

<https://doi.org/10.17221/132/2020-JFS>

## Differences in water relations and total carbohydrate content between precommercially thinned and unthinned *Pinus nigra* subsp. *pallasiana* stands

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Citation: Deligöz A., Bayar E., Genç M., Karatepe Y. (2021): Differences in water relations and total carbohydrate content between precommercially thinned and unthinned *Pinus nigra* subsp. *pallasiana* stands. J. For. Sci., 67: 125–133.

**Abstract:** Variations in seasonal responses in water relations and total carbohydrate content (TCC) in one-year-old shoots from precommercially thinned (PCT) and unthinned Anatolian black pine stands were assessed during three seasons (sampling in May, July and September) in 2015–2017. Three different treatments were established: unthinned control with 4 941 stems·ha<sup>-1</sup> and two thinned spacing levels (2–2.5 and 3–3.5 m) where 2 133 stems·ha<sup>-1</sup> and 1 093 stems·ha<sup>-1</sup> were left, respectively. Differences in osmotic potential at turgor loss point ( $\Psi\pi_{\text{TLP}}$ ) between the thinned and unthinned plots appeared only during a water shortage (September) in the second season, with the thinned stands showing lower  $\Psi\pi_{\text{TLP}}$  than the unthinned stands. Seasonal variation in terms of  $\Psi\pi_{\text{TLP}}$  was detected in the 3–3.5 m spacing trees. PCT were effective on osmotic potential at full turgor ( $\Psi\pi_{100}$ ), relative water content (RWC), symplastic water at saturated point per dry weight of the shoot and dry weight fraction. In both the thinned and unthinned plots, a gradual decline was observed in RWC from May to September in all three years. Generally, although TCC was found to be higher in the 3–3.5 m spacing, control plots were also high in carbohydrates in some periods. Results reflect the ability of this species to survive in changing environments by PCT during dry periods in the three studied seasons. Although PCT has an effect on water potential components and TCC, it is not clear exactly how effective the PCT density is in osmotic adjustment.

**Keywords:** Anatolian black pine; osmotic potential; relative water content; soluble sugar; spacing

Forests are the most biologically diverse ecosystems on Earth, and therefore the most valuable natural resources for mankind. We must protect them to maintain natural balance and favourable living conditions (Odabaşı et al. 2007). The conservation, appropriate management and carbon storage of forests will also make a vital contribution to reduce the adverse effects of climate change. Tending is a form of treatment implemented to protect the forests and to ensure their survival under climate change. Precommercial thinning (PCT) is a silvi-

cultural operation performed at the thicket stage of managed forests. The thicket stage is a bottleneck for many tree species and for each individual of the stand (lack of sufficient light, temperature, water, etc.) (Çolak, Odabaşı 2004). Removing some trees from a stand at that stage can help improve its microclimate conditions (Aussenac 2000; Park et al. 2018). Also Chase et al. (2016) stated that the removal of trees from a stand through PCT reduces competition, resulting in a reduction of multiple stress or resource limitations (light, soil water, and

nutrients) for the remaining trees. In other words, PCT helps reduce the stress level of trees (Bayar 2018). Some studies showed that precommercially thinned stands have a significantly higher leaf water potential than control plots (Bréda et al. 1995; Stoneman et al. 1996; Gauthier, Jacobs 2009). However, the plant water potential depends on daily abiotic conditions (Wright et al. 2015). If stressed by lack of water, plants close their stomata and reduce  $\text{CO}_2$  assimilation to reduce water loss through their leaves (Chaves et al. 2002; Wright et al. 2015). On the other hand, plants subjected to long-term water stress make some other morphological (leaf orientation) or physiological (osmotic potential) adjustments to keep their carbon assimilation rates under control (Wright et al. 2015). Osmotic adjustment, which is defined as reducing the osmotic potential at full turgor due to net solute accumulation in response to water stress, allows plants to cope with water stress, and thus, to survive (Gebre, Tschaplinski 2002). Plants subjected to water stress accumulate soluble carbohydrates and soluble sugars, such as glucose and sucrose, as osmotic regulators to maintain turgor at low leaf water potentials (Çırak, Esendal 2006). Research shows that drought stress causes an increase in soluble sugar content (Liu et al. 2017; Deligöz, Bayar 2018; Zolfaghari, Akbarinia 2018).

