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Does soil nutrient availability influence night-time water flux of aspen saplings?

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ABSTRACT

Previous investigations have been demonstrated that night-time water flux may increase or remain unchanged at low mineral nutrient availability. At the same time, it is a well-known fact that night-time water flux is relatively high in fast-growing species, which typically grow in fertile soil. To test the impact of soil nutrient deficiency on night-time water flux and fine-root acclimation in saplings of hybrid aspen (*Populus tremula* L. × *Populus tremuloides* Michx.), a growth chamber experiment was carried out. We set up a hypothesis that night-time sap flux density (F) and night-time water use percentage from daytime water use (NWU) are more intense in fertile conditions, in order to enhance or sustain the high intrinsic growth potential of hybrid aspen. The main limiting element in the low nutrient availability treatment (low-n) was nitrogen. The nitrogen concentrations of leaves and fine-roots exhibited the strongest ($R^2 = 0.95$; $P < 0.001$) positive relationship with NWU and foliar biomass. Both the night-time F and NWU were several times higher in the case of fertilized soil (high-n treatment) compared to low-n treatment ($P < 0.01$). The differences in nocturnal (and in diurnal) F disappeared at the end of the period of sap flow measurements, when the foliage area of trees was almost full-grown. Endogenous increase in water flux during predawn hours was observable only in the high-n treatment. Significantly greater NWU ($P < 0.01$) and specific fine-root length ($P < 0.05$), but smaller fine-root biomass ($P < 0.05$) in saplings of the high-n treatment potentially allow plants to use mass flow in soil more efficiently for transportation nutrients towards roots and to decrease construction costs for fine-root biomass production. Our results suggest that decreased night-time water flux as a result of strong nutrient (especially nitrogen) deficit could be characteristic to fast-growing tree species, which are adapted to grow in fertile soil.

1. Introduction

In the last decade, the night-time transpiration phenomenon has been intensively studied as a potential driver of mineral nutrients (especially nitrogen) from the soil to tree roots and up to the foliage. It has been suggested that increased water flux reduces the nutrient depletion zone of mass flow mobile nutrients like that may otherwise develop in the rhizosphere as a consequence of active nutrient uptake. The mass flow of nutrients may be especially important for plants with low root densities, providing a mechanism for accessing nutrients in the absence of an extensively proliferated root system (Cramer et al., 2008). The reduction of xylem flow is also known to repress xylem loading of different nitrogen compounds (Delhon et al., 1995) and to inhibit the uptake of nitrate and ammonium in fine roots of different tree species at night (Gessler et al., 1998; Geßler et al., 2002).

However, the causality between nocturnal transpiration and mineral nutrition has remained rather unclear and has an ambivalent nature (Daley and Phillips, 2006; Caird et al., 2007; Dawson et al., 2007; Howard and Donovan, 2007, 2010; Marks and Lechowicz, 2007; Scholz et al., 2007; Christman et al., 2009). There is evidence that night-time transpiration increases at low mineral nutrient (N, P) availability (Scholz et al., 2007) or remains unchanged (Howard and Donovan, 2007, 2010; Christman et al., 2009). At the same time it is a well-recognized fact that night-time transpiration is characteristic to shade-intolerant species, which do have relatively high overall growth rate and leaf nitrogen concentration (Daley and Phillips, 2006; Marks and Lechowicz, 2007). Phillips et al. (2010) demonstrated that nocturnal water transport was greater in *Eucalyptus* trees with a higher proportion of young foliage. This suggests that night-time transpiration could be beneficial in periods of high nitrogen demand. Hence, recent findings seem to support the idea that night-time transpiration should be

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higher in trees growing in fertile soils than in the case of nutrient deficiency, because high growth rate and leaf nitrogen concentration will more likely be achieved in fertilized (and well watered) conditions. At the same time, one cannot exclude the possibility that trees growing in nutrient deficiency will transpire more intensively to acquire additional N and P at night, as suggested by Scholz et al. (2007). Caird et al. (2007) pointed out that the relationship between varying night-time leaf conductance responses to nutrients and particular life forms or ecological strategies is unknown and may be related to the underlying causes of nutrient status effects on day-time leaf conductance.

In the current study, impact of mineral nutrient availability on night-time water flux was analysed on hybrid aspen (*Populus tremula* L. × *Populus tremuloides* Michx.) saplings grown in a climate chamber. We set up a hypothesis that night-time sap flux density (F) and night-time water use percentage from daytime water use (NWU) are more intense in fertile conditions, in order to enhance or sustain the high intrinsic growth potential of hybrid aspen.

2. Materials and methods

2.1. Sample trees and experimental conditions

The experiment was carried out in a double-sided growth chamber Percival AR-95 HIL (Percival Scientific Inc., Perry, IA) from the beginning of April to the end of July 2009. Eight 3-year-old micropropagated hybrid aspen (*P. tremula* L. × *P. tremuloides* Michx.) saplings were dug out from Rõka experimental site (Kupper et al., 2011), Järvselja Experimental Forest District (58°24′N, 27°29′E, altitude 40–48 m) in south-eastern Estonia before bud break in April 2009. The average diameter (at the base of the stem) and height of the sample trees was 10.2 mm and 1.06 m, respectively. The root system of each transplant was washed carefully to remove soil particles and the saplings were planted into the 10-l pots. The pots were without drainage holes in order to prevent the leakage of water and the leaching out of mineral nutrients.

