

UDC 577.355.3:581.115/116.1

PHOTOSYNTHETIC RESPONSES OF *Amygdalus arabica* Olivier AND *Atriplex canescens* (Pursh) Nutt. TO DROUGHT STRESS UNDER FIELD CONDITIONS

B. Akgün, E. Yazar, F. Kocacinar

Kahramanmaraş Sütçü İmam University
Batu Çevreyolu Bulv., 251 A, Onikişubat Kahramanmaraş, 46100 Turkey

E-mail: bakgun2002@gmail.com, emreyazar@ksu.edu.tr, kocacinarf@gmail.com

Received 30.01.2018

The central Anatolian region of Turkey is exposed to increasing temperatures and severe drought stress. Due to aridity and desertification brought about by global warming, climate change and overutilization, plant species in these regions are under the risk of extinction. Thus, plant species have to adapt to these harsh environmental conditions of extremely high temperatures and low precipitation. In this study, gas exchange and water potentials of the Arabian almond tree *Amygdalus arabica* Olivier (C_3 -photosynthesis) and four-winged saltbush *Atriplex canescens* (Pursh) Nutt. (C_4 -photosynthesis), two drought-tolerant woody species planted previously in an effort to reduce desertification at Karapınar, Konya, and Central Anatolian Region, were periodically measured from May until September under field conditions. Net photosynthesis and transpiration rates, mid-day water potential and water use efficiency were determined throughout the vegetation period in 2015. Maximum net photosynthetic rates were $12.4 \mu\text{mol m}^{-2} \text{s}^{-1}$ in the Arabian almond tree and $29.7 \mu\text{mol m}^{-2} \text{s}^{-1}$ in four-winged saltbush, measured in July and September, respectively. Also, the highest transpiration rates were $4.8 \text{ mmol m}^{-2} \text{s}^{-1}$ in the Arabian almond tree and $7.1 \text{ mmol m}^{-2} \text{s}^{-1}$ in four-winged saltbush. Maximum water use efficiency values were measured in June in both species, which made up 5.7 and 7.7 $\text{mmol CO}_2 \text{ mol}^{-1} \text{ H}_2\text{O}$ for the Arabian almond tree and four-winged saltbush, respectively. Lowest midday water potentials for both species were recorded in August. The results indicate that both species have the ability to tolerate drought stress in the region, though due to its C_4 nature of photosynthesis, the four-winged saltbush might overcome those stresses more efficiently than the Arabian almond tree in arid and barren areas.

Keywords: gas exchange, drought stress, arid and barren lands, Arabian almond tree, four-winged saltbush, central Anatolian region, Turkey.

How to cite: Akgün B., Yazar E., Kocacinar F. Photosynthetic responses of *Amygdalus arabica* Olivier and *Atriplex canescens* (Pursh) Nutt. to drought stress under field conditions // *Sibirskij Lesnoj Zurnal* (Sib. J. For. Sci.). 2018. N. 6: 103–111 (in English with Russian abstract). DOI: 10.15372/SJFS20180609

DOI: 10.15372/SJFS20180609

INTRODUCTION

While 75 % of Turkey's total land area is categorized as arid and semi-arid areas, it has been stated that these areas spend from 5 to 8 months of the year in dry and semi-arid climatic conditions, especially during the vegetation period (Çalikoğlu, Tilki, 2004). This period coincides with the growth period of April through October, when the forest trees and other woody and herbaceous vegetation are active (Taşdemir, 2012; Çalikoğlu, Tilki, 2004).

In most of Turkey's land, the rainfall is low during this time interval, and the potential transpiration is aggravated by high temperatures, thus yielding a low amount of rainfall. Hence, soil water decreases rapidly, and extreme droughts occur, especially in July, August and September. Moreover, stress conditions are increasing even more in saline and barren areas, where drought stress is experienced (Akgün, 2017).

Stress conditions have negative effects on the growth and development of plants and their productivity, causing their mortality (Kozłowski, Pallardy,

1997; Taiz, Zeiger, 2002; Kocacinar, Sage, 2004; McDowell et al., 2008; Allen et al., 2009). In addition, extreme stress conditions limit the choice of species in the afforestation and significantly decrease the progress of planted saplings.

Plants lose water excessively due to transpiration during photosynthesis. Thus, during the vegetation period, especially in conditions of high temperature and water stress in semi-arid areas with low rainfall and high salinity, droughts cause a serious water shortage. Some plants are completely absent in such areas, and those that survived undergo physiological adaptations (Akgün, 2017). As a result, the plants adapt by means of various physiological and anatomical characteristics to arid and semi-arid areas, and continue their lives, while those which cannot adapt will die due to natural factors.

These barren and arid areas, especially at Konya-Karapınar territory, underwent forestation with woody species reported to be drought tolerant. According to the data obtained between the years 1980–2015, the average annual precipitation amount characteristic of Karapınar region was 276 mm with the annual average temperature amounting to 12.2 °C (Akgün, 2017). This area was assigned to desert since it demonstrates a small variation in plant diversity and is hardly habitable (Dirik, 1994). However, in recent years, a large part of forest lands of Central Anatolian Region was reassigned to semi-arid areas (Güner et al., 2011).