Anatolian black pine [*Pinus nigra* Arn. subsp. *pallasiana* (Lamb.) Holmboe] has a wide range of ecological tolerance (Atalay, Efe 2010), and is distributed as both monospecific or mixed forests across 4.7 million hectares in Turkey (OGM 2015). Due to its topographical, main material, climatic, soil, and vegetative characteristics, Anatolian black pine is ubiquitous in different habitats. However, very little is known about its tending. Ecophysiological research on the reaction of a species in a natural stand or plantation to environmental conditions (light, water, nutrients, etc.) is needed to better understand the impacts of silvicultural interventions, such as tending, on it (Bayar 2018). Therefore the two primary aims of this study were (1) to quantify the effect of PCT treatments on the parameters of water relations and total carbohydrate content (TCC), and (2) to describe the osmotic adjustment between precommercially thinned and unthinned stands by the seasonal variation in these parameters of Anatolian black pine trees. The adjustment of PCT intensity can help stands survive the climate change and thus contribute to the protection of forests.

## MATERIAL AND METHODS

**Study site and experimental design.** The study was conducted in a natural *Pinus nigra* subsp. *pallasiana* stand at the thicket stage in the Gölhisar district (Ibecik forests) of Burdur province in Turkey (36°54'N and 29°22'E). The Northeast/East study area is located at an average altitude of 1 700 m a.s.l. on a 35% slope on average. Its soil texture ranged from sandy-clay loam to loam. Temperature and precipitation data during 2015–2017 were obtained using a mini meteorological station (Watchdog Spectrum Technologies, Inc., USA) installed at the study site. The highest mean monthly temperature was 20.7 °C (July) in 2017. The total rainfall between May and September was 277 mm in 2015, 258.7 mm in 2016, and 131 mm (from May until the 6<sup>th</sup> September) in 2017, with 170.2 mm (May) of the highest monthly rainfall in 2016 (Figure 1). According to the long-term climate data of Gölhisar Meteorological Station, the study area had an annual total rainfall of 1 276 mm and an average temperature of 12.1 °C (Deligöz et al. 2019).

The experiment was established in 21-year young stand in April 2015. Three PCT treatments such as unthinned and two thinned ones (hereafter referred to as control, 2–2.5 m spacing and 3–3.5 m spacing) were applied in three replications of each treatment using a randomized block design. Within each of the three blocks, the three PCT treatments were randomly assigned to the plots. The areas of the plots varied from 150 to 200 m<sup>2</sup> with a buffer zone between the plots. The control (unthinned) plots had an average of 4 942 individuals per hectare. On the plots thinned to spacing of 2–2.5 and 3–3.5 m 2 133 and 1 094 individuals per hectare were left, respectively.

**Water relation parameters and total carbohydrate content.** From each replication of each treatment, one-year-old shoots were cut from south-facing branches of the middle thirds of the crown of ten trees to determine water potential components and total carbohydrate content (TCC) in May, July, and September for three years (2015, 2016 and 2017). The shoots were immediately put into polyethylene bags and placed in a mini fridge. The pressure-volume curve technique was used to estimate water potential components [osmotic potential at turgor loss point ( $\Psi\pi_{\text{TLP}}$ ), osmotic potential at full turgor ( $\Psi\pi_{100}$ ), free water content at turgor loss point ( $\text{FWC}_{\text{TLP}}$ ), relative water content at

