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Research Article

Testing Foliar Absorption in Black Spruce [*Picea mariana* (Mill.) BSP] Saplings

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Abstract

Foliar absorption is a known water acquisition mechanism in many species and ecosystems. Experiments in the field showed that mature black spruce [*Picea mariana* (Mill.) BSP] can surprisingly sustain periods of summer drought. A possible explanation for this phenomenon is that this species is able to rehydrate via its needles. In this study, we explored if black spruce saplings are able to absorb water via the needles or to increase their water potential and photosynthesis after needle wetting. Forty saplings were used, of which half were excluded from irrigation until water potential of -2.70 MPa. For the first part of the experiment, the saplings were sprayed at night with a colorant solution and water potential was measured the following day. No colorant was absorbed by the saplings and no difference in water potential was found between irrigated and non-irrigated individuals. The experiment was then repeated, spraying saplings with normal water and measuring water potential and photosynthesis. Once again there was no increase in water potential or photosynthesis following the canopy spraying. The results of this study show no evidence of foliar absorption in black spruce saplings. However this does not exclude the occurrence of foliar absorption via passive or active mechanisms in mature trees, which grow under different circumstances.

Keywords: Foliar absorption; *Picea mariana;* Boreal forest; Drought

1. Introduction

Throughfalling rainwater absorbed by the root system is usually considered to be the primary water supply in forest ecosystems. However, part of this water is intercepted by the canopy where it may be absorbed by the leaves (Barbier, Balandier, & Gosselin, 2009). The phenomenon of foliar absorption is being increasingly studied because the contribution of foliar absorption to the water status of trees may be particularly important during periods of water deficit (Breshears et al., 2008; Eller, Lima, & Oliveira, 2013). Moreover, trees may be able to relocate the absorbed water to belowground organs and tissues when the soil is dry (Eller et al., 2013). Conifers are known to

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intercept a higher quantity of rainwater than broadleaves and deciduous trees, possibly due to differences in leaf area index and needle arrangement (Barbier et al., 2009; Keim, Skaugset, & Weiler, 2006), and this can occur in many species and ecosystems. In the Mediterranean region, dew absorption by the evergreen shrubs *Lavandula stoechas* and *Rosmarinus officinalis* was studied by Munné-Bosch, Nogués, and Alegre (1999), in redwood forests 80% of the dominant species benefit from foliar absorption (Limm, Simonin, Bothman, & Dawson, 2009). Other examples include species such as *Picea abies* that can absorb water via its twigs (Katz, Oren, Schulze, & Milburn, 1989), *Juniperus* spp. (Breshears et al., 2008) and *Pinus strobus* (Boucher, Munson, & Bernier, 1995) are also known to absorb water via their needles.

Rain, dew or fog may reduce plant water loss via transpiration (Reinhardt & Smith, 2008) and may also directly improve the water content of the foliage (Carter Berry & Smith, 2014). Water can diffuse directly into the leaves via the cuticle, twigs and branches (Boucher et al., 1995; Katz et al., 1989; Limm et al., 2009). Foliar absorption can quickly improve a plant's water status by increasing its water potential. Other benefits are improved stomatal conductance, plant growth and survival (Boucher et al., 1995; Breshears et al., 2008; Limm et al., 2009). Although canopy wetting may negatively affect photosynthesis and growth due to the presence of a water film on the leaf surface that reduces CO_2 transport (Brewer & Smith, 1997), other studies point out ecophysiological improvements. Transpiration may decrease due to a lower vapour pressure deficit. In *Abies fraseri,* photosynthetic activity and water relations were strongly related with cloud conditions (Reinhardt & Smith, 2008) and fog interception resulted in better leaf water potential and photosynthesis for *Sequoia sempervirens* (Simonin, Santiago, & Dawson, 2009).

In a previous study, it was shown that black spruce [*Picea mariana* (Mill.) BSP] withstood repeated periods without direct water supply to the root system (Belien, Rossi, Morin, & Deslauriers, 2012, 2014). In that experiment plastic under-canopy roofs were installed on mature black spruce trees for three consecutive summers. The canopy thus remained exposed to frequent rainfall, which may have allowed the trees to cope with the soil drought. Black spruce is one of the most common tree species in the boreal forest of Eastern North America and it is more sensitive to water stress than other boreal conifers (Grossnickle & Blake, 1986). In spite of its importance, the water relations of black spruce are not yet well-understood. If root water is not directly available, foliar absorption is one alternative way to obtain water. The objective of this study was to explore if foliar absorption is a possible water absorption mechanism in black spruce saplings. We tested the hypothesis that black spruce is capable of absorbing rainwater and using it to improve its water relations and vital physiological processes. As it was expected that the foliar absorption would be more evident in saplings that were water-stressed, we measured water potential and photosynthesis in five-year old black spruce seedlings submitted to a drought treatment and nocturnal canopy wetting.

