SEASONAL CHANGES IN LEAF GAS EXCHANGE PARAMETERS IN PLATANUS ACERIFOLIA WILLD. AND ACER PSEUDOPLATANUS L. SEEDLINGS ON UNDEVELOPED ALLUVIAL SOIL /FLUVISOL/ JOV ANA KRSTIĆ 1
SAŠA ORLOVIĆ 1
ZORAN GALIĆ 1
ANDREJ PILIPOVIĆ 1
SRĐAN STOJNIĆ 1

Abstract: Seasonal changes of net photosynthesis (A), stomatal conductance (gs) and transpiration (E) were researched in Platanus acerifolia Willd. and Acer pseudoplatanus L. Measurements were carried out four times during vegetation period (July 16, August 20, September 5 and September 22) 2011 at seedling age 2+1, cultivated in the nursery. Soil in the nursery belongs to the type of undeveloped alluvial soil (fluvisol), sandy loam form, with the dominant fraction of fine sand (63.5%) and silt+clay fraction in a lower concentration (34.7%). A sharp reduction in net photosynthesis was observed in the second part of August and at the beginning of September, when both species exhibited their lowest net CO₂ assimilation. Minimum A was 7.27 and 7.0 μmol m⁻² s⁻¹ in P. acerifolia and A. pseudoplatanus, respectively. Stomatal conductance followed rise-and-fall pattern of net photosynthesis during the entire period of observation. The seasonal course of transpiration was similar in P. acerifolia and A. pseudoplatanus, with a peak at the beginning of September. Maximum transpiration rate was 2.87 and 3.62 mmol m⁻² s⁻¹ in P. acerifolia and A. pseudoplatanus, respectively. Statistically significant correlation between net photosynthesis and stomatal conductance, in both species, suggests that stomatal closure was the main factor controlling CO₂ assimilation. Incomplete recovery of stomatal conductance and net photosynthesis in A. pseudoplatanus, after the rainfall at the end of September, suggests remaining stomatal limitations. Inferiority of A. pseudoplatanus was probably related to the sensitivity of this species to summer heat and drought owing to the fact that this species is native for sites determined by large share of silt in the soil texture and high content of moisture and nutrients in the soil.

Keywords: Acer pseudoplatanus L., Platanus acerifolia Willd., net photosynthesis, transpiration, stomatal conductance.

1 Jovana Krstić, dipl. ing.; Prof. Saša Orlović, Ph.D., full professor; Andrej Pilipović, Ph.D., research associate; Zoran Galić, Ph.D., senior research associate; Srdan Stojnić, Ph.D., research associate, Institute of Lowland Forestry and Environment Novi Sad
in upwind velocity, shelter for wildlife, etc. Although reforestation programs have a long tradition in the province, satisfactory results have been achieved only in the cases of poplar and willow plantations. Unfortunately, there is still a lot of evidence regarding failures in reforestation attempts which involved other tree species.

After planting, seedlings are very often exposed to extreme conditions in soil and unfavorable climate conditions (Miller, D.B., 1983). Therefore, it is important to understand the interactions between physiological responses of seedling and site environmental conditions (Rafiyannis, Y. et al., 2006).

According to Anjum, S. et al. (2011), drought stress is the most harmful factor influencing a wide range of plant responses, ranging from cellular metabolism to changes in growth rates. However, except of drought stress, gas exchange in plants is also influenced by other factors, such as air temperature and vapor pressure deficit (Day, M.E., 2000). For example, as temperature increases above the optimum for photosynthesis, intercellular CO$_2$ concentration increases causing stomatal closure. Stomata of water-stressed plants may be particularly sensitive to increases in CO$_2$ concentration (Osonubi, O., Davies, W.J., 1980a). Likewise, vapor pressure deficit is recognized as one of the most important environmental sources of variation in stomatal conductance (Bunce, J.A., 1999).

Aranda, I. et al. (1996) state that net photosynthesis is an important indicator of vitality and competitive ability of species at the particular site. Investigating the relationship between physiological parameters and survival rate in the seedlings of *Acer pseudoplatanus*, *Castanea sativa* and *Quercus frainetto*. Rafiyannis, Y. et al. (2006) found that differences in mortality between species were the result of differences in tolerance to water stress. Authors concluded that superiority of oak was related to the fact that oak was the only species which occurs naturally at the place where afforestation is carried out, and therefore is adjusted to environmental conditions of the site. Also, net photosynthesis and related gas exchange parameters have been recognized as determinants of plant productivity. The studies of different authors show that research of these parameters can provide useful information about growth potential and plant productivity (Kundu, S.K., Tigerstedt, M.A., 1998; Orlovic, S. et al., 2001; Orlovic, S. et al., 2006).