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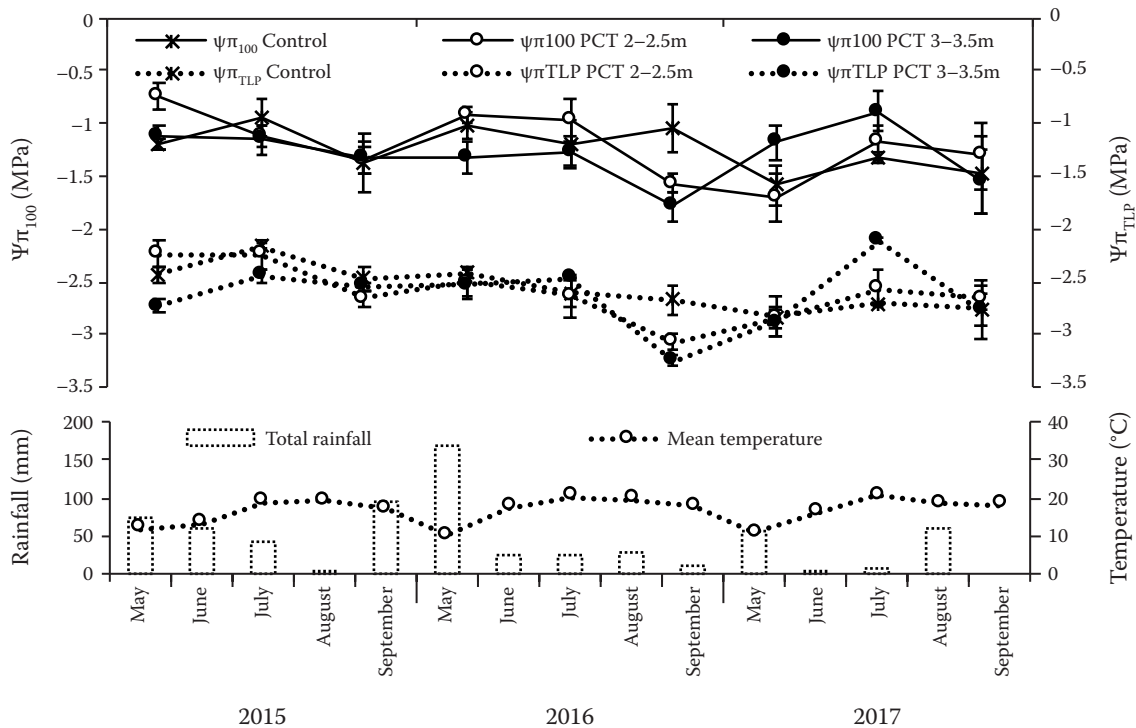


Figure 1. Seasonal osmotic potential at turgor loss point ( $\Psi\pi_{TLP}$ , mean + SE), osmotic potential at full turgor ( $\Psi\pi_{100}$ , mean + SE), rainfall and mean temperature following precommercial thinning (PCT) in an Anatolian black pine forest

turgor loss point ( $RWC_{TLP}$ ), relative water content ( $RWC$ ), symplastic water at saturated point per dry weight of the shoot ( $Vo/DW$ ), dry weight fraction ( $DWF$ ) (Tyree et al. 1978; Ritchie 1984; Doi et al. 1986; Grossnicle 1992). The corresponding water potential was measured with the pressure chamber described by Scholander et al. (1965).

For TCC, the shoots were dried at 65 °C for 48 h and then ground. For each sample, 100 mg of ground dry sample was incubated for 24 h in 10 ml of 80% ethanol and then it was centrifuged. The samples were first mixed with phenol solution and then with  $H_2SO_4$ , and then, kept at room temperature for 1 h. Afterwards, total carbohydrate content ( $mg\cdot g^{-1}$ ) was determined at a wavelength of 490 nm on a spectrophotometer using a phenol sulphuric acid method (Dubois et al. 1956).

**Statistical analysis.** The data were analysed using SPSS statistical package (Ver. 20.0, 2011). Analysis of variance (ANOVA) was used to determine the effects of PCT and sampling time on water potential components and total carbohydrate content. Data from each measurement year were analyzed separately. Differences between means were detected using Duncan's test at a significance

level of  $P \leq 0.05$ . At the end of the three years (2015, 2016 and 2017), the sampling year (SY), sampling time (ST), and PCT, and their interaction were analyzed using a generalized linear model.