2. Methodology

2.1 Experimental setup

The experiment was conducted on 40 black spruce saplings selected at the end of summer 2012. The five-year old saplings then passed the winter outside and were put into a heated greenhouse in January 2013. It was ensured that the saplings were in maximum growth during the experiment, which was conducted in March-April 2013. Day/night temperatures in the greenhouse were kept at 25/13 °C and relative humidity was 5-25% during the day and 30-40% at night. For the first part of the experiment, 20 experimental saplings were excluded from irrigation on DOY 73-95, while 20 control saplings were irrigated weekly with drip irrigation. On the evenings of DOY 92 and 94, half of the irrigated and non-irrigated saplings were sprayed with normal water and the other half with a solution of water and a non-toxic water-soluble food colorant using a manual spray bottle. Fifty-six ml of food colorant composed of Brilliant blue (Blue 1) and Allura red (Red 40) (McCormick, London, Canada) was dissolved per liter of water. For the second part, the experiment was repeated on the same saplings that were deprived of irrigation on DOY 122-149 and sprayed with normal water on the evenings of DOY 146-148. This time no colorant was used.

Each sapling was sprayed with approximately 0.5 l or until saturation of its needles (about five minutes per sapling), whichever was reached first. To avoid water simply being taken up by the roots, the stem base and root system of each sapling was covered with a plastic sheet sealed to the pot and stem.

Before the experiment, the roots of young black spruce saplings were plunged in the colorant overnight to test if the colorant could be absorbed by and observed in the plant tissues. These saplings were cut open lengthwise after 24 hours in the colorant solution and checked visually for colorant. The inside of branches and needles showed blue staining of the tissues, indicating that the colorant could be absorbed and transported within the plant.

2.2 Measurements

The volumetric water content (VWC) of the soil was measured with a time domain reflectometry soil moisture meter, shoot water potential was measured with a pressure chamber (model 610 Pressure Chamber, PMS instruments), and photosynthesis was measured using the LI-6400XT Portable Photosynthesis System (LICOR Biosciences, Lincoln, Nebraska) with the 6400-22L Lighted Conifer Chamber. Measurements were taken bi-weekly at mid-day as from one week before the irrigation exclusion until the end of the experiment, and every day after canopy wetting. Measurements were done on 5 plants per group (irrigated/non-irrigated) per sampling in the first part of the experiment and on 3 plants in the second part. The needles were completely dry during measurements to ensure that there was no indirect effect of the canopy wetting, such as a reduction in transpiration. At the end of the experiment, all saplings were abundantly irrigated and water potential was measured once again to verify that they had survived the treatment.

2.3 Statistics

Water potential and photosynthesis in the days before (DOY 92 and DOY 145) and after (DOY 93-95 and DOY 147-149) the canopy wetting were compared to see if there was an improvement of both parameters as a consequence of the treatment. A general linear model (GLM) followed by pairwise post-hoc t-tests in SAS (SAS institute Inc., Cary, North Carolina) was used to test for the effect of the canopy wetting on water potential and photosynthesis.

3. Results

In both parts of the experiment, the VWC of non-irrigated saplings decreased below 10% about 4 days after interruption of the irrigation (Figure 1). The VWC in irrigated plants fluctuated according to the times of irrigation. No increase in VWC was observed after the canopy wetting. When irrigation resumed at the end of the experiment, the soil rehydrated attaining the pre-treatment values.

The saplings that were sprayed with the colorant did not show any signs of staining of the tissues. After 19 and 11 days of irrigation exclusion in the respective experiments, the water potential of the non-irrigated saplings dropped below -2.70 MPa. During the first part of the experiment, water potential never exceeded -2.29 Mpa and went as low as -3.45 Mpa after the spraying. The spraying in the second part of the experiment resulted in an increase in water potential up to -1.89 Mpa, but during the following two days, after multiple wetting events, the water potential dropped again to lower values. The results of the GLM demonstrated significant differences (F=48.88, p<0.001 and F=13.05, p<0.0001 for the first and second experiment respectively, Figure 2). Post-hoc tests showed that there was a significant difference in water potential between the irrigated and non-irrigated saplings. However, there was no difference between the pre- and post-canopy wetting water potential within each treatment (Figure 2).

