

GAS-EXCHANGE RESPONSE OF NORWAY MAPLE (*ACER PLATANOIDES* L.) AND SILVER LIME (*TILIA TOMENTOSA* MOENCH) SAPLINGS TO FOREST THINNING

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Abstract

A species-specific initial response of gas-exchange and water use efficiency of Norway maple and Silver lime saplings were observed after a forest thinning. The photosynthetic rate increased significantly both in Norway maple and Silver lime leaves. The transpiration rate of Norway maple increased more intensively, in comparison to Silver lime. Norway maple saplings suffer both from intensive light and moisture deficit, while Silver lime saplings were more resistant to the patch opening. Stable water use efficiency in Silver lime leaves in response to the thinning may result from the better ability of this species to keep available water, which could be considered as the greater resistance to patch opening. These results may serve as a basis for improvement of forestry approaches in mixed deciduous forests with the presence of Norway maple and Silver lime.

Key words: patch, photosynthesis, transpiration, understory, water use efficiency.

Introduction

Thinning is the main forestry practice to increase tree growth by reducing stand tree density and competition for environmental resources. Further, small group selection harvests (small patch cuts) may be employed to increase the heterogeneity of forest conditions in a management area (Grebner et al. 2012). The physical environment within a small open area surrounded by forest differs from that under the canopy or in a large open area (Runkle 1985). Forest thinning increase the amount of incident light below the canopy, causing changes in temperature and water regimes inside the stand (Tang et

al. 2005), and probably can affect the nutrients availability (Blanco et al. 2005). Positive effects of thinning on tree growth are therefore caused by the reduction of a crown and belowground competition and the concentration of potential growth in only a reduced number of selected individuals (Martín-Benito et al. 2010).

Relatively few studies have compared plasticity in gas-exchange characteristics of woody plants in contrasting light environments after a forest thinning. The specific regimes of sub-canopy light, temperature, humidity, and nutrient availability within the patches can provide an advantage of shade-intolerant tree species, but at the same time can reduce

the physiological potential for adaptation and survival of sapling of shade-tolerant species (Kobe and Coates 1997). Competitive dynamics can then be assessed in eco-physiological context, wherein plant performance and distribution are assessed in relation to fine-scale, competitor-induced environmental variation (Burton and Bazzaz 1995). Burton and Bazzaz (1995) and Sipe and Bazzaz (1994) showed that specific differences in the physiological performance and plasticity of tree species lead to differences in their ability to invade and compete in open patches. The light acclimatization begins initially on the primary physiological processes, such as photosynthesis and transpiration. According to Chazdon (1992), an accurate picture of the photosynthetic characteristics of forest understorey plants must incorporate transient photosynthetic responses. Chow et al. (1991) observe that shade-tolerant species tend to have low maximum rates of photosynthesis, even when grown under conditions of high light availability, due to intrinsic mesophyll factors. Köstner (2001) established a linear increase in transpiration rate with increasing net radiation for spruce and beech canopies. He suggests that daily maximum of vapour pressure deficit is the best single atmospheric predictor of daily rate of transpiration. While the transpiration of gymnosperm correlated strongly with stand age (Köstner et al. 2002), in angiosperm remained almost constant over a wide range of age (Köstner 2001). In accordance to Wuenscher and Kozłowski (1971) water-use efficiency (WUE), the ratio of CO₂-uptake to water-loss, decreased along the gradient from xerophytic to mesophytic species.

The aim of this study was to compare the initial response of gas exchange and WUE of Norway maple (*Acer platanoides* L.) and Silver lime (*Tilia tomentosa* Moench) leaves after a patch opening. Both species are categorized in the literature as a non-pioneer, shade tolerant and tend to grow near other species in dense woodlands (San-Miguel-Ayanz et al. 2016, Schütt and Roloff 1994). We aimed to determine whether these two species have a species-specific early stress response and light plasticity, which could be considered as an indicator of different adaptive mechanisms.

