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Needle water potential of selected pine species during the off-season: A case study

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Abstract

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In this study we investigated the needle water potential of different pine species using a pressure chamber during winter months. Totally, seven pine species *Pinus jeffreyi* Greville & Balfour, *Pinus ponderosa* P. & C. Lawson, *Pinus uncinata* Ramond ex de Candolle, *Pinus nigra* Arnold, *Pinus sylvestris* Linnaeus, *Pinus heldreichii* Christ, *Pinus cembra* Linnaeus representing ecological variability of this genus were selected for measurements. Although the water potential is well documented in many tree species during the vegetation season, data from the off-season are scarce. During the investigated seasons (November 2014, January and February 2016), days with air temperature (T) above and below 0°C were selected for the measurement. During the days with air T above 0°C and global radiation reaching 3,000 $kJ \cdot m^{-2} \cdot day^{-1}$, the water potential averaged –0.6 ± 0.4 MPa. On the contrary, under T below 0°C and global radiation above 6,000 $kJ \cdot m^{-2} \cdot day^{-1}$, the needle water potential was close to zero (–0.3 ± 0.2 MPa) regardless of the pine species. The reason why the needle water potential reflects air T and is negatively correlated with the global radiation in winter will be an objective of our future investigations.

Keywords: water stress; *Pinus*; global radiation; climatic changes; stomatal closure; transpiration

Pinaceae species are important components of the vegetation over large parts of the northern hemisphere. The range of environmental conditions for the family Pinaceae is remarkably wide due to low water availability, surviving under extremely low air temperatures (T), on nutrient-poor acidic soils (Richardson, Rundel 1998).

The relatively rapid changes in climate may influence tree species composition and stability of an ecosystem. Forest trees cannot migrate or adapt fast enough to cope with such rapid climatic changes due to their long life cycle. The need to select forest tree species for the more drought-tolerant genotypes (ecotypes) is becoming obvious (Atzmon et al. 2004; Grant et al. 2013).

Water loss from leaves (needles) is fundamentally linked to assimilation. The ability of plants to adequately supply water to foliage is crucial for their success in dry habitats. Pine trees may tolerate habitats over a wide range of water availability, the response of different species to low tissue water potentials is remarkably similar, showing almost complete stomatal closure at low needle water potentials – Ψ (MPa) (Richardson, Rundel 1998).

Generally, pine species were confirmed as tolerant to drought. Not even is a significant decrease of stomatal conductance connected with obvious variation in Ψ. They usually exhibit drought-avoidance strategy typically with efficient stomatal control of transpiration loss, decrease of stomatal conductance (up to 30%) and no change in Ψ (Lebourgeois et al. 1998). Whereby water use per unit needle area is maximized under well-watered conditions but decreases rapidly as water becomes

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insufficient to avoid very low water potentials and maintain a favourable water balance. At low water potentials, cavitation of water inside xylem conduits causes their blockage by air embolisms. The hydraulic conductivity of the xylem is therefore reduced causing increasingly lower water potentials, further cavitation and decreased water transport (Tyree, Sperry 1989). Extreme water potentials can trigger extensive xylem cavitation resulting in foliage dieback or plant death (Tyree et al. 1993; Saliendra et al. 1995; Cochard et al. 2004).

Minimum Ψ as a good indicator of physiological water stress is correlated with the ratio of annual precipitation to annual potential evapotranspiration. This result implies that structural and physiological adjustments allowed the different species to maintain water potentials within relatively narrow limits (Martínez-Vilalta et al. 2004; Ditmarová et al. 2010).

Forest tree species are reported to withstand values of Ψ up to –11 MPa measured as 50% loss of conductive tracheids (Maherali et al. 2004), agricultural crops up to –2 MPa (Pockman et al. 1995) and saltwater plants are able to live under harsh osmotic pressure up to –8 MPa. The creosote bush *Larrea tridentata* (de Candolle) Coville shows an extraordinary vulnerability to water stress conditions as it is able to assimilate up to –8 MPa and its cells survive Ψ up to –11.5 MPa (Vasek 1980). There is a wide range of water potential values measured in different pine species across the globe: in *Pinus canariensis* C. Smith from –0.3 to –2.5 MPa according to the altitude and precipitation (Gieger, Leuschner 2004), in *Pinus mugo* Turra –3.4 MPa, *Pinus cembra* Linnaeus up to –3.5 MPa, *Pinus sylvestris* Linnaeus up to –2.6 MPa, in *Pinus nigra* Arnold up to –1.8 MPa (Cochard et al. 2004) and in *Pinus palustris* Miller from –0.8 to –1.8 MPa during the year (Addington et al. 2004) and similarly in *Pinus pinaster* Aiton during spring months (Delzon et al. 2004).

