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GAS-EXCHANGE DYNAMICS WITHIN THE CROWN OF NORWAY SPRUCE

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Abstract

The balance between CO_2 income during photosynthesis and H_2O release during transpiration is strongly influenced by differentiation of leaves within the canopy. Gas-exchange and water use efficiency (WUE) were studied in respect to branch position in the crown of 37-year-old Norway spruce [*Picea abies* (L.) Karst.] tree, growing in the Western Stara Planina. The needles of the middle-crown branches had significantly highest rate of net photosynthesis compared to the upper and lower crown. The rate of transpiration and vapour pressure deficit gradually decreased to the upper-crown branches. The highest water use efficiency was established for the needles in the top of the crown. The lowest photosynthesis and WUE, along with the highest transpiration and vapour pressure deficit of the branches in the crown base of the tree are indicative for the diminished adaptive capacity. The study results could contribute to better understanding of the physiological mechanisms of branch self-pruning.

Key words: photosynthesis, self-pruning, stomatal conductance, transpiration, water use efficiency.

Introduction

Recent models of canopy physiology (Cannell and Thornley 1998, Jones 2013) are based on the assumption that leaf physiological characteristics are constant throughout the tree crown. However, Rosell and Sanz (2012) have shown that variation in leaf geometry can result in photosynthetic variation related to changes in the surface area for light interception. The conifer needles are grouped closely together, so that photosynthesis is strongly affected by shading of one needle by another (Leverenz and Jarvis 1979) or of one branch by another (Norman and Jarvis 1974). Leaves that are shaded by other leaves of the same plant experience limitations similar to those experienced by a plant shaded by other plants (Berry 1975). Björkman (1981) explained that separate crown part of tree plants reacts differently to light variation. There are several reviews on the specific anatomical and morphological characteristics of the sun and shade leaves that provoke big variation in the physiological processes (Leverenz and Jarvis 1980, Masarovicová and Štefančík 1990, Thornley 2002, Terashima et al. 2006).

Furthermore, there are large changes in the microclimatic conditions with increasing of depth in the forest canopy (Campbell and Norman 1998). The light direction, light intensity and light spectrum are strongly affected by the crown and canopy architecture (Jones 2013). Bazzaz and Williams (1991) found out that the air concentration of CO_2 in the crown base is higher than that in the top of crown. The failure of conventional flux-gradient relationships in the crown space, which may be explained with the sporadic penetration of transporting eddies into the canopy (Denmead and Bradley 1985).

The data about the differences of the photosynthesis intensity for sun and shade shoots in Norway spruce are controversial. Wierzbicki (1980) has reported that maximal photosynthesis is higher in sun shoots. On the other hand Fuchs et al. (1977) found higher photosynthetic rate in the shade than in the sun crown. Hinckley and Ritchie (1970) showed that stomatal activity increased, but water stress decreased with increasing of branch position in the crown of spruce. Their results suggest that water levels within the crown are in spatial gradient. Sellin and Kupper (2004) define a hypothesis that stomatal conductance at the base of the crown is constrained not only by low light availability but also by plant's inner hydraulic limitations.

The aim of this study is to find out the specificity in the gas-exchange within the vertical crown profile of Norway spruce during the phase of intensive branch self-pruning. This knowledge could be useful for better understanding of the physiological mechanisms of branch self-pruning.

Table 1. Site description and plant material.

Site description		Plant material	
Altitude, m a.s.l.	825	Age, years	37
Latitude, °	43.15	Height of tree, m	20.0
Longitude, °	23.14	Height of crown, m	11.2
Slope, °	8	Diameter at breast height (DBH), cm	21.6
Exposure	East	Trees density, ha^{-1}	1150

Materials and Methods

Site description and plant material

The experiment was conducted in the Western Stara Planina. Site description and plant material characteristics are shown in Table 1.

The study was carried out in even-aged forest monoplantation in phase of branch self-pruning. The measurements were performed on an experimental tree, chosen on the basis of mean diameter at breast height (DBH) and mean crown length. Thirty-three yearling branches with three different geographical expositions were taken from eleven crown levels (at every one meter from the base to the top of the crown). The third leading shoot from the top of the branches were used for gas-exchange measurements.