## RESULTS

**Water potential components.** Sampling year and time had a significant effect on  $\Psi\pi_{TLP}$  ( $P < 0.001$ ). In all three years, sampling time had a significant effect only in the 3–3.5 m spacing. The highest  $\Psi\pi_{TLP}$  was observed in July 2015, May and July 2016, and July 2017. PCT had a significant effect on  $\Psi\pi_{TLP}$  in May 2015 ( $P < 0.05$ ), September 2016 ( $P < 0.05$ ), and July 2017 ( $P < 0.05$ ) (Figure 1). The 3–3.5 m spacing had a lower  $\Psi\pi_{TLP}$  in May 2015 than the control and the 2–2.5 m spacing. Both thinned stands had a lower  $\Psi\pi_{TLP}$  compared to control plots in September 2016. The 2–2.5 m spacing and control plots had the lowest  $\Psi\pi_{TLP}$  in July 2017. There was a significant difference in  $\Psi\pi_{100}$  in May 2015 and September 2016 between the two PCTs (Figure 1;  $P < 0.05$ ). The highest  $\Psi\pi_{100}$  was observed in May in the 2–2.5 m spacing and in September in control plots. In 2015, sampling time had a sig-

nificant effect on  $\Psi\pi_{100}$  only in the 2–2.5 m spacing ( $P < 0.01$ ). The highest and the lowest  $\Psi\pi_{100}$  were observed in May and September, respectively.

Control plots had a significantly higher  $FWC_{TLP}$  in May 2015 than the values shown in the 2–2.5 and 3–3.5 m spacing plots ( $P < 0.05$ ) (Figure 2a). Sampling time had a significant effect on  $FWC_{TLP}$  only in 2–2.5 m spacing stands in 2015. The values in May were lower than those in July and September. Both PCT and sapling time had a significant effect on  $RWC_{TLP}$  only in 2016 (Figure 2 b). The 2–2.5 m spacing and control plots had higher  $RWC_{TLP}$  in May but lower  $RWC_{TLP}$  in July than the 3–3.5 m spacing. In terms of sampling time, the 3–3.5 m spacing had lower  $RWC_{TLP}$  in May than in July and September. In September 2016,  $RWC$  differed significantly between PCT treatments (Figure 2c).

Both thinned stands had the highest  $RWC$  in September. Sampling time had a significant effect on  $RWC$  in all three years.

PCT had a significant effect on  $Vo/DW$  in May 2016 (Figure 3). The 2–2.5 m spacing showed the lowest  $Vo/DW$  whereas the 3–3.5 m spacing had the highest  $Vo/DW$ . In 2016, the 3–3.5 m spacing had higher  $Vo/DW$  in May than in July and September.

A significant difference in DWF between PCT treatments was found only in May 2015 ( $P < 0.05$ ). The 2–2.5 m spacing and control plots had the highest DWF. Sampling time had an effect on DWF in 2015 in the 3–3.5 m spacing, in 2016 in all treatments, and in 2017 in the 3–3.5 m spacing (Figure 4). The 3–3.5 m spacing had lower DWF in July than in May and September in 2015. DWF was