The amount of growth substrate was different for the two nutrient availability treatments, being 9 and 7 l for the high nutrient availability (high-n) and the low nutrient availability (low-n) treatments, respectively. The difference in soil volume enabled us to equalize the plant size/soil volume ratio and also ensured similar soil moisture conditions in both treatments. The pots were filled with a growth substrate of calcimined sphagnum peat with a particle size of up to 20 mm. The organic content of the peat was 98% and the degree of decomposition was between 2 and 4 according to the Von Post classification. Each pot contained up to 3% gravel with a particle size of 2–5 mm. The initial concentration of macro- and micronutrients in the growth substrate (Appendix A) was about two times higher in the high-n treatment than in the low-n treatment, whereas the dominating N source was NO_3^- nitrogen. In addition, the growth substrate of the high-n treatment was enriched with a water dissolved fertilizer (containing 6.6% NO_3^-, 2.4% NH_4^+, 9% P_2O_5, 27% K_2O, 3% MgO, 0.01% B, 0.01% Cu, 0.06% Fe, 0.04% Mn, 0.001% Mo and 0.01% Zn) nine times during a growth period. Each tree was fertilized with a 300 ml of solution (0.1%). The average soil water pH_{H_2O} measured with a digital pH meter (Model 60; Lazar Research Laboratories, Inc., Los Angeles, CA) was 5.8 and 4.9 for high-n and low-n treatments, respectively.

To water the trees, the pots with saplings were weighed, usually every evening and the amount of daily consumed water was added to the pots to restore the soil water reserve. The threshold of soil water content was set to 60% of the field capacity. The 20% larger soil volume in the pots of the fertilized trees enabled 20% more water to be added to the pots at the same soil water content threshold, and a presumable decline in soil matric potential (Ψ_S) as a result of greater water consumption due to the larger size of fertilized trees to be partially avoided. The average Ψ_S did not fall below −25 kPa during the whole study period. During sap flow measurements the daily average Ψ_S was −11.5 and −12.9 kPa in high-n and low-n treatments, respectively.

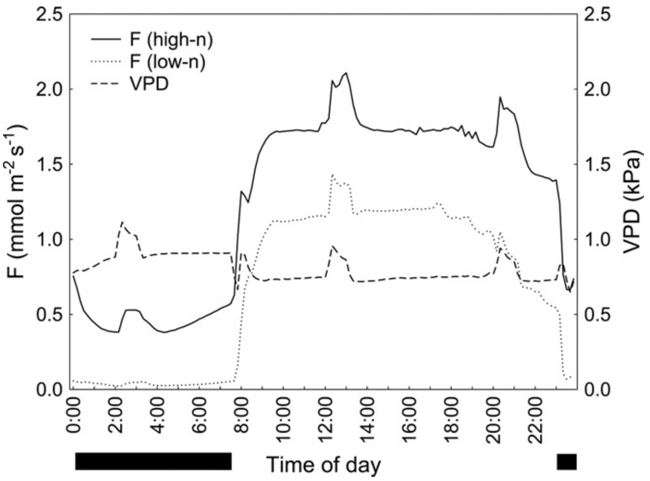

Fig. 1. Average daily course of the stem sap flux density (F) in high nutrient availability treatment (high-n) and low nutrient availability treatment (low-n) and air vapour pressure deficit (VPD) in growth chamber during period of sap flow measurements. Both lines of the F represent the average value of four measured trees. The line of the VPD represents the average value in the growth chamber. The black strip expresses night-time.

The night/day length in the chamber was 8.5/15.5 h, and the light was switched off from 23:00 to 7:30 h. The daily photosynthetically active radiation (PAR) was kept constant at 400–800 μmol m^{-2} s^{-1} for the upper foliage of the saplings. Both the relative humidity (RH) and temperature of the air (T_a) varied between the opposite sides of the growth chamber. The average RH and T_a were 71.3% and 20.6 °C in left side of the chamber but 65.1% and 22.4 °C in the right side of the chamber. However, the trees from the different treatments were distributed equally between the two sides of the chamber (four sample trees on both sides: two from high-n and two from low-n treatment) and therefore the two nutrient availability treatments are comparable to each other. The average RH was kept ca 5% lower at night than in the daytime, in order to induce nocturnal transpiration flux in sample trees (Fig. 1). The air temperature of the chamber was kept constant during the night and day. Vapour pressure deficit of the atmosphere (VPD) was calculated as the difference between the saturation and ambient vapour pressures using RH and T_a data. RH and T_a were measured with four HMP45A sensors (Vaisala, Helsinki, Finland) located at two heights (70 and 120 cm) on the two sides of the growth chamber. The readings of the HMP45A probes were recorded with a DL2e data logger (Delta-T Devices, Burwell, UK). Ψ_S was measured with dielectric water potential sensors (MPS-1; Decagon Devices, Pullman, WA), one per each pot, located at a depth of 10–15 cm and connected to the Em50 data loggers (Decagon Devices). The readings of all sensors were collected every 1 min and stored as average values every 10 min with the data loggers.

2.2. Measurements of sap flow and leaf area

The xylem sap flow of saplings (N = 8) was recorded with a sap flow system T4.2 (EMS Brno, Brno, Czech Republic), furnished with 'Baby Kucera' sap flow sensors for 8–12 and 12–18 mm stem diameter. Each sample tree was fitted with one sensor installed ca 40–50 cm above the ground. The sap flow data was recorded every 1 min and stored as 10-min averages from 37 to 57 days after bud break in May and June. Nevertheless, only the 11 days