According to Markovic, J., Tatalovic, I. (1995), the area of Vojvodina is suitable for a wide range of woody species and new forests should be established of various forest trees and shrubs. Conserving forest biodiversity is a prerequisite for the long-term and broad flow of forest ecosystem services (Secretariat of the Convention on Biological Diversity, 2009). Therefore, this study presents the results of seasonal changes in net photosynthesis, transpiration and stomatal conductance, in three year old seedlings of *Platanus acerifolia* Willd. and *Acer pseudoplatanus* L., cultivated on undeveloped alluvial soil (fluvisol). As fluvisol occupies approximately 9% of total land area in Vojvodina (Galic, Z. et al., 2011), the aim of research was to examine the physiological response of given species to environmental conditions which prevail in a large part of the province. Although fluvisol is the most appropriate for establishment and growing of poplar plantations, the possibility of planting other tree species on this soil type should not be neglected. The selection of appropriate tree species will be of great importance for establishing and survival of new forests and shelterbelts.
2. MATERIAL AND METHODS

Experimental site and plant material

Research was conducted in the nursery of Experimental Estate “Kaćka Šuma” of the Institute of Lowland Forestry and Environment, which is located in Kać (N 45°17; E 19°53; 76 m a.s.l.). The climate records are obtained from the weather station “Rimski Šančevi” (N 45°20’, E 19°51’; 84 m a.s.l). Temperature and precipitation were averaged for the period between 1966 and 2004. Mean annual temperature is 11.1°C, annual sum of precipitation is 624 mm. During the vegetation period (April-September) mean air temperature is 17.8°C and the precipitation amounts 369 mm.

The study involved seedlings of two tree species: *Platanus acerifolia* Willd. and *Acer pseudoplatanus* L., age 2+1. The space between the plants in the row was 35-40 cm, while the space between rows was 120 cm.

Soil analysis and climate observations

The soil physical characteristics were determined according to standard laboratory analyses. Particle size distribution (%) was determined by the international B-pipette method with the preparation in sodium pyrophosphate (Bošnjak, Đ. et al., 1997), while the determination of soil textural classes was carried out based on particle size distribution using Atteberg classification (Hadžić, V. et al., 2004).

Climate parameters, such as air temperature (°C) and precipitation (mm) were taken from the meteorological station “Rimski Šančevi” (N 45°20’, E 19°51’; 84 m a.s.l). (RHMZ, 2012). Because the measurements were performed in the morning, we used morning temperatures, recorded at 7 a.m. Daily variations of these variables, in the referent period (July, August and September), were presented. Vapor pressure deficit (VPD) was calculated on the basis of values of air temperature and relative humidity.

Physiological parameters

Measurements were conducted in 2011, four times during the vegetation period (July 16, August 20, September 5 and September 22). Net photosynthesis (A), transpiration (E) and stomatal conductance (gs) were recorded using portable photosynthesis system “ADC Bioscientific Ltd. LCpro+”. All measurements were taken between 07:00 and 09:00 a.m., on 10 individuals per species. Fully expanded leaves of the same developmental age, with the same orientation, placed in the upper part of the crown were used as samples. Leaves were enclosed in the broad leaf chamber until the values of net CO₂ accumulation and stomatal conductance stabilized (usually about 60 seconds). Photosynthetic active radiation (P.A.R.) was set to volume of 1000 μmol m⁻² s⁻¹, while the temperature, humidity and the concentration of CO₂ in the chamber were taken ambient from the atmosphere.

Statistical analysis

Data were processed using Statistica 10 software (StatSoft, Inc.). One-way
ANOV A was applied to determine the significant differences between group means. In order to investigate the relationship between observed physiological parameters in studied species, as well as relationship between the physiological parameters and climate variables (air temperature and vapor pressure deficit), linear regression analysis was applied. Regression analysis was performed using the mean values of variables.

3. RESULTS AND DISCUSSION

Soil characteristics

The results of the soil analysis determined the type of undeveloped alluvial soil (fluvisol), sandy loam form (A\textsubscript{p,a} - A\textsubscript{a IG} so - IG so - IIG so). Particle size composition and textural class of soil are given in Table 1.