Thresholds of Ψ values are usually expressed for the growing season (Addington et al. 2004; Atzmon et al. 2004; Gieger, Leuschner 2004; Hubbard et al. 2013; Kuster et al. 2013; Kerr et al. 2015). Higher global radiation and higher air T are connected with a low water potential as the transpiration demand usually exceeds the water supply from the roots (Law et al. 2000; Cinnirella et al. 2002; Durán et al. 2014). There is enough information about the lower water potential in pine species during the growing season, nevertheless the values of water potential during the off-season are missing. The goal of this study is to find: (*i*) differences in Ψ between the days with different solar radiation and t conditions, (*ii*) differences in Ψ between different pine species in relation to different meteorological conditions.

MATERIAL AND METHODS

Plot description. Water potential measurements on seven pine species were done at the Czech University of Life Sciences Prague campus which was established as an educational ground for dendrology courses. The campus elevation is 280 m a.s.l. positioned at 14°22'N and 50°08'E. There is a black soil with modal subtype, fine loam, neutral pH. Average annual air T is 9°C, average annual amount of precipitation 500 mm. There are 123 trees and bush species growing at the campus of the university. In our experiment we focused on the following pine species: *Pinus jeffreyi* Greville & Balfour, *Pinus ponderosa* P. & C. Lawson, *Pinus uncinata* Ramond ex de Candolle, *P. nigra*, *P. sylvestris*, *P. heldreichii* Christ, *and P. cembra*. According to Debreczy and Racz (2012) there are differences in the ecological valence within the studied pine groups.

P. cembra prefers sites with a continental climate and it is able to survive T differences between the warmest and the coolest month up to 60°C. Indigenous individuals can withstand average annual air T around zero and enormous frost (up to –47°C). Next to the bushy and smooth needles, extremely high viscosity of the cell plasma is responsible for such high frost tolerance.

P. heldreichii – a species native to mountainous areas of the Balkans and southern Italy. Solitaire trees can be observed up to the 2,200 m a.s.l. The wide ecological amplitude is typical of this tree. It grows mostly on limestone, grows slowly in open stands and the ecological requirements are even lower compared to *P. nigra*.

P. ponderosa – a North American pine species, which is the common tree in highlands and mountains up to 3,200 m a.s.l. It is tolerant to dry conditions but relatively sensitive to hard frost. Soil moisture spreading out from the Pacific Ocean is a limiting factor for its growth.

P. jeffreyi – a North American pine species. It grows from the west coast up to the mountains (from 60 up to 3,000 m a.s.l.), it is tolerant to dry conditions and grows even at a lower altitude. It copes better with climatic extremes and drought compared to *P. ponderosa*.

P. uncinata – a European pine species which is native to the Pyrenees and Western Alps up to the altitude of 2,200 m a.s.l. where the upper tree line is often constituted of this tree species. It is very durable under harsh climatic and soil conditions especially on nutrient-poor and acid soils.

P. nigra grows well southern Europe, in the Mediterranean and in North Africa. It demands continental climate. Compared to *P. sylvestris*, it withstands extreme sites better as it is able to lower the daily sum of transpiration by 21% in one-year needles and up to 50% in two-year needles.

P. sylvestris – the pine with a wide range of distribution across central and northern Europe to the Caucasus Mountains and from sea level up to 2,600 m a.s.l. and the only pine native to northern Europe. It survives the climate extremes as well as on shallow and poor soils. It grows well on stony soils as wells as on peat or salinized soils.

Water potential measurement. The measurement was done on seven pine species in winter months in November 2014 and December/January 2015/2016. On average six samples per one pine species and day were measured. More samples per species were measured (up to 10) but some of the data showed extreme values (they were out of the measurement scale) and they were removed before the statistical analysis. The age of investigated trees was 12–15 years, they were growing individually out of competition in an open area. The values of Ψ were estimated between 1 and 2 PM. For Ψ measurement a pump-up pressure chamber (PMS Instrument Company, Albany, USA) was used. The range of the water potential measurement of this chamber is from 0 to –2.1 MPa. The needles were taken from the sun adapted part of north oriented branches of different whorls. The selection of the whorl for water potential measurement was dependent on the height of the tree – usually samples from 10th or 12th whorl were taken (counted from the top of the tree). The precise collection of samples was dependent on accessibility to the crown. Needles were cut in one third of their length, put into a plastic bag and into the pressure chamber immediately. The cut part of the needle was outside of the chamber. Using mechanical power the pressure inside the chamber was increasing. A magnifier was used for the exact moment of water drop occurrence on the cut surface. At this point accurate pressure was read from the device – the amount of water appearing on the cut surface of the needle correlated with the water pressure potential of the leaf.