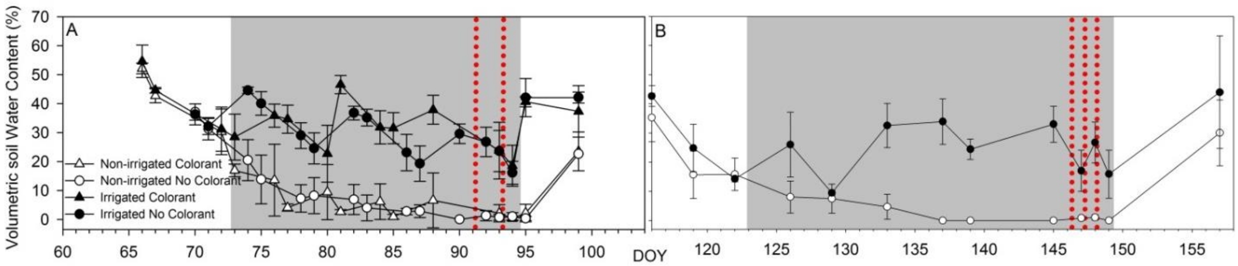

Fig. 1. Volumetric soil water content during the first (A) and second (B) part of the experiment in the non-irrigated (open) and irrigated (solid) plants with (circles) and without (triangles) colorant reported as means with the standard deviations. The shaded background represents the periods with no irrigation. The dotted vertical lines show the times of canopy wetting.

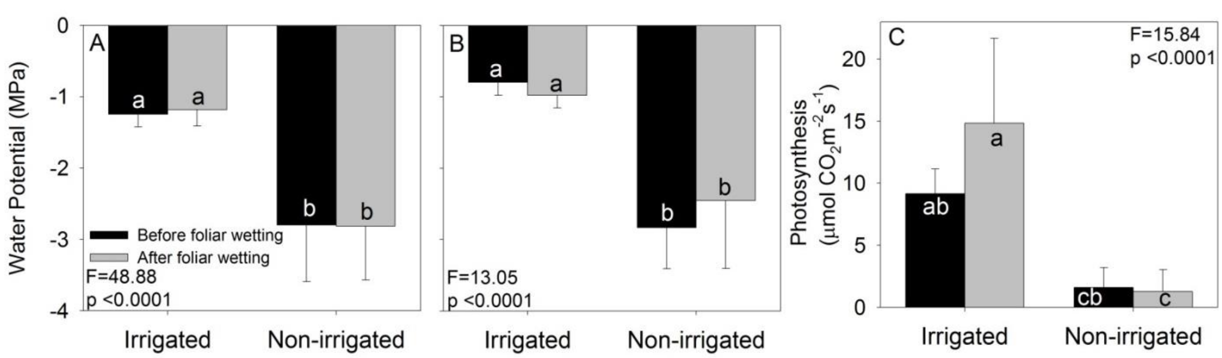

Fig. 2. The stem water potential before (black bars) and after (grey bars) the canopy wetting in irrigated and non-irrigated plants during the first (A) and second (B) part of the experiment. Plus photosynthetic rate (C) before (black bars) and after (grey bars) the canopy wetting in irrigated and non-irrigated plants during the second part of the experiment. Vertical lines show the standard deviation, letters indicate significant differences according to the post-hoc test (p< 0.05), F and p-values of the GLM are given in each graph.

Photosynthesis decreased in the non-irrigated saplings to 0.12 µmol CO2m-2s-1 after 17 days of treatment, whereas the irrigated saplings had a photosynthetic rate of 11.33 µmol CO2m-2s-1 on the same day. The GLM showed significant effects of the irrigation treatments and canopy wetting ($F=15.84$, $p<0.001$), the post-hoc tests showed that there was no significant effect of the canopy wetting. There was a significant difference between irrigated and non-irrigated saplings after the canopy-wetting (Figure 2c). In both experiments, the saplings recovered water potentials and photosynthetic activity similar to the irrigated saplings within one week after irrigation was resumed.

4. Discussion

The results of this experiment showed no evidence of foliar absorption by black spruce saplings subjected to water deficit. The first experiment showed that there was no significant change in water potential, and no absorption of the blue colorant via the needles. It was then considered that even though there was no direct water absorption, and thus no improvement in water potential, the saplings might have been able to recuperate enough water to maintain basic physiological processes such as photosynthesis. The second experiment however confirmed canopy wetting did not affect water potential and photosynthesis. Even though the colorant could be absorbed and transported by the plant tissues, no staining was found in the xylem. The hypothesis that black spruce would be able to absorb rainwater through needles and use it to improve its water relations was definitely rejected by this experiment.

4.1 Absorption

The blue food colorant could be absorbed by the plant tissues of young black spruce as demonstrated by the preliminary test. Katz et al. (1989) observed that dye could be absorbed via the twig xylem, but not via the needles after canopy wetting. In our experiment however, the colorant was not found in any plant tissues after canopy wetting.