<table>
<thead>
<tr>
<th>Horizon</th>
<th>Depth (cm)</th>
<th>Particle size composition (%)</th>
<th>Textural class</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ap</td>
<td>0-10</td>
<td>&gt;0.2: 5.5 0.2-0.02: 60.8 0.02-0.002: 28.2 &lt;0.002: 5.5</td>
<td>Sandy loam</td>
</tr>
<tr>
<td>Ap</td>
<td>10-20</td>
<td>&gt;0.2: 1.7 0.2-0.02: 59.1 0.02-0.002: 29.8 &lt;0.002: 9.4</td>
<td>Sandy loam</td>
</tr>
<tr>
<td>Ap\textsubscript{IG}so</td>
<td>20-30</td>
<td>&gt;0.2: 1.1 0.2-0.02: 61.5 0.02-0.002: 29.9 &lt;0.002: 7.5</td>
<td>Sandy loam</td>
</tr>
<tr>
<td>Ap\textsubscript{IG}so</td>
<td>30-50</td>
<td>&gt;0.2: 0.4 0.2-0.02: 60.8 0.02-0.002: 29.1 &lt;0.002: 9.7</td>
<td>Sandy loam</td>
</tr>
<tr>
<td>Ap\textsubscript{IG}so</td>
<td>50-70</td>
<td>&gt;0.2: 0.1 0.2-0.02: 75.2 0.02-0.002: 17.8 &lt;0.002: 6.9</td>
<td>Sandy loam</td>
</tr>
<tr>
<td>Average</td>
<td>1.8</td>
<td>63.5 27.0 7.8</td>
<td>34.8 Sandy loam</td>
</tr>
</tbody>
</table>

Climate characteristics

Daily variations in air temperature and sums of precipitation, during the observed period, are presented in Figure 1. In order to estimate the influence of climate occurrences in the moments of measurement on observed gas exchange parameters, data of air temperature and relative air humidity were used to calculate vapor pressure deficit (Table 2). VPD was used instead of relative air humidity because vapor pressure deficit presents a much more sensitive indicator of water vapor conditions of the atmosphere and gives an indication of the evaporation rates (Anderson, D.B., 1936).
Figure 1. Daily variations in mean air temperatures and sums of precipitation during: a) July, b) August and c) September 2011. Vertical dash lines represent days on which measurements were performed.

Slika 1. Dnevna varijabilnost prosečnih temperature vazduha i količine padavina tokom: a) jula, b) avgusta i c) septembra 2011. godine. Vertikalne isprekidane linije predstavljaju datume u kojima su merenja rađena.
Table 2. Air temperature, relative air humidity and vapor pressure deficit at the moment of measurement

<table>
<thead>
<tr>
<th>Date</th>
<th>Air temperature (°C)</th>
<th>Relative air humidity (%)</th>
<th>Vapor pressure deficit (kPa)</th>
</tr>
</thead>
<tbody>
<tr>
<td>16th July</td>
<td>18.9</td>
<td>76</td>
<td>0.52</td>
</tr>
<tr>
<td>20th August</td>
<td>21.1</td>
<td>81</td>
<td>0.48</td>
</tr>
<tr>
<td>5th September</td>
<td>22.8</td>
<td>58</td>
<td>1.17</td>
</tr>
<tr>
<td>22nd September</td>
<td>15.6</td>
<td>94</td>
<td>0.11</td>
</tr>
</tbody>
</table>

Physiological parameters

According to ANOVA results, it was found that all physiological parameters, in both species, showed highly significant statistical differences concerning the date of measurements. Throughout the observation period, both species showed similar seasonal patterns of investigated physiological parameters. On 16 July, the mean net photosynthesis of *P. acerifolia* and *A. pseudoplatanus* was 10.10 and 10.58 μmol m$^{-2}$ s$^{-1}$, respectively (Figure 2). A sharp reduction in $A$ was observed in the second part of August and at the beginning of September, when both species exhibited their lowest net CO$_2$ assimilation. Minimum $A$ was 7.27 and 7.0 μmol m$^{-2}$ s$^{-1}$ in *P. acerifolia* and *A. pseudoplatanus*, respectively. Significant increase in $A$, in both species, was recorded on 22 September when mean values of *P. acerifolia* and *A. pseudoplatanus* were 11.85 and 9.22 μmol m$^{-2}$ s$^{-1}$.