Arid and barren ecosystems may consist of diverse functional types of plants as they have different responses to climate change (Wertin et al., 2015). Different species, which occur together in these ecosystems often adopt different ecophysiological strategies to overcome excessive drought stress (Tiemuerbieke et al., 2018). Desert species have undergone similar adaptations, in terms of internal structure and morphological characteristics (Li et al., 2017). But, species with different photosynthetic pathways with similar life forms which had different morphological characteristics could have different physiological responses to drought stress in desert conditions. In this study, two woody species, the Arabian almond tree *Amygdalus arabica* Olivier and four-winged saltbush *Atriplex canescens* (Pursh) Nutt., planted previously to reduce desertification at Karapınar, Konya, Central Anatolian Region in Turkey were chosen not only for their drought tolerance characteristics but also their different photosynthetic pathways. The four-winged saltbush is native to the Southwestern deserts of the United States, a drought and salinity tolerant

C_4 -photosynthesis (C_4) plant with a high performance in terms of ecophysiological traits (Hao et al., 2013). On the other hand, (C_3) the Arabian almond tree with C_3 -photosynthesis was reported as drought tolerant but had moderate performance compared to the four-winged saltbush (Rajabpoor et al., 2014). These respective studies were focused specifically on either the four-winged saltbush or the Arabian almond tree.

As described above, two species different in terms of morphology and photosynthetic pathways were observed under similar natural conditions; we assume that differences in terms of physiological traits could occur. Moreover, we hypothesize that even under similar conditions with similar adaptations different C_3 and C_4 species yield different gas exchange performances. Thus, in this study, we aimed to make gas exchange measurements on the Arabian almond tree and four-winged saltbush to investigate and compare the performance of these woody species.

MATERIALS AND METHODS

Study site and physiological measurements. The study was carried out in Central Anatolia, Konya Soil, Water and Desertification Research Institute, Karapınar Station (37°42'48.9"N, 33°31'40"E, altitude 1016 m a. s. l.), at the sites planted with the Arabian almond tree and four-winged saltbush sites (Fig. 1, 2).

These species introduced to the study site by previous researchers and were not native to the study area. Although the species were from the same study site, they were from different parts of the study site, with the distance between the species equal 20 km.

Gas exchange measurements were made at an average air temperature of 24–25 °C in May, 26–27 °C in June, 28–30 °C in July and August, and 24–25 °C in September (Fig. 3.).

All the measurements were made at 2000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ light intensity, under atmospheric CO_2 concentrations ($\approx 400 \mu\text{mol mol}^{-1}$) and at about 55 % relative midday humidity. The measurements were made with the rate of photosynthesis reaching a steady state. With these species, under natural conditions, during 2015 vegetation period (May–September); net assimilation rates (net photosynthesis rates, A) and transpiration rates (E) were measured using a portable GFS-3000, photosynthesis, and fluorescence gas-exchange meter (GFS-3000, Heinz Walz GmbH, Effeltrich, Germany).



Fig. 1. Gas exchange measurements of the Arabian almond tree in the field of Konya Karapınar.



Fig. 2. Gas exchange measurements of four-winged saltbush in the field of Konya Karapınar.

Leaf weight method was used for gas-exchange measurements according to G. D. Farquhar et al. (1982); water use efficiency (WUE) was calculated from A_n/E ratio and intrinsic WUE (iWUE) was determined A_n/g_s ratio. Measurements were made for 6 different plants of each species in field conditions. Leaf weight was measured on a selected branch of both species, then a similar branch was used for gas exchange measurements. After the measurements the values were converted applying GFS-3000 software to leaf area data (GFS-win V3.70). Leaf area values were changed until the same gas exchange values were obtained using the software.

Predawn and midday water potentials were measured using PMS pressure chamber (PMS Instrument Co., Albany OR, USA). The midday leaf water potentials were measured at solar noon, while the predawn water potentials were measured 20 min before sunrise, according to H. Xu et al. (2007) method.

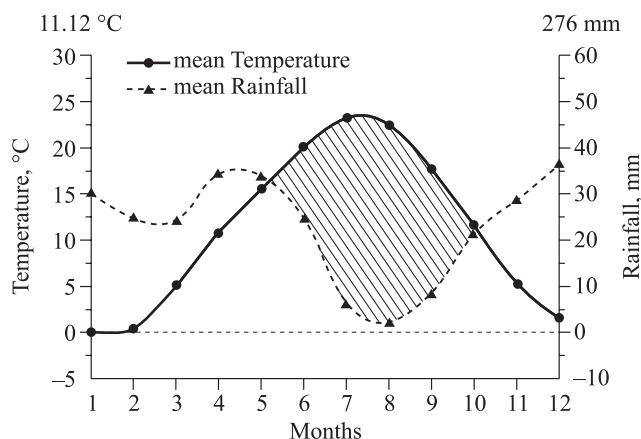


Fig. 3. Walter diagram of Karapınar, 1980–2015. Data from the Turkish State Meteorological Service, Karapınar Station. Shaded area indicates water deficit between May and October and corresponds to the vegetation period of many species that grow in the study field.

Data analysis. The results of gas exchange and water potential measurements at midday and predawn were subjected to one-way analysis of variance (ANOVA) followed by Fisher LSD comparison test ($p < 0.05$ significance level) (Systat Software Inc., CA, USA).

RESULTS AND DISCUSSION

The net assimilation rate, transpiration rate, stomatal conductance, WUE and iWUE measurements of the species are shown at Fig. 4–8. The net photosynthesis rate increased in the C_3 species of the Arabian almond tree in May and July, though it decreased in the warmer months of August and September (Fig. 4).