Materials and Methods

Site description and plant material

The experiment was conducted in the arboretum of the University of Forestry, Bulgaria (Table 1).

After a small patch opening in a mixed broadleaf bio-group, dominated by Norway maple and Silver lime, a part of the understorey saplings of the experimental species were exposed to full sunlight, whereas the other part remained in a shade. Norway maple is a fast-growing species, which germinates and grows quickly in shade, even under closed canopy (San-Miguel-Ayanz et al. 2016). Silver lime is relatively resistant to persistently low humidity because the dense hairiness of the young leaves and shoots reduces transpiration. Young trees endure shadows, but older ones have high light requirements and must be free (Schütt and Roloff 1994).

Table 1. Site and stand characteristics.

Site characteristics	
Latitude, ° ' ''	42° 39' 09" N
Longitude, ° ' ''	23° 21' 30" E
Altitude, m a.s.l.	590
Soil type (Jordanova and Jordanova 1999)	Pellic Vertisol
Mean annual temperature, °C (Alexandrov et al. 2004)	9.9
Annual amounts of precipitation, mm (Alexandrov et al. 2004)	571
Stand characteristics	
Height, m	17
Diameter at breast height (DBH), cm	20
Leaf area index (LAI), m ² ·m ⁻²	5.57
Patch area, m ²	48

Note: Height and DBH were measured on ten Norway maple and ten Silver lime trees from the main stand. LAI was calculated in accordance to Beer's law and following Monsi and Saeki (2005): $LAI = \cos\theta \cdot \ln(I/I_0) \cdot k^{-1}$, where θ is the zenith angle, I_0 is the incident radiation, I is the radiation transmitted below canopy, k is the extinction coefficient, and LAI is the leaf area index. According to Bréda et al. (2003) k assumed to constant: $k=0.50$.

Gas exchange measurements and micro-environmental conditions

The measurements of leaf gas exchange and recording of micro-environmental conditions were performed a week after thinning. Twenty randomly chosen saplings (five per plant species, both from the understory and from the patch) were used for the measurements. The values of examined variables were measured on the third and the fourth fully developed main stem leaves from the top of each sapling (Sesták 2012).

The photosynthetic rate (A_N , $\mu\text{mol}\cdot\text{CO}_2\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) and transpiration rate (E , $\text{mmolH}_2\text{O}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) of each leaf (two per sapling) were measured with a portable infrared gas analyser Li-6400 (Li-Cor Biosciences, Lincoln, NE, USA) equipped with shielded thermocouples, quantum sensor (LI-190) and red light-emitting diode light source (6400-02) in the chamber. Ambient photosynthetic photon flux density ($PPFD$, $\mu\text{E}\cdot\text{mol}^{-1}\cdot\text{air}$), CO_2 concentra-

tion ($\mu\text{molCO}_2\cdot\text{mol}^{-1}\cdot\text{air}$), air temperature (T_A , °C) and relative humidity (HD , %) were recorded simultaneously during measurements through Li6400 sensors. The air pumped into the Li-6400 was passed through a buffering tank (10 L) with a constant flow rate ($500\ \mu\text{mol}\ \text{air}\cdot\text{s}^{-1}$) to reduce the time for measurement stabilization. Due to determine light-saturated photosynthesis, the PPFD in the chamber was maintained at $1000\ \mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. The data were recorded after a stabilization time of minimum 5 minutes and lowering the total coefficient of variation to less than 0.5 %. Water use efficiency (WUE , $\mu\text{molCO}_2\cdot\text{m}\cdot\text{mol}^{-1}\text{H}_2\text{O}$) was calculated in each case of measurements as a proportion of A_N and E (Barrs 1968).