Stomatal conductance followed a similar pattern to $A$ (Figure 2). Reduction in $g_s$ caused by summer heat wave was more pronounced in *A. pseudoplatanus*. Minimal $g_s$ in both species were measured on 5 September and amount to 0.122 mol m$^{-2}$ s$^{-1}$ in *P. acerifolia* and 0.112 mol m$^{-2}$ s$^{-1}$ in *A. pseudoplatanus*. The highest $g_s$ in *P. acerifolia* was recorded on 22 September (0.286 mol m$^{-2}$ s$^{-1}$), while in *A. pseudoplatanus* it was on 16 July (0.189 mol m$^{-2}$ s$^{-1}$). Comparing to other followed parameters, stomatal conductance showed the highest values of coefficient of variation. Also, it varied in the broadest ranges of all parameters.

The seasonal course of transpiration, in both species, followed a rise-and-fall pattern with a peak at the beginning of September (Figure 2). Transpiration rates of *P. acerifolia* and *A. pseudoplatanus* had initial mean values of 1.46 and 2.53 mmol m$^{-2}$ s$^{-1}$ on 16 July. After first period of measurements, $E$ increased until 5 September up to 2.87 and 3.62 mmol m$^{-2}$ s$^{-1}$ and then sharply decreased on 22 September.

Results of correlation analysis revealed presence of significant relationship between net photosynthesis and stomatal conductance, in both species (Figure 3). In order to identify how environmental variables influenced leaf gas exchange, regression analysis between observed physiological parameters and climate variables (air temperature and vapor pressure deficit) in the moment of measurement was applied. Results of regression analysis showed that relationship between investigated physiological parameters and climate parameters had similar pattern in *P. acerifolia* and *A. pseudoplatanus*. Statistically significant correlation was observed only in between air temperature and $A$ and $g_s$ in *P. acerifolia* and *A. pseudoplatanus*. Statistically significant correlation was observed only in between air temperature and $A$ and $g_s$ in *P. acerifolia* and *A. pseudoplatanus*. Physiological parameters and climate variables had similar pattern in *P. acerifolia* and *A. pseudoplatanus*. Statistically significant correlation was observed only in between air temperature and $A$ and $g_s$ in *P. acerifolia* and *A. pseudoplatanus*.
Figure 2. Seasonal courses of net photosynthesis (A), stomatal conductance (gs) and transpiration (E) in the leaves of *P. acerifolia* Willd. (closed squares, solid line) and *A. pseudoplatanus* L. (open square, dotted line). Symbols represent means ±1 SE.
Figure 3. Correlation analysis among investigated physiological parameters (p<0.05) in *Platanus acerifolia* Willd. (closed squares, solid line) and *Acer pseudoplatanus* L. (open square, dotted lines).

Slika 3. Korelaciona analiza između istraživanih parametara (p<0.05) kod *P. acerifolia* Willd. (crni kvadrati, puna linija) i *A. pseudoplatanus* L. (beli kvadrati, isprekidana linija).
Figure 4. Linear regression between investigated physiological parameters and air temperature (°C) (p<0.05) in *P. acerifolia* Willd. (closed squares, solid line) and *A. pseudo-platanus* L. (open square, dotted line). Parameter acronyms are defined in Material and Methods.
Figure 5. Linear regression between investigated physiological parameters and VPD (kPa) in *P. acerifolia* Willd. (closed squares, solid line) and *A. pseudoplatanus* L. (open square, dotted lines). Parameter acronyms are defined in Material and Methods.
The availability of soil water to plants depends predominantly on the soil structure and texture. The water-holding capacity of soils is the lowest in sandy soils and increases with decreasing soil particle and pore size as in a clay loam soil (Orcutt, D. M., Nielsen, E. T., 2000). In this study, the fraction of fine sand was represented with an average of 63.5%. A large share of the texture classes of sand causes termination of the capillary rise of water in the driest part of the growing season (Rončević, S. et al., 1999) and thus affects the physiological processes in plants. For example, Stojnić, S. et al. (2011) found that rooted cuttings of *Populus x euramericana cl. Pannonia*, planted on soil with sandy-clay loam texture, showed significantly higher rates of net photosynthesis and stomatal conductance, compared to rooted cuttings planted on soil characterized by sandy loam texture.