On the contrary, the net photosynthesis rate in C_4 four-winged saltbush was higher than its counterpart in all months and increased through the vegetation period. During the vegetation period, the

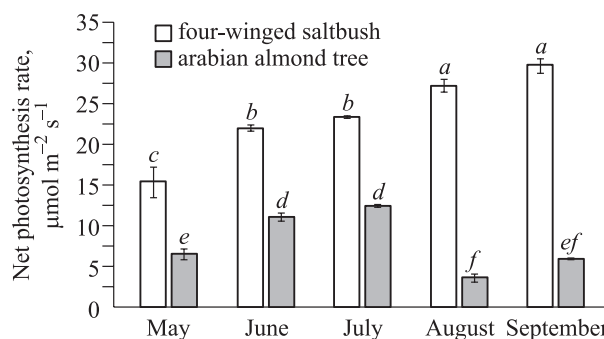


Fig. 4. Net photosynthesis rate (A_n) of four-winged saltbush and the Arabian almond tree. Columns indicate mean values ($n = 6$), bars denote \pm SE, letters stand for the difference between species and months ($p < 0.05$). As temperature increased, the net assimilation rate of C_4 species of four-winged saltbush also increased. On the contrary, the net assimilation rate of C_3 species of the Arabian almond tree increased until July and later it drastically decreased.

rate of photosynthesis slowly increased in the Arabian almond tree reaching a maximum at a certain level, which was about 2–3 times lower than that for the four-winged saltbush. In all the months of the survey until July, there was a significant difference between the species, and the net assimilation rate of the C_4 species was 1.5-fold compared to its counterpart C_3 species. However, after July, there was a nearly 10-fold difference between the species in August and September. The C_4 species reached maximum assimilation rate in September ($29.67 \mu\text{mol m}^{-2} \text{s}^{-1}$) and its minimum in May ($15.6 \mu\text{mol m}^{-2} \text{s}^{-1}$). On the other hand, the C_3 species reached maximum assimilation rate in the warmest month of July when it reached 12.44, while the minimum assimilation rate amounted to $3.59 \mu\text{mol m}^{-2} \text{s}^{-1}$ in August, which was as warm as July in 2015 at the study site (Fig. 4).

The transpiration rate for the Arabian almond tree was found to be lower in May, June, August, and September and higher in July. In the case of four-winged saltbush, it started to increase in May and reached its maximum in September (Fig. 5). Also, the transpiration rate of the Arabian almond tree and four-winged saltbush followed a similar trend, with the net assimilation rate as shown in Fig. 4. In the beginning of summer, in May and June, there was no significant difference between the species. In July, in the warmest month, the transpiration rates of the species were nearly similar. But, after July, there was a nearly 6-fold difference between four-winged saltbush and the Arabian almond tree respectively (6.63 and $1.19 \text{ mmol m}^{-2} \text{s}^{-1}$). In September this trend also continued (Fig. 5).

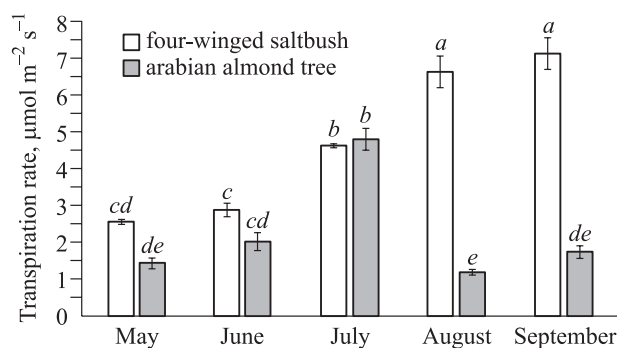


Fig. 5. Transpiration rates (E) of the four-winged saltbush and the Arabian almond tree. Columns indicate mean values ($n = 6$), bars denote \pm SE, letters stand for the difference between species and months ($p < 0.05$). In May, June and July there was no marked difference between the species, but in August and September the difference in transpiration rates between the species made up nearly 6-fold.

As seen in Fig. 6, the stomatal conductance of the species followed a similar trend as that for the assimilation and transpiration rates. In May, there was a 2-fold difference between the Arabian almond tree and four-winged saltbush s , but in August and September, this difference increased to 6-fold.

In June and July, however, there was no marked difference between the species. In June, stomatal conductance of four-winged saltbush and the Arabian almond tree amounted to 0.116 and $0.112 \text{ mol m}^{-2} \text{s}^{-1}$ respectively, and in July it reached 0.144 and $0.133 \text{ mol m}^{-2} \text{s}^{-1}$ (Fig. 6).

Water use efficiency (WUE) was calculated as the ratio of the net photosynthesis rate to the transpiration rate. Accordingly, in C_4 four-winged saltbush, WUE was higher than in its counterpart, the Arabian almond tree, during the summer period. There was no significant difference between the two species both in September and in August. In both species, WUE was highest in June and lowest in August. Through May to June, WUE increased in both species, however, through August to September WUE of four-winged saltbush decreased gradually, while WUE of the Arabian almond tree increased gradually.

Moreover, there was no significant difference in terms of intraspecific WUE between July to September, and in August and September there was no significant difference in terms of interspecific WUE (Fig. 7).