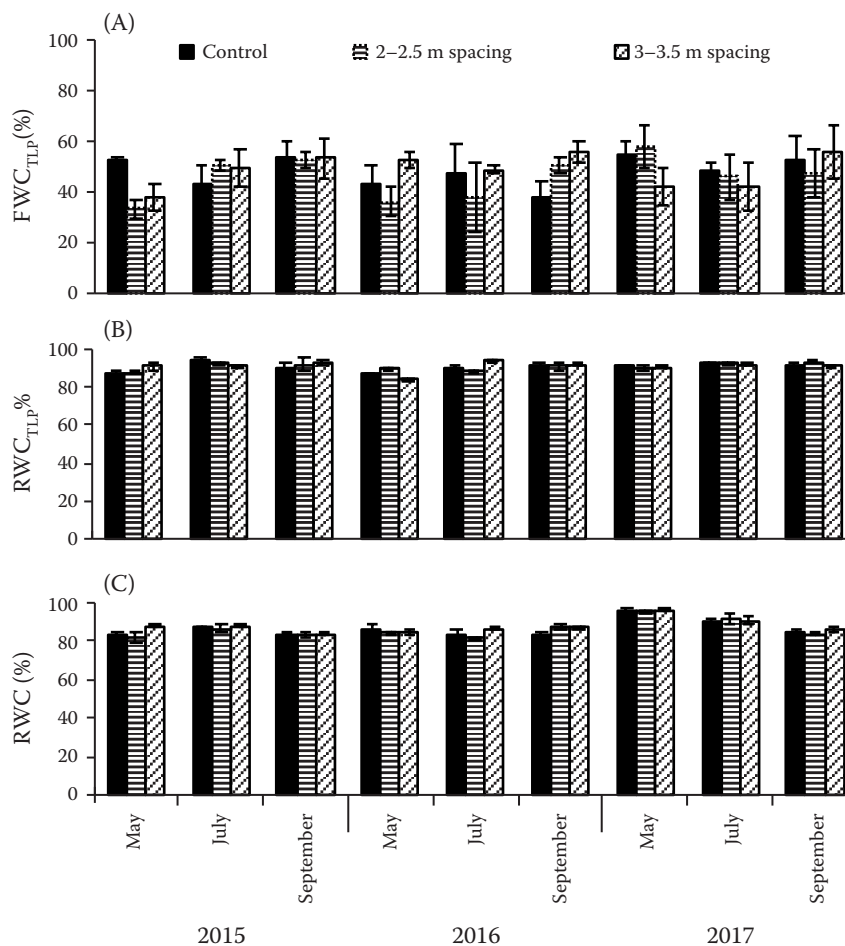


Figure 2. Seasonal free water content at turgor loss point ( $FWC_{TLP}$ , mean + SE) (A), relative water content at turgor loss point ( $RWC_{TLP}$ , mean + SE) (B) and relative water content ( $RWC$ , mean + SE) (C) following PCT in an Anatolian black pine forest

<https://doi.org/10.17221/132/2020-JFS>

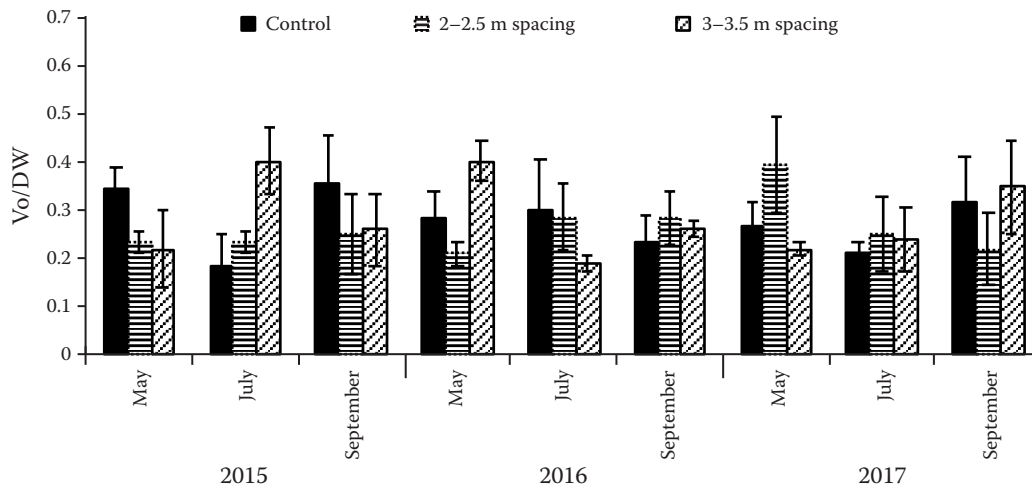


Figure 3. Seasonal symplastic water at saturated point per dry weight of the shoot ( $V_o/DW$ , mean + SE) following PCT in an Anatolian black pine forest