Obtained results showed that *P. acerifolia* and *A. pseudoplatanus* responded similarly to prolonged dry period during the growing season. Parallel decreasing in *A* and *gs* in August and at the beginning of September, were observed in both species, suggesting a regulative function of stomata in minimizing water loss under limited water supply (Li, S. et al., 2004; Gallé, A., Feller, U. 2007). Also, a strong positive relationship between net photosynthesis and stomatal conductance, for seasonal courses, suggests that stomatal closure was the main factor controlling CO$_2$ assimilation. According to Leuzinger, S. et al. (2005), trees regulate their water balance by closure of the stomata during drought, thereby decreasing xylem sap flow rate. Similar results have been reported for beech and sessile oak by Raf托n尼斯, Y., Rαdouλou, K. (2002). In contrast to the findings in *P. acerifolia*, the recovery of *gs* and *A* in *A. pseudoplatanus* were still incomplete, after the rainfall in the end of September, suggesting remaining stomatal limitations.

Except of water stress, reduction of net photosynthesis and stomatal conductance could be the consequence of stomatal closure caused by other abiotic factors (Rαf托n尼斯, Y. et al., 2006). Our study showed that increased air temperature had a negative effect on net photosynthesis and stomatal conductance, especially in the case of *P. acerifolia* ($R^2_A = 0.99; R^2_{gs} = 0.99$). This is in agreement with findings of Schulze, E. D. et al. (1973) who demonstrated that the stomata of water-stressed plants, of several species, closed in response to increasing temperature. Subjecting seedlings of *Betula pendula* and *Gmelina arborea* to variation in temperature and irradiance, Oσonbi, O., Davie, W. J. (1980a) proved that water stress reduce the rate of photosynthesis, particularly at high temperatures. Similarly, Grαtαni, L. et al. (2003) found that the highest rates of net photosynthesis and stomatal conductance in *Quercus ilex* provenances were monitored in the range of 17–19°C and that further increasing of temperature led to decrease of these parameters. However, the relatively small responses of *A* and *gs* to increasing temperature ($R^2_A = 0.41; R^2_{gs} = 0.22$), observed in *A. pseudoplatanus*, suggest that modest increases in temperatures during the growing season are unlikely to disrupt gas exchange in this species. Day, M. E. (2000) reported similar results for *Picea rubens*, when both *A* and *gs* exhibited a relatively flat response to temperatures between 16° and 32°C and only temperatures between 32° and 36°C markedly decreased *A* and *gs*.
Responses of stomatal conductance to increasing vapor pressure deficit generally follow an exponential decrease, although the magnitude of the decrease varies considerably both within and between species (Oren, R. et al., 1999). Decreasing of stomatal conductance with increasing of VPD could be the consequence of two features: abscisic acid (ABA) in the leaves which trigger this response or increasing in transpiration that lowers the leaf water potential (Bunce, J. A., 1996; Streck, N. A., 2003). Our study showed that net photosynthesis and stomatal conductance parallely decreased with increasing of VPD, even though this relationship was not statistically significant. Similar results were obtained by Day, M. E. (2000) on red spruce seedlings, who found that influence of VPD on $g_s$ was weak at VPDs lower than 2 kPa. Shirke, P. A., Pathre, U. V. (2004) reported that inhibitory effects of high VPD on net photosynthesis and stomatal conductance at P. juliflora were visible only when the VPD level exceeded a threshold of $>3$ kPa. Nevertheless, as the vapor pressure deficit between leaf and air increases, stomata respond by partially closure, preventing excessive dehydration and physiological damage (Lange, O. L. et al., 1971; Meinzer, F. C., 1982). Study of Osonubi, O., Davies, W. J. (1980b) showed that stomatal conductance in mildly water-stressed seedlings of Betula pendula decreased as VPD was increased and that this response seemed to be closely linked to the water status of the air rather than to the water status of the plant.

Decrease of $A$ and $g_s$ in response to elevated VPD in P. acerifolia was characterized by steeper slope, comparing to physiological response in A. pseudoplatanus. Also, P. acerifolia had higher stomatal conductance at low vapor pressure deficit. According to Oren, R. et al. (1999), species with high stomatal conductance at low vapor pressure deficit show a greater sensitivity to VPD, as required by the role of stomata in regulating leaf water potential. The rate of transpiration is directly related to the degree of stomatal opening and to the evaporative demand of the atmosphere surrounding the leaf (Tahery, Y. et al., 2011). According to Fletcher, L. A. et al. (2007), atmospheric evaporative demand and consequently plant transpiration increase with increasing atmospheric vapor pressure deficit. Results of our study confirmed this observation, as the transpiration rate in both species, generally, increased with the increasing of VPD. Also, transpiration was negatively correlated with stomatal conductance (linear increasing function of stomatal conductance). According to Bunce, J. A. (1996), high transpiration could cause stomatal closure by increasing the water potential gradient between the guard cells and other cells, or by lowering leaf water potential.