Intrinsic water use efficiency (iWUE) differed from WUE. The differences between species in WUE seemed to lessen in iWUE. Intraspecifically, there was less difference between different months of the summer season in 2015. But, the iWUE trend

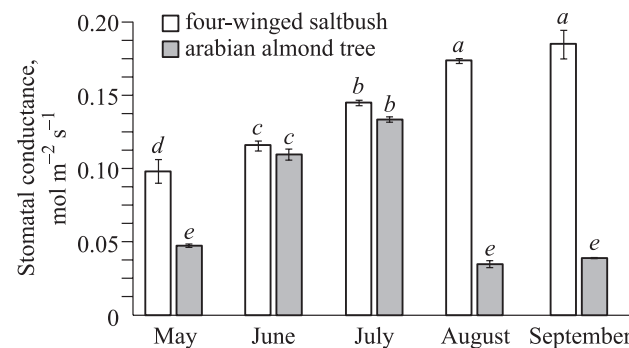


Fig. 6. Stomatal conductance (g_s) of four-winged saltbush and the Arabian almond tree. Columns indicate mean values ($n = 6$), bars denote \pm SE, letters designate the difference between species and months ($p < 0.05$). In June and July, there was no significant difference between the species. But in the other months, values of stomatal conductance of the species slightly differed from each other.

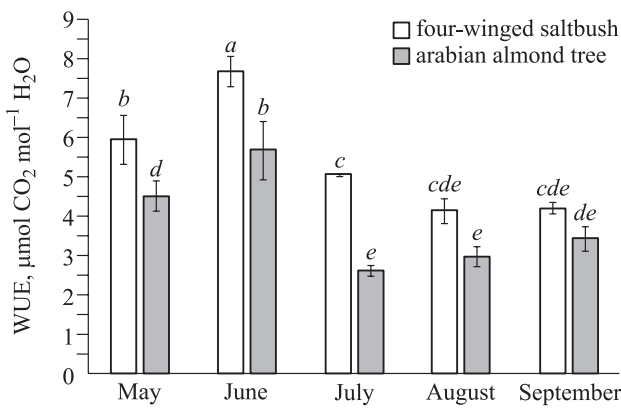


Fig. 7. Water use efficiencies (WUE) of four-winged saltbush and the Arabian almond tree, as calculated from A_n/E . Columns denote mean values ($n = 6$), bars stand for \pm SE, letters denote the difference between species and months ($p < 0.05$). The difference between the species slightly increased from May to July. After July, in terms of WUE, there was no significant difference between the species.

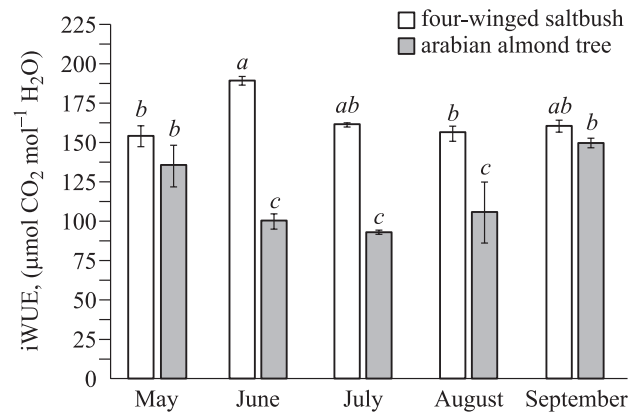


Fig. 8. Intrinsic water use efficiencies (iWUE) of four-winged saltbush and the Arabian almond tree, as calculated from A_n/g_s . Columns indicate mean values ($n = 6$), bars denote \pm SE, letters stand for the difference between species and months ($p < 0.05$).

of four-winged saltbush showed some similarities with WUE, such as reaching its maximum value of 189.53 mmol CO₂ mol⁻¹ H₂O in June. WUE of the Arabian almond tree gradually increased from July to September, and reached its maximum value in September with 149.88 mmol CO₂ mol⁻¹ H₂O (Fig. 8).

Predawn and midday water potentials of C₃ and C₄ plant are shown in Fig. 9 and 10.

The midday and predawn water potentials were measured and the data compared to understand the recovery of these species under drought stress conditions. The midday water potentials were below -1.5 MPa, which indicated severe drought stress for both plants for the vegetation period (Fig. 10). Moreover, predawn water potential values between the plants were significantly different and lower in the C₃ plant, when compared to C₄ plant (Fig. 9).

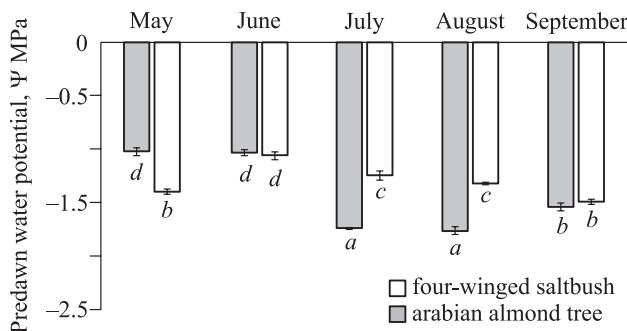


Fig. 9. Predawn water potential of four-winged saltbush and the Arabian almond tree in vegetation period of 2015. Columns indicate means of 6 plants, \pm bars are SE, letters stand for marked difference ($p < 0.05$). In July and August, in the middle of the summer period, predawn water potentials of both species decreased.

In terms of predawn water potential, there was no significant difference between the species in June and September. In the other months of the study, there was a significant difference between the species. In July and August, the predawn water potential of both species decreased, when compared to other months. For instance, the predawn water potential of the Arabian almond tree decreased from -1.02 MPa to -1.74 MPa, from May to July respectively. The predawn water potential of four-winged saltbush increased from May to June and decreased again from June to September (Fig. 9).