Meteorological measurement. As the transpiration process could be functioning during the winter, the water potential reflected the irradiance of the crown and soil moisture availability next to the tree species. Therefore we express the variability of individual tree crowns using the standard deviation for every tree species and investigation period.

For meteorological measurement these instruments were used: (*i*) air T and relative humidity probe HMP45C (Vaisala Inc., Finland), (*ii*) SR03 precipitation gauge (FIEDLER AMS s.r.o., Czech Republic), (*iii*) CM11 pyranometer (Kipp & Zonen B.V., Netherlands).

The days were divided into two groups according to global radiation (GR) and T: the first group gathering the days with relatively high mean daily T (above 0°C) and low GR (below 3,000 $kJ \cdot m^{-2} \cdot day^{-1}$), the second one with T below 0°C and high GR (above 5,000 $kJ \cdot m^{-2} \cdot day^{-1}$). Relative humidity was stable during investigated days and reached 74 ± 4%.

Statistical analysis. For statistically significant differences between the groups, factorial ANOVA and Scheffe's test were used. The Pearson correlation coefficient for strength and direction of the linear relationship between the groups was used. Data were evaluated on the level $\alpha = 0.05$ using STATISTICA software (Version 13, 2015).

RESULTS

The average air T during the investigation period in November 2014 was –1.2 ± 0.8°C and 2.3 ± 2.1°C during the next year. The course of the air temperature before and within the measurement campaigns is shown in Fig. 1. Excluding several days at the beginning and in the middle of January the average air T was above 0°C and the availability of water within the soil profile was not influenced.

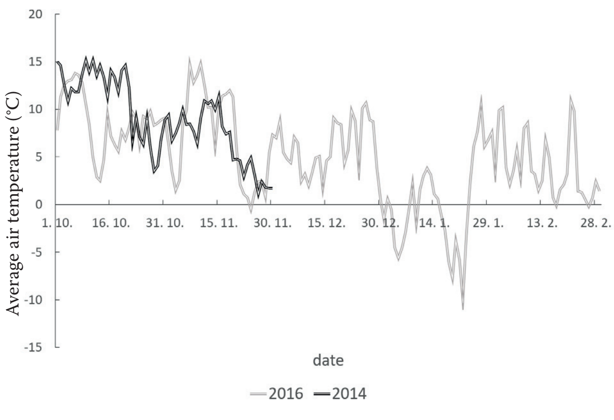

Fig. 1. Course of the air temperatures before and during the measurement campaigns in 2014 and 2015/2016 at the Czech University of Life Sciences Prague campus

High relative humidity during the whole time of measurement (72 and 79%, respectively) was measured. The global radiation was strongly dependent on the day and it ranges from 2,815 to 6,197 $kJ \cdot m^{-2} \cdot day^{-1}$. During the growing season high T is usually connected with high GR, which leads to a lower water potential. Besides GR the water potential depends on vapour pressure deficit and soil water availability as well. During winter months a different situation was typical: water potential −0.6 ± 0.4 MPa was found out during days with high T (around 0°C or slightly above 0°C) together with lower GR (around 3,000 $kJ \cdot m^{-2} \cdot day^{-1}$). On the opposite under T below 0°C and GR above 6,000 $kJ \cdot m^{-2} \cdot day^{-1}$ the leaf water potential was close to zero (−0.3 ± 0.2 MPa) regardless of the pine species (Fig. 2). The differences between the selected groups were statistically significant (Scheffe's test, $P << 0.01$). Considering the pine species, *P. nigra*, *P. ponderosa* and *P. uncinata* differed significantly (Scheffe's test, $P < 0.05$) from the rest of pines regardless of T or GR (Table 1).

Using factorial ANOVA we found out that there was a difference between two groups in the needle water potential between two days with different GR and T but no difference in interaction between species and T ($P = 0.21$) was found (Table 1). During winter months the lower water potential (−0.6 MPa) is connected with T above 0°C, on the other hand days with negative mean daily T led to the less negative leaf water potential (close to 0°C).