4. CONCLUSION

Statistically significant correlation between net photosynthesis and stomatal conductance was found in both species. The incomplete recovery of stomatal conductance and net photosynthesis in A. pseudoplatanus, after the rainfall at the end of September, suggests the remaining of stomatal limitations. Higher VPD (lower air humidity) means that the air has a higher capacity to hold water, stimulating water vapor transfer from the leaf to the atmosphere. This can result in a decrease in net photosynthesis and stomatal conductance.

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Statistically significant correlation between net photosynthesis and stomatal conductance was found in both species. This indicates that stomatal closure is a major factor controlling CO$_2$ assimilation. The incomplete recovery of stomatal conductance and net photosynthesis in A. pseudoplatanus, after the rainfall at the end of September, suggests the remaining of stomatal limitations. Higher VPD (lower air humidity) means that the air has a higher capacity to hold water, stimulating water vapor transfer from the leaf to the atmosphere. This can result in a decrease in net photosynthesis and stomatal conductance.
transfer (transpiration) into the air. 

P. acerifolia showed greater sensitivity to VPD characterizing by high stomatal conductance at low VPD. Also, lower values of transpiration rate in P. acerifolia compared to A. pseudoplatanus, under a high vapor pressure deficit would result in water conservation, allowing for both increased growth and water use efficiency. Although, neither P. acerifolia, nor A. pseudoplatanus are adapted to growth on fluvisol, inferiority of A. pseudoplatanus could be related to the sensitivity of this species to summer heat and drought and very high demands to habitat conditions (large share of silt in the soil texture and high content of moisture and nutrients in the soil).

Acknowledgment

This paper was realized as a part of the project “Biosensing Technologies and Global System for Long-Term Research and Integrated Management of Ecosystems” (43002) financed by the Ministry of Education and Science of the Republic of Serbia within the framework of integrated and interdisciplinary research for the period 2011-2014.

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WILLD. и A. pseudoplatanus L. НА НЕРАЗВИЈЕНОМ аспекти биљака зависи од других фактора и генетичког материјала. Усмено учешће фракције песка у земљишту критеријум калигарно пањење воде и на тај начин утиче на физиолошке процесе у биљака. У раду је приказана сезонска промена за два варијета (А) и стоматална проводљивост (С) и транспирација (Е) код саднина Platanus acerifolia и Acer pseudoplatanus. Фотосинтетска активност је израђена у два саднина са различитим умешним врстама (өө), али спроведена у радском периоду „Кафка шума” Института за низијско шумарство и животну средину у Кану, Република Србија. Мерења су обављене на садницима старости 2-4 године, четири пута током вегетационог периода 2011. године (10. јула, 20. августа, 5. септембра и 22. септембра). Земљиште на којем су саднице расле и прима типу неразвијеног алувијалног земљишта (флувисол) – текстурне класе песковитих иловац, са доминантном фракцијом ситног песка (63.5%), док је фракција иловаца + глина заступљена у мањем проценту (34.7%). Заједничка редукција одних фотосинтетских показатеља је у току половине августа и почетком септембра, и...
повољешем температуре ваздуха и дефицит засићености водене паре, растојао је и интензитет транспирације код обе врсте. Мање вредности транспирације код P. acerifolia, при вишим вредностима дефицита засићености водене паре утиче на конзервативније коришћење воде, омогућавајући повећану ефикасност коришћења воде. Инфериорност A. pseudoplatanus у по ређењу са P. acerifolia је вероватно повезана са осетљивости ове врсте на летње врућине и сушу, с обзиром су оптимални услови за раст јавора условљени високим садржајем релативне влаге, у влажној, хладнијој клими, на земљиштима иловастог текстурног састава која су богате хранљивим материјама.

Кључне речи: Acer pseudoplatanus F(Platanus acerifolia О аерисе Ес Улуси Омбеси ру — тална проводљивост, транспирација.