Gas-exchange measurements

Foliar gas-exchange measurements were acquired using a LI-6400 portable infrared gas analyzer (LI-COR Ltd., Lincoln, Nebraska, 68504 USA) with the conifer chamber (6400-05) on mature needles at ambient conditions: rate of photosynthetically active radiation, CO_2 concentration, air temperature and relative humidity (Table 2).

The rate of photosynthesis (An), transpiration rate (E), stomatal conductance (gs)

Table 2. Microclimatic conditions during the gas-exchange measurements.

Parameter	Value ± SE
Air temperature, °C	23.35 ± 0.09
Air humidity, %	50.82 ± 0.18
PAR, $\mu mol \cdot m^{-2} \cdot s^{-1}$	867.8 ± 9.4
Air CO_2 concentration, ppm	402.9 ± 0.1

and vapour pressure deficit of leaves (VpdL) were measured in mid-October, in a clear and sunny day. The water use efficiency (WUE) as ratio between An and E and the intrinsic water-use efficiency (iWUE), defined as ratio between An and gs, were calculated. Data were taken after a minimum 30-minute LI6400 calibration period. Readings were logged when gas-exchange was become stable as marked by: (a) visually stable intracellular CO_2 concentration and net CO_2 assimilation rates values and (b) a total coefficient of variation less than 0.5 %, according to the Li-6400 manual (2012). For recalculation of the measured elements of gas-exchange, the projected area of the needles of the experimental shoots was determined with open source software ImageJ (Rasband 2016).

Data analysis

Due to a random distribution of the physiological data (Shapiro-Wilk Normality Test), the medians and median absolute deviations were calculated. The quadratic polynomial regression was used for the analysis of the relationships between branch position throughout the crown and the rate of particular physiological parameter. The significance of the regression coefficients (R^2) was tested by F-statistics. Only significant coefficients were discussed.

Results and Discussion

The highest rate of photosynthesis was measured within the range from 35 % to 90 % of the crown length (Fig. 1). The rate of photosynthesis decreased along with light attenuation in the base of crown and also a sharp decrease was found in the top of crown. Such tendency may refer to the specific crown architecture of Norway spruce, which is adapted to efficient light utilization (Schulze 2005). The photosynthetic rate at light limitation is largely determined, apart from the light, and by the air temperature (Kirschbaum and Farquhar 1984), whereas at light saturation is mostly determined by CO_2 concentration and ribulose-1.5-bisphosphate carboxylase/oxygenase (Rubisco) activity (von Caemmerer et al. 2009).

The transpiration rate decreased gradually from the base to the top of crown, showing big variation among the separate crown levels. However, the greatest variation and lack of significant tendency within the crown were found about gs. Present results are in agreement with the findings of Hinckley and Ritchie (1970) that in the top of spruce crown water stress increased, but do not confirm the hypothesis of Sellin and Kupper (2004) for a gradient of stomatal conductance. The highest E in the base of the crown is probably due to favourable air humidity in this canopy level. In the same time the highest E and lowest light intensity in the base of crown probably reflect in a decrease of An. VpdL decreased gradually from the base to the top of the crown. The big VpdL in the lower crown parts provokes an intensive transpiration and limited photosynthesis. The clearest tendency was found out in the vertical dynamics of WUE. The low efficiency of water utilization of the branches in the base of the crown is probably evidence for a suppressed wa-