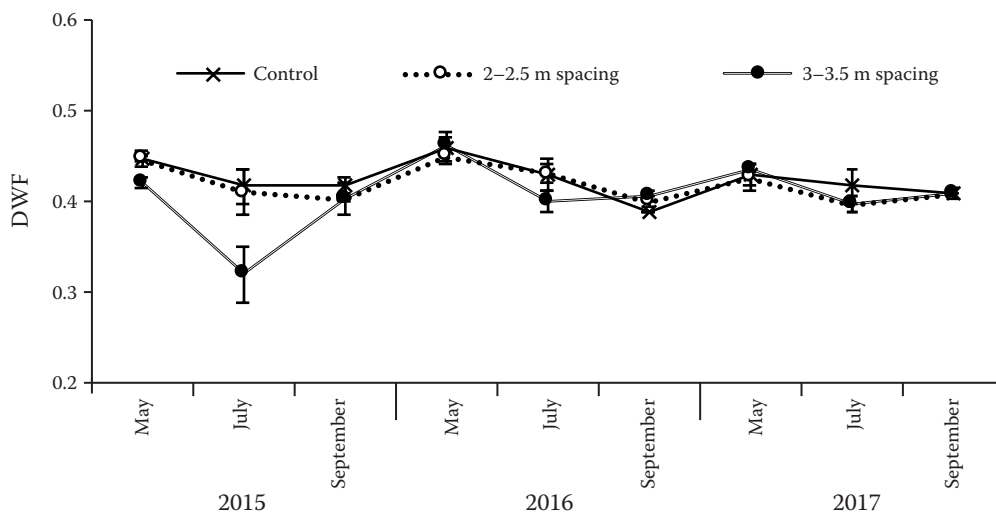


Figure 4. Seasonal dry weight fraction (DWF, mean + SE) following PCT in an Anatolian black pine forest

higher in May 2016 and 2017 than in July and September. In 2016, the lowest DWF was observed in the 2–2.5 m spacing and control plots in September.

**Total carbohydrate content.** PCT had a significant effect on TCC in all months but July in 2015 (Figure 5). In May 2015, control plots and the 2–2.5 m spacing had similar TCC, which was lower than that in the 3–3.5 m spacing. Control plots had the highest TCC in September 2015. In 2016, control plots also had lower TCC in May but higher TCC in July than in the 2–2.5 m and the 3–3.5 m spacing. However, the 3–3.5 m spacing had the

highest TCC in September 2016. The 3–3.5 m spacing had higher TCC in May and September 2017. In July 2017, both thinned stands had similar TCC, which was higher than that of control plots.

Sampling time had a significant effect on TCC ( $P < 0.05$ ) (Figure 5). TCC, which was high in May 2015, decreased in July and September in control plots. There was, however, no statistical difference in TCC between July and September. The 2–2.5 m spacing had similarly high TCC in May and July, which decreased in September. TCC, which was high in May, decreased towards September in the

