.
- Martin-Benito, D., Del Rio, M., Heinrich, I., Helle, G., Canellas, I., 2010. Response of climate-growth relationships and water use efficiency to thinning in a *Pinus nigra* afforestation. *For. Ecol. Manage.* 259, 967–975.
- McDowell, N., Brooks, J.R., Fitzgerald, S.A., Bond, B.J., 2003. Carbon isotope discrimination and growth response of old *Pinus ponderosa* trees to stand density reductions. *Plant Cell Environ.* 26, 631–644.
- McJannet, D., Vertessy, R., 2001. Effects of thinning on wood production, leaf area index, transpiration and canopy interception of a plantation subject to drought. *Tree Physiol.* 21, 1001–1008.
- Medhurst, J.L., Battaglia, M., Beadle, C.L., 2002. Measured and predicted changes in tree and stand water use following high-intensity thinning of an 8-year-old *Eucalyptus nitens* plantation. *Tree Physiol.* 22, 775–784.
- Misson, L., Tang, J.W., Xu, M., McKay, M., Goldstein, A., 2005. Influences of recovery from clear-cut, climate variability, and thinning on the carbon balance of a young ponderosa pine plantation. *Agric. For. Meteorol.* 130, 207–222.
- Moon, M., Kim, T., Park, J., Cho, S., Ryu, D., Kim, H.S., 2015. Variation in sap flux density and its effect on stand transpiration estimates of Korean pine stands. *J. Forest Res.* 20, 85–93.
- Moon, M., Kim, T., Park, J., Cho, S., Ryu, D., Suh, S., Kim, H.S., 2016. Changes in spatial variations of sap flow in Korean pine trees due to environmental factors and their effects on estimates of stand transpiration. *J. Mountain Sci.* 13, 1024–1034.
- Moreno-Gutierrez, C., Barbera, G.G., Nicolas, E., De Luis, M., Castillo, V.M., Martinez-Fernandez, F., Querejeta, J.L., 2011. Leaf delta 18O of remaining trees is affected by thinning intensity in a semiarid pine forest. *Plant, Cell Environ.* 34, 1009–1019.
- Nadezhkina, N., David, T.S., David, J.S., Ferreira, M.I., Dohnal, M., Tesar, M., Gartner, K., Leitgeb, E., Nadezhdin, V., Cermak, J., Jimenez, M.S., Morales, D., 2010. Trees never rest: the multiple facets of hydraulic redistribution. *Ecohydrology* 3, 431–444.
- Novick, K.A., Ficklin, D.L., Stoy, P.C., Williams, C.A., Bohrer, G., Oishi, A.C., Papuga, S.A., Blanken, P.D., Noormets, A., Sulman, B.N., Scott, R.L., Wang, L.X., Phillips, R.P., 2016. The increasing importance of atmospheric demand for ecosystem water and carbon fluxes. *Nat. Clim. Change* 6, 1023–1027.
- Oberhuber, W., Stumbock, M., Kofler, W., 1998. Climate tree-growth relationships of Scots pine stands (*Pinus sylvestris* L.) exposed to soil dryness. *Trees-Struct. Function* 13, 19–27.
- Pérez-de-Lis, G., García-González, I., Rozas, V., Arévalo, J.R., 2011. Effects of thinning intensity on radial growth patterns and temperature sensitivity in *Pinus canariensis* afforestations on Tenerife Island, Spain. *Ann. For. Sci.* 68, 1093–1104.
- R Core Team, 2016. *R: A language and environment for statistical computing*. In: R Foundation for Statistical Computing, Vienna, Austria.
- Reid, D.E.B., Silins, U., Lieffers, V.J., 2006. Sapwood hydraulic recovery following thinning in lodgepole pine. *Ann. For. Sci.* 63, 329–338.
- Richardson, A.D., Black, T.A., Ciais, P., Delbart, N., Friedl, M.A., Gobron, N., Hollinger, D.Y., Kutsch, W.L., Longdoz, B., Luysaert, S., Migliavacca, M., Montagnani, L., Munger, J.W., Moors, E., Piao, S., Reimann, C., Reichstein, M., Saigusa, N., Tomelleri, E., Vargas, R., Varlagin, A., 2010. Influence of spring and autumn phenological transitions on forest ecosystem productivity. *Philos. Trans. R Soc. Lond. B Biol. Sci.* 365, 3227–3246.
- Rigling, A., Braker, O., Schneider, G., Schweingruber, F., 2002. Intra-annual tree-ring parameters indicating differences in drought stress of *Pinus sylvestris* forests within the Erico-Pinion in the Valais (Switzerland). *Plant. Ecol.* 163, 105–121.
- Ryu, D., Moon, M., Park, J., Cho, S., Kim, T., Kim, H.S., 2014. Development of allometric equations for V age-class *Pinus koraiensis* in Mt. Taehwa plantation Gyeonggi-do. *Kor. J. Agric. For. Meteorol.* 16, 29–38.
- Sohn, J.A., Hartig, F., Kohler, M., Huss, J., Bauhus, J., 2016. Heavy and frequent thinning promotes drought adaptation in *Pinus sylvestris* forests. *Ecol. Appl.* 26, 2190–2205.
- Son, Y., Hwang, J.W., Kim, Z.S., Lee, W.K., Kim, J.S., 2001. Allometry and biomass of Korean pine (*Pinus koraiensis*) in central Korea. *Bioresour. Technol.* 78, 251–255.
- Trenberth, K.E., 2011. Changes in precipitation with climate change. *Climate Res.* 47, 123–138.
- Warren, C.R., McGrath, J.F., Adams, M.A., 2001. Water availability and carbon isotope discrimination in conifers. *Oecologia* 127, 476–486.
- Yang, B., Pallardy, S.G., Meyers, T.P., Gu, L.H., Hanson, P.J., Wullschlegel, S.D., Heuer, M., Hosman, K.P., Riggs, J.S., Sluss, D.W., 2010. Environmental controls on water use efficiency during severe drought in an Ozark Forest in Missouri, USA. *Glob. Change Biol.* 16, 2252–2271.
- Yang, Y.T., Guan, H., Batelaan, O., McVicar, T.R., Long, D., Piao, S.L., Liang, W., Liu, B., Jin, Z., Simmons, C.T., 2016. Contrasting responses of water use efficiency to drought across global terrestrial ecosystems. *Scientific Reports* 6.
- Zhang, J.W., Webster, J., Young, D.H., Fiddler, G.O., 2016. Effect of thinning and soil treatments on *Pinus ponderosa* plantations: 15-year results. *For. Ecol. Manage.* 368, 123–132.
- Zhang, S.Y., Chauret, G., Swift, D.E., Duchesne, I., 2006. Effects of precommercial thinning on tree growth and lumber quality in a jack pine stand in New Brunswick, Canada. *Can. J. For. Res.-Revue Canadienne De Recherche Forestiere* 36, 945–952.
- Zhang, X., Moran, M.S., Zhao, X., Liu, S.H., Zhou, T., Ponce-Campos, G.E., Liu, F., 2014. Impact of prolonged drought on rainfall use efficiency using MODIS data across China in the early 21st century. *Remote Sens. Environ.* 150, 188–197.