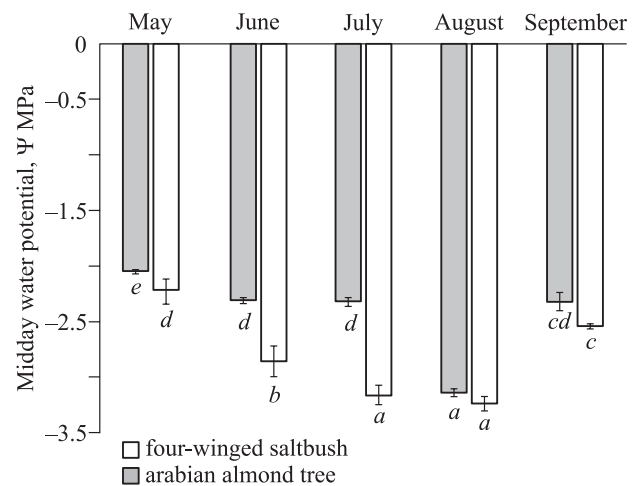


Fig. 10. Midday water potential of four-winged saltbush and the Arabian almond tree in vegetation period of 2015. Columns indicate means of 6 plants, \pm bars are SE, letters designate marked difference ($p < 0.05$). Midday water potentials of both species decreased as the mean temperatures increased in 2015. Especially in August, the mid-day water potential values of the species were similar to each other.

The midday water potentials of the species are given in Fig. 10. In both species there was a significant increase in the midday water potentials from May to August. In September, midday water potential of both species decreased to the May values. In August and September, there was no significant difference between the species.

Drought stress is generally mentioned as water shortage and drying of the plants (Smirnoff, 1993). Water deficiency limits gas exchange and causes stomata to close. Independent of the biochemical pathway drought stress negatively affects the photosynthetic rate, transpiration rate, stomatal conductance and water use efficiency (Örs, Ekinçi, 2015). Under drought conditions C_4 species are more resistant than C_3 species. This is caused by high WUE, high net assimilation rates, low transpiration and stomatal conductance in C_4 plants (Kocacinar, 2015). In contrast, plants with both photosynthetic pathways continue to survive in arid and semi-arid areas. These plants exhibited physiological, morphological and anatomical adaptations to these areas (Xu, Li, 2006).

In our study, especially the increase of temperatures through June to August, caused a decrease of photosynthesis and an increase in transpiration in the Arabian almond tree, while in four-winged saltbush, it caused an increase of photosynthesis and transpiration. Also, through the vegetation period the net photosynthesis rate tended to decrease in the Arabian almond tree (C_3), while the rate of photosynthesis of (C_4) four-winged saltbush was significantly higher (Fig. 4).

S. Rajabpoor et al. (2014) reported that net assimilation rate of the Arabian almond tree decreased, while the drought stress increased. For instance, in their study, after -1.3 MPa mid-day water potential the Arabian almond tree yielded $15.48 \mu\text{mol m}^{-2} \text{s}^{-1}$ in terms of the net assimilation rate. The Arabian almond tree showed a decrease in net photosynthesis rates as the water potentials decreased (Rajabpoor et al., 2014). In this study, drought levels were much higher (Fig. 10) and as expected, the net assimilation rates were much lower as shown in Fig. 4. On the other hand, J. C. Oakley et al. (2014) reported that similar four-winged saltbush species with similar life forms was not affected by severe drought stress and demonstrated a stable performance both in drought stress and well-watered conditions. In our study similar results are obtained for the four-winged saltbush (Fig. 4).

There is a direct relationship between the transpiration rate and stomatal conductance. Generally,

the rate of transpiration is lower in C_4 plants than in C_3 plants (Calikoglu, Tilki, 2004; Osborne, Sack, 2012).

In terms of WUE, it was seen that the difference is approximately 1.5 times (Fig. 7). This effect may be due to that the amount of water required per unit of photosynthesis is lower in C_4 species than in C_3 species because of narrower stoma openings than C_3 plants, which is likely to be the cause for lower transpiration rates in C_4 plants (Sage, Pearcy, 1987; Wang et al., 2005). This study was carried out in Karapınar, in one of the most drought stressed and water-deficit areas in Turkey (Fig. 1), where it was found that the four-winged saltbush had a higher transpiration rate than its C_3 counterpart in some months. This difference could be related with the C_4 plant high photosynthesis rate during arid conditions (Fig. 6–8). At increased photosynthesis and decreased transpiration rates, WUE of the plants seems to increase (Kocacinar, Sage, 2003). Similar results were obtained in this field study, where the temperature and the drought stress effect were high, while water use efficiency of C_4 was higher than that for C_3 (Fig. 7).

Moreover, stomatal conductance and transpiration rate of C_3 species also increase with temperature (Caemmerer, Evans, 2015). This can also be seen in Fig. 5 and 6. In cooler months, such as May, there was no significant difference between the species in terms of stomatal conductance and transpiration rates, but in September, there was a large gap between the species (Fig. 5, 6). This difference could be caused by different temperatures, when gas-exchange measurements were made; though, mean temperatures were comparable in May and September, the value was different on the days of measurement.

Martin et al. (1991) reported that during a dry season transpiration and WUE for (C_4) species were found to be lower than those for other plants (C_3). Similar results were obtained in this study in terms of high photosynthesis rate and WUE (Fig. 4, 7). Recent studies suggest that there was a decoupling between stomatal conductance and the net assimilation rates, especially at high temperatures (Urban et al., 2017). Thus, this difference also affects transpiration rates of the plants. Urban et al. (2017) investigated two C_3 coniferous species and concluded that stomatal conductance and transpiration rates disagree with the net assimilation rates after the plants were influenced by higher temperatures. In our study, this pattern could be seen in mid-summer, especially in July and August (Fig. 4–6). Sin-

ceWUE and iWUE were calculated from stomatal conductance and transpiration rates, this fact could have influenced these parameters. The iWUE increase should have been affected by g_s decrease, which was accepted as a strategy to avoid excessive water loss in dry environments.