Statistical analysis

Shapiro-Wilk test (P -value < 0.05) was used to determine whether the outcome variables were normally distributed. Vari-

ables were reported as medians and quartiles because the hypothesis of normal distribution was rejected in each case. The Mann-Whitney rank sum test (P -value < 0.001) was used to test for differences between the medians of micro-environmental parameters in both patches. A Kruskal-Wallis one-way analysis of variance on ranks (P -value < 0.001) was used to determine differences in the median values of the investigated physiological parameters among the treatment groups. A multiple-comparison procedure (Tukey Test, P -value < 0.05) was used to isolate the group or groups that differ from the others. All statistical proceedings were performed with MS Excel (Office 2016, Microsoft, Redmond, WA, USA) and user-defined functions in Visual Basic for Applications (MS VBA 7.1, Microsoft, Redmond, WA, USA).

Results

Micro-climatic conditions

Photosynthetic photon flux density ($PPFD$) was the most varying micro-climatic factor between patch and understory. The $PPFD$ increased almost 120 times in patch in compare to understory (Table 2).

Table 2. Micro-environmental characteristics of understory (U) and patch (P).

Micro-climatic factors	U	P
$PPFD$, $\mu E \cdot m^{-2} \cdot s^{-1}$	4.0 a	479.0 b
T_a , $^{\circ}C$	25.3 a	26.2 b
RH , %	49.1 a	46.7 b
CO_2 , $\mu molCO_2 \cdot mol^{-1}air$	384.6 a	379.9 a

Note: Values shown are medians ($n = 20$). The same letters on each row indicate that there is no statistically significant difference (Mann-Whitney rank sum test, P -value < 0.001) between medians in both areas.

Both the higher T_a and lowest RH in the patch are due to higher illumination in comparison to understory. The lack of variation in CO_2 -concentration between two areas was presumably due to small area of the patch.

Gas-exchange

The photosynthetic rate increased significantly after the patch opening both in leaves of Norway maple and Silver lime (1.9 and 1.7 times respectively). The understory saplings of Silver lime photosynthesize more actively than saplings of Norway maple and this difference has kept after a thinning (Fig. 1).

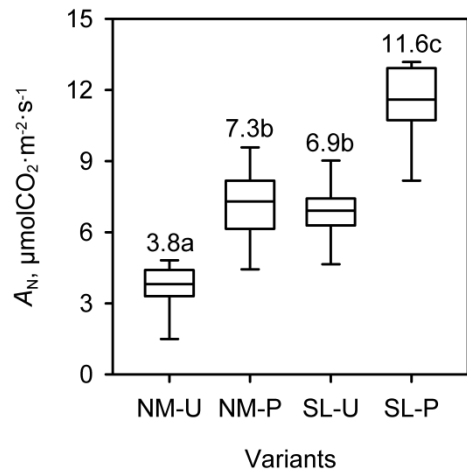


Fig. 1. Photosynthetic rate (A_N) of Norway maple (NM) and Silver lime (SL) in the understory (U) and in the patch (P).

Note: Medians and 25th and 75th percentiles are shown in boxes, and minimum and maximum values are shown as whiskers. The median values above boxes, indexed by the same letter, are not significantly different (Tukey test, P -value < 0.05).

After a patch opening the transpiration rate both of Norway maple and Silver lime

also increased significantly. In the leaves of patch saplings of Norway maple, E increased 5.72 times, while in the Silver lime leaves this increase is only 2 times (Fig. 2).

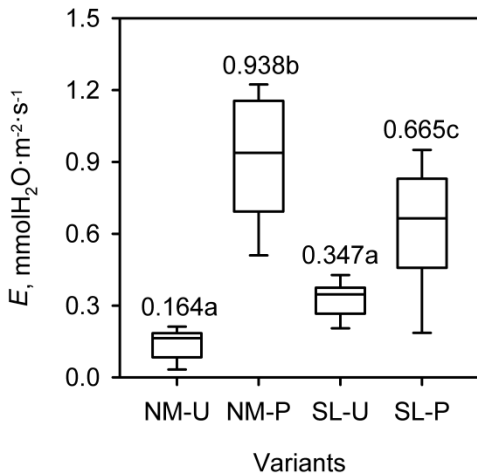


Fig. 2. Transpiration rate (E) of Norway maple (NM) and Silver lime (SL) in the understory (U) and in the patch (P).