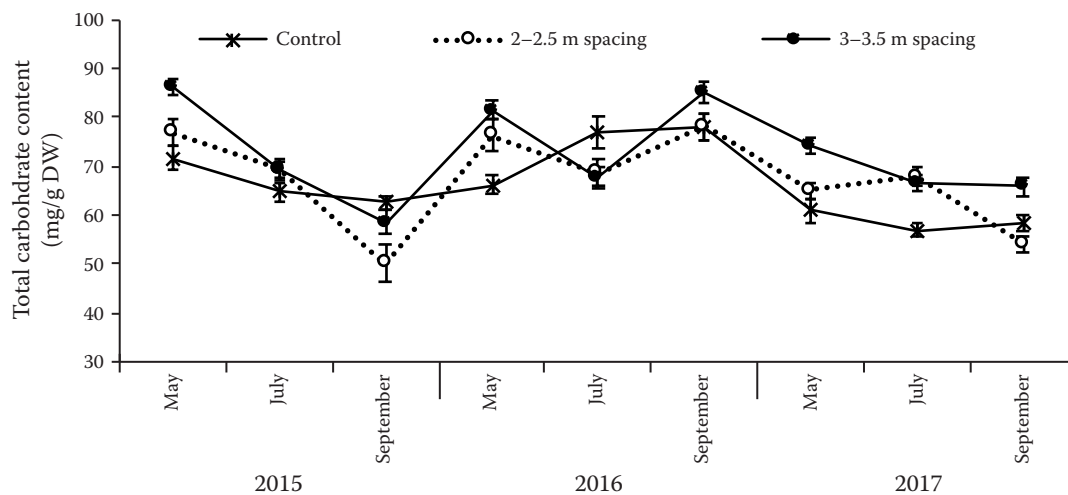


Figure 5. Seasonal total carbohydrate content ( $\text{mg}\cdot\text{g}^{-1}$  DW, mean + SE) following PCT in an Anatolian black pine forest

3–3.5 m spacing. TCC, which was low in May, was high in July and September in control plots in 2016. Both thinned stands had high TCC in May and September, which decreased in July. Sampling time had no significant effect on TCC in control plots in 2017. The lowest TCC was observed in both thinned stands in September, and in July and September, respectively.

## DISCUSSION

Silvicultural treatments are an effective strategy that can be used to reduce the impact of drought on trees (Chmura et al. 2011; Sohn et al. 2016). In other words, it is argued that such treatments can reduce the number of trees and increase the resistance of the remaining trees to drought (D'Amato et al. 2013). Moreno and Cubera (2008) stated that such treatments can be used to regulate stand density and prevent trees from dying due to severe drought. A reduction of stand density results in the increased amount of soil water, and hence, in the xylem water potential (Bréda et al. 1995). In fact, an increase in the water level leads to changes in the level of water stress (Aussenac, Granier 1988). Osmotic potential at turgor loss point is an important physiological indicator that can be used to assess water stress and drought tolerance (Farrell et al. 2017). Our results showed that sampling year and time had a significant effect on  $\Psi\pi_{\text{TLP}}$  whereas only sampling time had a significant effect on  $\Psi\pi_{100}$  at the end of the three years. The 3–3.5 m spacing had a rather low  $\Psi\pi_{\text{TLP}}$  in May 2015 and

July 2016 but a high  $\Psi\pi_{\text{TLP}}$  in July 2017. Control and 3–3.5 m spacing treatments had lower  $\Psi\pi_{100}$  than in the 2–2.5 m spacing in May 2015. Stands thinned to spacing of 3–3.5 m had the lowest  $\Psi\pi_{100}$  in September 2016. Aranda et al. (2001) stated that an increase in light intensity may result in a decrease in osmotic potential at turgor loss point and osmotic potential at full turgor and that reducing the stand density through thinning led to a decrease in osmotic potential. Pothier and Margolis (1990) found that a thinned plot had lower osmotic potential at turgor loss point and osmotic potential at full turgor than a control plot after a year. Our results showed that PCT in general had no significant effect on other water potential components, such as  $\text{FWC}_{\text{TLP}}$ .