Increasing temperatures contribute to the increase of iWUE (Granda et al., 2018). In our study, however, the C_3 species also followed this tendency, and the C_4 species had an increase in iWUE as well as g_s (Fig. 6, 10). Thus, the increase in iWUE was due to the increase in A_n (Fig. 4), which indicates that C_4 plant could have consumed more groundwater than its counterpart (Fig. 9) (Arend et al., 2013).

Leaf water potential is an important factor that indicates the extent to which a plant is exposed to drought. Generally, values below -1.5 MPa should be associated with drought stress, while values below -2 MPa are to be considered as severe drought or desert conditions (Taiz, Zeiger, 2002; Kocacinar, Sage, 2003, 2004). As can be seen from the results, plants in the study area are under severe drought stress (Fig. 10). The ability of the desert plants to recover from the midday to predawn leaf water potentials is an important factor to estimate their drought tolerance (Su et al., 2012). In our case, however, the ability of C_4 plants to recover was slightly higher than that of C_3 plants, the C_3 species also recovered from drought conditions and showed drought-tolerant characteristics (Fig. 9, 10).

Lebourgeois et al. (1998) reported that a decrease in photosynthesis could occur when leaf water potential decreases in the middle of the day. Therefore, in the areas where lower leaf water potentials are characteristic of plants, the species resistant to drought should be preferred. In addition, Ward et al. (1999) compared C_3 and C_4 plants with similar life form under severe drought stress. In their study, when the stress level increased, leaf water potential decreased, especially in C_4 species. Moreover, stomatal conductance of the C_4 plant was higher in the recovery period after the drought stress. In our study, a similar trend could be seen in water potentials through the season.

In this study, stomatal conductance and transpiration rate of C_4 plant gradually increased, when compared to its counterpart. This could be due to different strategies characteristic of different photosynthetic types, which could also be associated with the changes xylem conductivity in these plants. This phenomenon must be addressed in future studies with similar or the same plants.

CONCLUSIONS

It is hard to understand long-term or daily basis of effects of drought from the results, because of the limitations of field conditions. Nonetheless, our study provides a relative comparison of C_3 and C_4 species with similar life forms under severe drought stress. Photosynthetic rates, transpiration rates, stomatal conductance, water use efficiencies and water potential parameters will shed light on restoration and rehabilitation studies that are planned to be performed in similar marginal areas.

As it is seen from the study, in arid areas, afforestation using C_4 species, especially, those resistant to heat and drought, should be preferred. However, in addition to these species, the use of C_3 species that have adapted to these conditions should not be overlooked.

Moreover, as a result of afforestation with these species, wind erosion threatening the settlement areas can be prevented. Similar arid and semi-arid areas should be meticulously protected, especially in the study area, and ecophysiological studies on natural or afforested plantations and adaptation of plants should be increased without delay. The ecophysiological properties of the studied woody plants are a good indicator for the selection of the correct species in the future afforestation.

This research was supported by the Kahramanmaraş Sütçü İmam University project grant, no. 2014/2 39 M awarded to F. Kocacinar by the Scientific Research Projects Coordination Unit. The authors would like to thank Oğuzhan Bilgili and Lütfi Er from Karapınar Desertification and Erosion Research Centre.

REFERENCES

- Akgün B. Kurak ve çorak alanların ağaçlandırılmasında kullanılan bazı türlerin ekofizyolojik özellikleri (A study on ecophysiological properties of some woody species used for rehabilitation of arid and barren lands): PhD. thesis. Grad. School Nat. Appl. Sci., Dpt. For. Engineer. Kahramanmaraş Sütçü İmam Univ., 2017. 125 p. (in Turkish).
- Allen C. D., Macalady A. K., Chenchouni H., Bachelet D., McDowell N., Vennetier M., Kitzberger T., Rigling A., Breshears D. D., Hogg E. H. (Ted), Gonzalez P., Fensham R., Zhang Z., Castro J., Demidova N., Lim J. H., Allard G., Running S. W., Semerci A., Cobb N. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests // For. Ecol. Manag. 2009. V. 259. Iss. 4. P. 660–684.