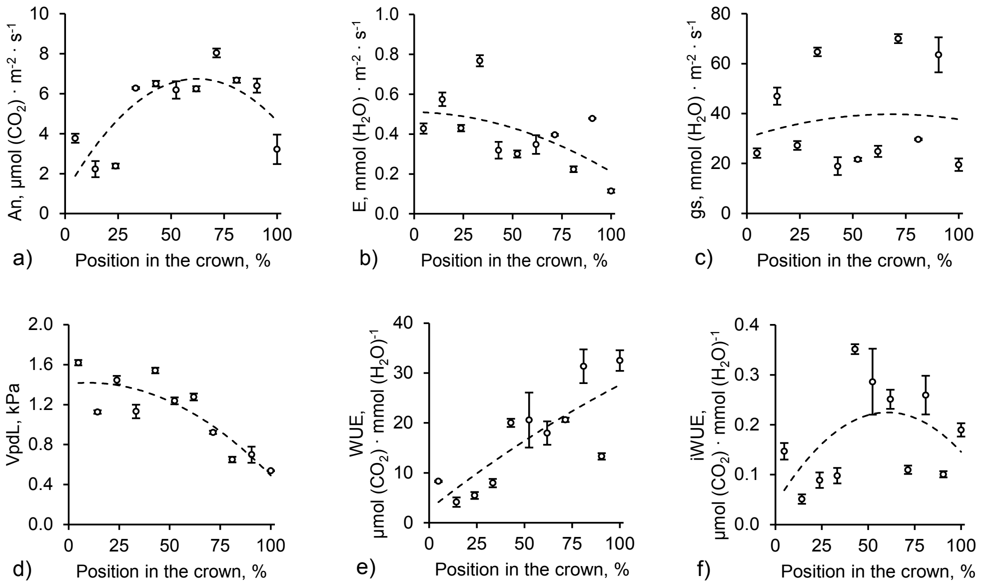

Fig. 1. Vertical gradient of: a) rate of photosynthesis (An); b) rate of transpiration (E); c) stomatal conductance (gs); d) vapour pressure deficit of leaves (VpdL); e) water use efficiency (WUE); f) intrinsic water-use efficiency (iWUE) within Norway spruce crown.

Note: Median (○) ± median absolute deviation and quadratic polynomial regression (---) is presented.

ter and CO_2 balance. Such tendency may lead to intensive self-pruning of the trees. The iWUE is influenced by the high variation of gs and the well-defined trend of An

Table 3. Coefficients of determination and F-statistics of polynomial regressions between branch position in Norway spruce crown and photosynthetic rate (An), transpiration rate (E), stomatal conductance (gs), vapour pressure deficit of leaves (VpdL), water use efficiency (WUE) and intrinsic water use efficiency (iWUE).

Physiological parameters	R^2	F test	*P* value
An	0.497	14.831	< 0.001
E	0.396	9.823	< 0.001
gs	0.007	0.103	0.902
VpdL	0.737	42.036	< 0.001
WUE	0.551	18.442	< 0.001
iWUE	0.211	4.013	0.029

within the crown profile. The lowest levels of iWUE in the base crown part contributes to restricted ability for survival of these branches. Great variance in measured physiological parameters obtained in the present study definitely do not support the idea for the permanence of leaf physiology throughout the crown, which is the basis of some models of canopy physiology.

The regression analysis revealed significant dependence of An, E, VpdL, WUE and iWUE on branch position within the vertical profile of crown (Table 3).

The highest dependence for VpdL (R^2 = 0.737) is probably due to morphological gradient of the needles within the crown. The volume of intercellular space increases with increasing of light and tree height (Niinemets and Kull 1995, Grassi and Bagnaresi 2001). The WUE of needles is depended close to linearly on the branch positions within the crown. The needles in the top of crown had highest WUE, i.e. the most adequate CO_2 and H_2O balance compared to needles in the crown base. Apart from the light deficit in the base of the crown (Sorrensen-Cothern et al. 1993), the lowest WUE along with the highest VpdL probably have a key role for branch self-pruning.

Conclusions

The following tendency within the Norway spruce crown is found:

- The results obtained in the present study definitely do not support the idea of permanence of leaf physiology throughout the crown.
- The needles of the middle-crown branches showed significantly higher rate of net photosynthesis compared to the upper- and lower-crown branches.
- The rate of transpiration and vapour pressure deficit gradually decreased to the upper-crown branches.
- The highest water use efficiency was established for the needles from the top of the crown.
- The gas-exchange dynamics within the vertical crown profile approved the inability of base-crown branches to keep a positive H_2O balance, which is probably the significant reason for self-pruning.

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