The absorption of water and solutes into the leaves depends on several factors, like the wettability of the cuticle. The systematic build-up of aerosol depositions on the leaf surfaces decreases their hydrophobicity, and thus increases their wettability (Grantz, Garner, & Johnson, 2003). Certain species have specialized morphological structures to facilitate water uptake like hydathodes or thrichomes. In species that lack these structures, such as black spruce, water can diffuse into the leaf via the cuticle (Gouvra & Grammatikopoulos, 2003) or via the stomata. Hydraulic activation of stomata can then take place when a continuous thin water film forms on the stomatal walls, enabling the bidirectional transport of water and solutes between the leaf interior and its surface (Burkhardt, 2010). On the other hand, the presence of a water film on the leaf may reduce its photosynthetic carbon uptake (Brewer & Smith, 1997).

4.2 Duration of canopy wetting event and timing of measurements

The plants were sprayed until water started dripping down from the needles, and it was ensured that all leaves and branches were wetted. It is considered that this is sufficient to have an effect on the plant water status, as previous experiments showed the occurrence of foliar absorption in *Pinus strobus* and *Juniperus spp.* after a short-time canopy wetting (Boucher et al., 1995; Breshears et al., 2008). The concentration of suspended materials on leaves is highest at the beginning of rain events, which may quickly facilitate uptake by the plant (Grantz et al., 2003). Black spruce exhibits nighttime stomatal conductance that is strongly dependent on decreasing temperature. It is therefore possible that there was a short-term improvement in the plant water potential, but no effect during the following days. Breshears et al. (2008) took measurements immediately after canopy wetting but hypothesized that the change in water potential could persist over more than a day. Plants were allowed to dry, as in Boucher et al. 1995, to avoid an indirect effect of the canopy wetting such as reduced transpiration. An increase in gas exchange was also to be expected after leaf drying (Gouvra & Grammatikopoulos, 2003; Simonin et al., 2009).

4.3 Drought treatment

No different reaction was observed between irrigated and non-irrigated saplings, however it was expected that there would be a larger foliar water uptake in plants with lower water potential (Breshears et al., 2008; Katz et al., 1989). The water potential of the saplings dropped below -2.70 MPa, which is defined as severe water deficit for black spruce (Balducci, Deslauriers, Giovannelli, Rossi, & Rathgeber, 2013). When soil water potential drops below plant water potential, water can theoretically move down the soil-plant-atmosphere continuum through the passive conduits of roots and stems, which may facilitate the foliar absorption (Nadezhdina et al., 2010). Black spruce often keeps its stomata open, even during drought stress (Stewart, Elabidine, & Bernier, 1995). However, extreme water stresses may limit foliar uptake when the epidermis and cuticle contract due to dehydration (Burgess & Dawson, 2004; Limm et al., 2009).

4.4 Age of saplings

In earlier experiments, it was shown that young black spruce saplings had a reaction to drought, whereas mature trees surprisingly seemed more resistant to its effects (Balducci et al., 2013; Belien et al., 2012). Young needles have higher physiological activity, like a higher stomatal conductance because there is less wax accumulated in stomata (Ludlow & Jarvis, 1971; Rayment & Jarvis, 1999); this may facilitate foliar absorption in younger plant parts. However, the young needles are more hydrophobic than older ones because less particulate matter has been built up on the surfaces (Grantz et al., 2003). In adult plants in a natural environment however, there may be other factors promoting the occurrence of foliar absorption. The presence of mosses and lichens, in particular on twigs and branches, increases the water holding capacity in the forest. Low vapour pressure deficit during rainfall may contribute to an improved plant water status irrespective of stomatal effects (Berry & Smith, 2013) and cloud formation may reduce transpiration. In particular for late successional species, like black spruce, the amount of throughfalling rainwater is lower, whereas the amount of water intercepted by the canopy is higher than in earlier successional species (Barbier et al., 2009).

Although foliar absorption occurs in different species and ecosystems, black spruce may not have developed this mechanism because root water is always available and is a much more efficient water acquisition strategy. Other reasons for not exploiting foliar absorption are that accumulation of leaf water may favour pathogen attacks and inhibit photosynthesis. It is possible that, despite the lack of active absorption of water via the needles, a passive absorption mechanism may be present in mature trees.

This study consists of a greenhouse experiment in which black spruce saplings were excluded from irrigation and then sprayed at night to test if foliar absorption occurred. In contrast to the hypothesis the results showed no evidence of foliar absorption or improvement of water potential and photosynthesis in black spruce saplings. There was no difference in the reaction to foliar wetting between saplings that were water-stressed or well-irrigated. Although the saplings did not show foliar absorption, there is the possibility that mature trees in natural conditions may benefit from foliar wetting because of specific environmental circumstances.

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