- Arend M., Brem A., Kuster T. M., Günthardt-Goerg M. S. Seasonal photosynthetic responses of European oaks to drought and elevated daytime temperature // *Plant Biol.* 2013. V. 15. Iss. 1. P. 169–176.
- Caemmerer S. von, Evans J. R. Temperature responses of mesophyll conductance differ greatly between species // *Plant, Cell Environ.* 2015. V. 38. Iss. 4. P. 629–637.
- Çalkoğlu M., Tilki F. Transpiration analyses in *Quercus libani* Olivier and *Quercus frainetto* Ten. seedlings in dry season // *Rev. Fac. For., Univ. Istanbul.* 2004. V. 54. N. 1. P. 133–142.
- Dirik H. Üç yerli çam türünün (*Pinus brutia* Ten., *Pinus nigra* Arn. ssp. *pallasiana* Lam., *Pinus pinea* L.) kurak peryoddaki transpirasyon tutumlarının ekofizyolojik analizi (An ecophysiological analysis of transpiration in three native Pinus species (*Pinus brutia*, *Pinus nigra* (Arn.) ssp. *pallasiana* Lamb Holmboe, *Pinus pinea* L.) under drought stress) // *İstanbul Üniversitesi Orman Fakültesi Dergisi (Rev. Fac. For. Univ. Istanbul).* 1994. V. 44. Iss. 1. P. 111–121 (in Turkish).
- Farquhar G. D., O'Leary M. H., Berry J. A. On the relationship between carbon isotope discrimination and the intercellular carbon dioxide concentration in leaves // *Aust. J. Plant Physiol.* 1982. V. 9. P. 121–137.
- GFS-3000 Portable gas exchange & fluorescence system for the assessment of plant photosynthesis, 2018. http://www.walz.com/products/gas_exchange/gfs-3000/introduction.html
- Granda E., Alla A. Q., Laskurain N. A., Loidi J., Sánchez-Lorenzo A., Camarero J. J. Coexisting oak species, including rear-edge populations, buffer climate stress through xylem adjustments // *Tree Physiol.* 2018. V. 38. Iss. 2. P. 159–172.
- Güner Ş. T., Özkan K., Çömez A., Çelik N. İç Anadolu Bölgesi'nde Anadolu Karaçamının (*Pinus nigra* subsp. *pallasiana*) verimli olabileceği potansiyel alanların odunu gösterge türleri (Woody indicator species in the potential zones of Central Anatolia Region, where the use of black pine (*Pinus nigra* subsp. *pallasiana*) could be efficient) // *Ekoloji Dergisi (Ecol. Magaz.).* 2011. V. 20. N. 8. P. 51–58 (in Turkish).
- Hao G.-Y., Lucero M. E., Sanderson S. C., Zacharias E. H., Holbrook N. M. Polyploidy enhances the occupation of heterogeneous environments through hydraulic related trade-offs in *Atriplex canescens* (Chenopodiaceae) // *New Phytol.* 2013. V. 197. Iss. 3. P. 970–978.
- Kocacinar F. Photosynthetic, hydraulic and biomass properties in closely related C₃ and C₄ species // *Physiol. Plant.* 2015. V. 153. Iss. 3. P. 454–466.
- Kocacinar F., Sage R. F. Photosynthetic pathway alters xylem structure and hydraulic function in herbaceous plants // *Plant, Cell & Environ.* 2003. V. 26. Iss. 12. P. 2015–2026.
- Kocacinar F., Sage R. F. Photosynthetic pathway alters hydraulic structure and function in woody plants // *Oecologia.* 2004. V. 139. Iss. 2. P. 214–223.
- Kozlowski T. T., Pallardy S. G. *Physiology of woody plants.* 2nd ed. San Diego, CA, USA: Acad. Press, 1997. 411 p.
- Lebourgeois F., Levy G., Aussenac G., Clerc B., Willm F. Influence of soil drying on leaf water potential, photosynthesis, stomatal conductance and growth in two black pine varieties // *Ann. For. Sci.* 1998. V. 55. N. 3. P. 287–299.
- Li C., Shi X., Mohamad O. A., Gao J., Xu X., Xie Y. Moderate irrigation intervals facilitate establishment of two desert shrubs in the Taklimakan Desert Highway Shelterbelt in China // *Plos One.* 2017. V. 12. N. 7. P. 1–17: e0180875.
- Martin C. E., Harris F. S., Norman F. J. Ecophysiological responses of C₃ forbs and C₄ grasses to drought and rain on a tallgrass prairie in Northeastern Kansas // *Int. J. Plant Sci.* 1991. V. 152. N. 3. P. 257–262.
- McDowell N., Pockman W. T., Allen C. D., Breshears D. D., Cobb N., Kolb T., Plaut J., Sperry J., West A., Williams D. G., Yezzer E. A. Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? // *New Phytol.* 2008. V. 178. Iss. 4. P. 719–739.
- Oakley J. C., Sultmanis S., Stinson C. R., Sage T. L., Sage R. F. Comparative studies of C₃ and C₄ *Atriplex* hybrids in the genomics era: physiological assessments // *J. Exp. Bot.* 2014. V. 65. Iss. 13. P. 3637–3647.
- Osborne C. P., Sack L. Evolution of C₄ plants: a new hypothesis for an interaction of CO₂ and water relations mediated by plant hydraulics // *Phil. Trans. R. Soc. B.* 2012. V. 367. Iss. 1588. P. 583–600.
- Örs S., Ekinci M. Kuraklık stresi ve bitki fizyolojisi (Drought stress and plant physiology) // *Derim.* 2015. V. 32. N. 2. P. 237–250 (in Turkish).
- PMS Instrument Comp., 2018. <https://www.pmsinstrument.com/>
- Rajabpoor S., Kiani S., Sorkheh K., Tavakoli F. Changes induced by osmotic stress in the morphology, biochemistry, physiology, anatomy and stomatal parameters of almond species (*Prunus* L. spp.) grown *in vitro* // *J. For. Res.* 2014. V. 25. Iss. 3. P. 523–534.
- Sage R. F., Pearcy R. W. The nitrogen use efficiency of C₃ and C₄ plants. I. Leaf nitrogen, growth, and biomass partitioning in *Chenopodium album* (L.) and *Amaranthus retroflexus* (L.) // *Plant Physiol.* 1987. V. 84. Iss. 3. P. 954–958.
- Smirnoff N. The role of active oxygen in the response of plants to water deficit and desiccation // *New Phytol.* 1993. V. 125. Iss. 1. P. 27–58.
- Su P., Yan Q., Xie T., Zhou Z., Gao S. Associated growth of C₃ and C₄ desert plants helps the C₃ species at the cost of the C₄ species // *Acta Physiol. Plant.* 2012. V. 34. Iss. 6. P. 2057–2068.
- Systat software. Tools for science, 2018. <https://systatsoftware.com/>
- Taiz L., Zeiger E. **Plant physiology.** 3rd ed. Sunderland, MA, USA: Sinauer Associates, Inc., 2002. 690 p.
- Taşdemir C. Kurak mntıka ağaçlandırmaları ve Doğu-Güney Doğu Anadolu Bölgelerinin bu açıdan değerlendirilmesi (Arid area plantations and evaluation of East-South Eastern Anatolia Regions) // *Güney Doğu Anadolu Ormancılık Araştırma Enstitüsü Yayınları (Publ. South-Eastern Anatolia For. Res. Inst.).* 2012. V. 14. P. 39–55 (in Turkish).
- Tiemuerbieke B., Min X.-J., Zang Y.-X., Xing P., Ma J.-Y., Sun W. Water use patterns of co-occurring C₃ and C₄