Note: Medians and 25th and 75th percentiles are shown in boxes, and minimum and maximum values are shown as whiskers. The median values above boxes, indexed by the same letter are not significantly different (Tukey test, P -value < 0.05).

As a result, WUE of Silver lime was not significantly different between patch and understory, while the understory Norway maple saplings used water 3.15 times more effectively in comparison to patch saplings (Fig. 3).

Discussion

The initial response in photosynthesis of two species to the patch opening was almost similar, while the response of transpiration was species-specific. Rapid light

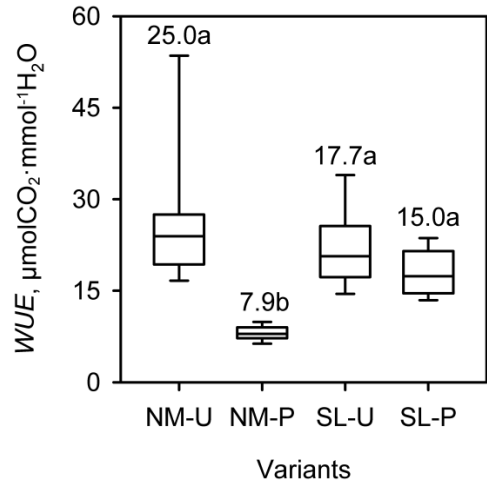


Fig. 3. Water use efficiency (WUE) of Norway maple (NM) and Silver lime (SL) in the understory (U) and in the patch (P).

Note: Medians and 25th and 75th percentiles are shown in boxes, and minimum and maximum values are shown as whiskers. The median values above boxes, indexed by the same letter are not significantly different (Tukey test, P -value < 0.05).

saturation of the leaves of these shade-tolerant species (San-Miguel-Ayanz et al. 2016, Schütt and Roloff 1994) was probably the leading factor of photosynthesis increase. Chow et al. (1991) even observe prone to photoinhibition in sudden exposure to high irradiance, which presumably leads to further limit the increase in photosynthesis when the understory opened. Despite of the higher rate of photosynthesis of Silver lime within the patch, Norway maple saplings may better cope with the high illumination. The established variation in photosynthesis agrees with the finding of Chazdon and Field (1987) that photosynthetic capacity shows a little variation among leaves of understorey plants, despite high variation in light availability among leaf microsites.

The transpiration rate of thin leaves in Norway maple respond much stronger, than in the morphologically more adapted leaves of Silver lime. Bréda et al. (2006) point out that during drought for most tree species, a more severe limitation occurred for E than for A_N , and as a result, water use efficiency generally increases. However, the Norway maple saplings tried to maximize carbon assimilation by keeping stomata opened even in severe drought stress. Such strategy leads to dramatic decrease of WUE after patch opening. In the same time, stable WUE in Silver lime leaves in response to the changed conditions may result from the ability of this species to keep available water, which could be considered as the greater resistance to patch opening, probably due to xeromorphic features of the leaves.

Conclusions

The short-term response of gas-exchange of tree saplings balances a complex set of site constraints to each microenvironment patch type. Immediately after the patch opening, the Norway maple saplings suffer heavily both from intensive light and moisture deficit. The Silver lime saplings showed better resistance to the increased amount of incident light and related changes in temperature and humidity. This study presents an early initial response of the Norway maple and Silver lime saplings to the suddenly increased light. Further research is necessary to understand the whole plant physiological response in the understorey for a longer period and to evaluate the effect of subsequent thinning practices on the balance between assimilation and transpiration of the two species.

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