Table 1. Water potential of different pine species in homogeneous groups (columns 1 and 2 with asterisks) according to the mean water potential in needles during the off-season

Species	Water potential mean	Water potential SD	1	2
Pinus nigra Arnold	−0.42	0.35		*
Pinus ponderosa P. & C. Lawson	−0.44	0.34	*	*
Pinus uncinata Ramond ex de Candolle	−0.37	0.22	*	*
Pinus sylvestris Linnaeus	−0.42	0.35	*	
Pinus jeffreyi Greville & Balfour	−0.39	0.21	*	
Pinus heldreichii Christ	−0.27	0.18	*	
Pinus cembra Linnaeus	−0.23	0.15	*	

SD – standard deviation

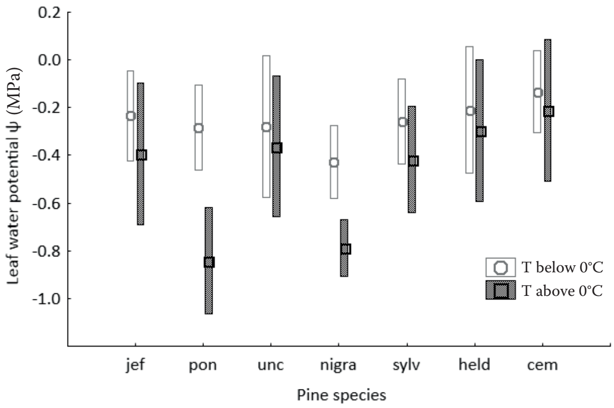

Fig. 2. The leaf water potential of different pine species divided into two groups according to the air temperature (T above or below 0°C) during the off-season

jef – *Pinus jeffreyi* Greville & Balfour, pon – *Pinus ponderosa* P. & C. Lawson, unc – *Pinus uncinata* Ramond ex de Candolle, nigra – *Pinus nigra* Arnold, sylv – *Pinus sylvestris* Linnaeus, held – *Pinus heldreichii* Christ, cem – *Pinus cembra* Linnaeus

Surprisingly the water potential was negatively correlated with GR (Pearson correlation coefficient $r = 0.57$, $P << 0.01$) during winter months. Irradiance of all investigated pine species was very similar as all the investigated trees are solitaires.

DISCUSSION

During winter months the values of Ψ are always low due to osmotic substances in the plant tissue, nevertheless, exact values are missing. Low Ψ is accompanied by the accumulation of osmotic substances such as glycine or betadine (Ashraf, Foolad 2007) together with LEA (late embryogenesis abundant) proteins synthetized during low T (Walker et al. 2010). There is also a higher concentration of proteins such as for example DREB – dehydration-responsive element-binding factors (Ma et al. 2014). McDowell et al. (2008) and Sala et al. (2010) suggested that the amount of carbohydrate storage was neither a good predictor of mortality nor a good indicator of available reserves to outlast the drought because the lower plant water potential could lead to problems mobilizing and transporting carbohydrates. Interference with carbohydrate transport could, in turn, starve living plant cells even with abundant plant reserves.

Concerning the global radiation and Ψ relationship we assume that according to extremely high T compared to the long-term period over Europe during the whole winter 2013/2014 (Tang et al.

2013) and 2014/2015, the roots did not probably stop sucking the water from the soil. The high levels of global radiation driving the transpiration could enhance transpiration rates and Ψ at the same time. We suppose this is the reason for less negative Ψ values during the day with high global radiation compared to the day with low global radiation. Moreover, several pine species native to North America such as *Pinus radiata* D. Don, *P. ponderosa* or *Pinus strobus* Linnaeus have the ability to survive more than one month longer in a soil with ultimate wilting point (Boucher et al. 1995). Surviving under such condition is possible due to the exploitation of dew. This ability corresponds with a wider range of Ψ in *P. ponderosa* compared to other pines as the value of Ψ depends not only on the soil moisture but also on relative air humidity (Boucher et al. 1995). A variety of physiological processes respond at different plant water potentials, so that the severity of the drought will influence the physiological response (Ditmarová et al. 2010). Besides the dew, ectomycorrhizal fungi in plant species play an important role during water stress and subsequent recovery (Lehto, Zwiazek 2011; Rapparini, Penuelas 2014). Differences in the water potential between inoculated and uninoculated seedlings of *P. pinaster* during severe stress reach up to 2 MPa (Lamhamedi et al. 1992). If there is any relationship of the pine water potential to the isohydrid plant group (i.e. to the strategy of maintaining a constant leaf water potential in case of water abundance as well as under drought conditions).

CONCLUSIONS

During winter months the lower water potential (–0.6 MPa) in pines is connected with air T above 0°C, on the other hand, days with negative mean daily air T led to the less negative leaf water potential (close to 0°C). Above 0°C, under higher irradiance – photosynthesis as well as transpiration can be functioning, thus lost water of needles and their potential decrease. During winter months the leaf water potential is negatively correlated with global radiation – high global radiation (above 6,000 $kJ \cdot m^{-2} \cdot day^{-1}$) signifies a less negative water potential. When the soil is not frozen, then transpiration on the whole tree level can be functional. Therefore needles can exhibit a less negative water potential as they are refilled with water. Among all investigated pine species *P. uncinata*, *P. ponderosa* and *P. nigra* lowered their water potential up to −1 MPa during winter days with air T above 0°C.

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