- shrubs in the Gurbantonggut desert in northwestern China // Sci. Total Environ. 2018. V. 634. P. 341–354.
- Urban J., Ingwers M. W., McGuire M. A., Teskey R. O. Increase in leaf temperature opens stomata and decouples net photosynthesis from stomatal conductance in *Pinus taeda* and *Populus deltoids* x *nigra* // J. Exp. Bot. 2017. V. 68. Iss. 7. P. 1757–1767.
- Wang R. Z., Liu X. Q., Xing Q., Bai Y. Photosynthesis, transpiration, and water use efficiency of *Leymus dasystachys* on the Hunshandake desert // Photosynthetica. 2005. V. 43. Iss. 2. P. 289–291.
- Ward J. K., Tissue D. T., Thomas R. B., Strain B. R. Comparative responses of model C₃ and C₄ plants to drought in low and elevated CO₂ // Glob. Ch. Biol. 1999. V. 5. Iss. 8. P. 857–867.
- Wertin T. M., Reed S. C., Belnap J. C. C₃ and C₄ plant responses to increased temperatures and altered monsoonal precipitation in a cool desert on the Colorado Plateau, USA // Oecologia. 2015. V. 177. Iss. 4. P. 997–1013.
- Xu H., Li Y. Water-use strategy of three central Asian desert shrubs and their responses to rain pulse events // Plant and Soil. 2006. V. 285. Iss. 1–2. P. 5–17.
- Xu H., Li Y., Xu G., Zou T. Ecophysiological response and morphological adjustment of two Central Asian desert shrubs towards variation in summer precipitation // Plant, Cell & Environ. 2007. V. 30. Iss. 4. P. 399–409.

УДК 577.355.3:581.115/116.1

ФОТОСИНТЕТИЧЕСКИЕ РЕАКЦИИ МИНДАЛЯ АРАБСКОГО *Amygdalus arabica* Olivier И ЛЕБЕДЫ СЕРЕЮЩЕЙ *Atriplex canescens* (Pursh) Nutt. НА ВЛИЯНИЕ ЗАСУХИ В ПОЛЕВЫХ УСЛОВИЯХ

Б. Акгун, Е. Язар, Ф. Кокасинар

Университет им. Имама Кахраманмараши Сутсу
Турция, 46100, Оникисубат Кахраманмараши, Бульвар Бати Чевреелу, 251 А

E-mail: bakgun2002@gmail.com, emreyazar@ksu.edu.tr, kocacinarf@gmail.com

Поступила в редакцию 30.01.2018 г.

Центральный Анатолийский регион Турции подвержен повышенным температурам воздуха и сильной засухе. В связи с засушливостью и опустыниванием в результате глобального потепления и изменения климата при усугубляющем воздействии истощительного использования многие растения в этом регионе находятся под угрозой исчезновения. Вместе с тем некоторые виды растений смогли адаптироваться к суровым условиям чрезвычайно высоких температур и малого количества осадков. В статье обсуждаются результаты полевых исследований и периодических измерений в период с мая по сентябрь газообменных и водных потенциалов миндаля арабского *Amygdalus arabica* Olivier (C₃-фотосинтез) и лебеды сереющей *Atriplex canescens* (Pursh) Nutt. (C₄-фотосинтез) – двух засухоустойчивых древесных пород, высаженных ранее в целях борьбы с опустыниванием в районе Карапинар, провинция Конья, в центральном Анатолийском регионе. В течение вегетационного периода 2015 г. определяли показатели чистого фотосинтеза, скорости транспирации, водного потенциала в полдень и эффективности использования воды растениями. Максимальные показатели чистого фотосинтеза и наибольшая скорость транспирации, измеренные в июле и сентябре у миндаля арабского и лебеды сереющей, составили: 12.4 и 29.7 мкмоль м⁻² с⁻¹ (фотосинтез); 4.8 и 7.1 ммоль м⁻² с⁻¹ (транспирация) соответственно. Максимальные значения эффективности использования воды миндалем и лебедой, измеренные у обоих видов в июне, составили 5.7 и 7.7 ммоль СО₂ моль⁻¹ Н₂О соответственно. Наименьшие значения полуденного водного потенциала у обоих видов зафиксированы в августе. Результаты исследований показывают, что оба вида растений обладают способностью переносить условия засухи в регионе, однако по природе C₄-фотосинтеза лебеда сереющая обладает более высокой засухоустойчивостью, чем миндаль арабский, произрастающий на засушливых землях и пустошах.

Ключевые слова: газообмен, влияние засухи, засушливые земли и пустоши, *Amygdalus arabica*, *Atriplex canescens*, центральный Анатолийский регион, Турция.