Moreover,  $\Psi\pi_{\text{TLP}}$  showed a seasonal change in the 3–3.5 m spacing. Kubiske and Abrams (1991), Mitchell et al. (2008) and Deligöz (2011) reported that  $\Psi\pi_{\text{TLP}}$  changed from season to season. It can be stated that  $\Psi\pi_{\text{TLP}}$  is generally higher in July than in May and September. The total rainfall reported in the experimental plot was 43.0 mm in July 2015, 24.7 mm in 2016, and 7.7 mm in 2017.  $\Psi\pi_{\text{TLP}}$  was high in July, probably related to the shoot elongation continued until July. The decrease in  $\Psi\pi_{\text{TLP}}$  in September may be due to the osmotic adjustment as a response to the dry period. In fact, the total rainfall in September 2016 was 11.9 mm. There were no seasonal changes in  $\Psi\pi_{\text{TLP}}$  in the 2–2.5 m spacing and control plots for three years. However, a seasonal change in the  $\Psi\pi_{100}$  was determined in 2015 in the 2–2.5 m spacing because it decreased

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from May to September. Lo Gullo and Salleo (1988) also found that  $\Psi\pi_{100}$  was higher in May than in September in *Olea oleaster* Hoffm. et Link. and *Laurus nobilis* L. Deligöz and Cankara (2020) reported the highest  $\Psi\pi_{100}$  in *Pinus nigra* subsp. *pallasiana* and *Pinus brutia* Ten. in July. Our results showed that Vo/DW, which is another water potential component, was highest in May 2016 whereas DWF was highest in May 2016 and 2017. The high Vo/DW may be a result of the beginning of the growing period. Tognetti et al. (2000) stated that Vo/DW was high in late spring but decreased over the summer.

Our results showed that PCT had a significant effect on TCC. Although the 3–3.5 m spacing had the highest TCC in general, control plots had the highest TCC in September 2015 and July 2016. The 3–3.5 m spacing generally had high TCC, which may be due to the fact that PCT resulted in a reduction in the number of trees, allowing the remaining trees to benefit more from water, food, light, etc. Zhang et al. (2013) and Wang et al. (2015) argue that the more the light and irradiation, the higher the concentration of soluble sugar and starch in plant leaves. Pothier and Margolis (1990) also reported that plots treated with PCT had higher sugar content. The high values observed in the control plots in July and September may be due to environmental stress. Stress factors (low light, water deficit, etc.) may also have increased TCC in control plots. Plants can increase their soluble sugar content as a response to stress (Hessini et al. 2009; Kuang et al. 2017). Our results showed that TCC decreased from May to September in both thinned and control plots in 2015, but increased in the latter from May to September 2016, which may be due to osmotic adjustment as a response to the arid period. Both thinned stands had higher TCC in May and September than in July 2016. However, it decreased from May to September in 2017. Piispanen and Saranpää (2001) reported that the shoot elongation in May caused a decrease in non-structural carbohydrates. Kaelke and Dawson (2005) also found that bud burst and elongation of new shoots led to a decrease in total non-structural carbohydrates in spring and summer (during the growing period). Furze et al. (2019) argued that non-structural carbohydrates are generally high in winter, decrease towards summer, and then increase again and reach a maximum in winter. Numerous studies also show that soluble sugar content changes from season to season (Gaucher et al. 2005; Gruber et al.

2011), which may also be due to seasonal temperature, water regime or phenological events resulting from them (Würth et al. 2005).

## CONCLUSION

Our results showed that differences between the thinned and unthinned treatments appeared only during a water shortage (September) in the second season as the thinned stands had lower  $\Psi\pi_{TLP}$ . Tree density did not seem to affect  $FWC_{TLP}$  and  $RWC_{TLP}$  of *Pinus nigra* subsp. *pallasiana*.  $\Psi\pi_{TLP}$  in samples from the 3–3.5 m spacing varied seasonally for three seasons following PCT, but there were no seasonal changes for either the 2–2.5 m spacing or unthinned plots. A gradual decrease in RWC was observed from May to September in the thinned and unthinned plots in the third year of the study. The 3–3.5 m spacing generally had high TCC. However, unthinned plots also had high TCC in some time periods. These results are likely to reflect the ability of the species to survive in changing environmental conditions caused by PCT.

**Acknowledgement:** We would like to thank the Directorate of Gölhisar Forest Operations, and Necati AKÇORA, the Chief of İbecik Orman Operations, and its staff for their assistance in the field.

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Received: August 24, 2020

Accepted: January 7, 2021