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Gas Exchange Parameters of 8-Year-Old *Abies fraseri* (Pursh) Poir. Seedlings Under Different Irrigation Regimes

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ABSTRACT

Eight-year-old *Abies fraseri* seedlings were grown under different irrigation regimes to determine how drought stress might affect the seedlings in terms of gas exchange parameters. In this study, net photosynthesis (*Anet*), transpiration rate (*E*), stomatal conductance (*gs*), intercellular CO_2 (*Ci*), *Ci* to ambient CO_2 (*Ca*) concentration ratio (*Ci*/*Ca*), intrinsic water use efficiency (*iWUE*), and water use efficiency (*WUE*) were measured on August 11 and 27. Irrigation and measurement time were statistically significant on all gas exchange parameters except *WUE* for irrigation and measurement time and *Anet* for measurement time. *E* and *gs* were significant under the irrigation and measurement time interactions. In this study, increasing irrigation generally decreased *Anet*, and *gs*, while increased *E*, *iWUE*, and *Ci*/*Ca*. On August 27, *A. fraseri* had higher *Anet*, *gs*, *E*, *Ci*, *Ci*/*Ca*, and lower *iWUE* values than August 11. However, there was a robust positive correlation between *gs* and *Anet*, while a negative correlation between *gs* and *iWUE* in *A. fraseri* seedlings. In general, prolonged water deficiency leads plants to decrease *Anet*, *gs*, and *E* while *iWUE* increases, contrary to the current study. A well-developed and deeper root system, especially in plants under less or no-irrigation regimes, may alleviate drought stress effects in the long run and provide an advantage in leaf gas exchange parameters. In addition, the fact that soil moisture did not differ much between treatments, although irrigation levels were different, may explain the similar behavior among individuals measured in terms of gas exchange parameters.

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Introduction

Among *Abies* species, *Abies fraseri* [Pursh] Poir. (Fraser fir) is an economically important plant species for the production of Christmas trees and landscapes in the Eastern and Midwest of the USA (Nzokou et al., 2010; Kulaç et al., 2012; Wilson et al., 2013; Pettersen et al., 2015; NCTA, 2019). *A. fraseri* naturally grows at high elevation (between 1500 and 2037 m asl) in the southern Appalachian Mountains, where the weather conditions are chill and humid. In their natural distribution, *A. fraseri* species receive 1900-2500 mm precipitation annually, and the average temperature is between 6-15°C (Cory et al., 2017).

In the USA market, each tree costs approximately $ 75-80, and a total of 26 million Christmas trees were sold in 2019 (NCTA, 2019). *A. fraseri* has been extensively planted in the Eastern and Midwest USA because of its economic viability, being a fast-grown species, and its aesthetic appearance (Cregg and O'Donnell, 2020). As a result of the plantation tree species far away from their natural distribution sites, they face some environmental stresses such as drought stress due to low rainfall and higher summer temperatures. The increasing effect of global warming under climate change scenarios will be more severe in *A. fraseri* plantation areas outside their natural range, where the temperature will increase, and the rainfall reduces, especially throughout the summer (Melillo et al., 2014).

Temperature, precipitation, wind, and other environmental factors play a critical role in plant morphology, anatomy, and phenotypic features (Koç, 2021a; Ozel et al., 2021). Water may be one of the most crucial environmental stressors observed in the 21st century worldwide (Mutlu and Kurnaz, 2018; Tokatli et al., 2021; Kutlu and Mutlu, 2021). Increased temperature increases the water usage by plants, resulting in a decline in water content in the soil called drought and water deficit. Progress of water deficit or drought in the soil causes a decline in turgor, followed by reduced stomatal closure and transpiration (Dayer et al., 2020; Yang et al., 2021). Drought as one of the abiotic stressors' constraints plant germination, growth (Koc and Nzokou, 2018), physiology (Sevik and Erturk, 2015; Li et al., 2020; Guo et al., 2021; Koç et al., 2021), and nutrient uptake (Shults et al., 2020).

The intensity and frequency of drought will reduce soil moisture and affect plants much more in the future due to global warming as a result of increased greenhouse gas concentrations (Xu et al., 2020; Canturk and Kulaç, 2021; IPCC, 2021; Varol et al., 2021). According to IPCC (2021), the air temperature may increase by 2.5°C in 2050 and 4.8°C in 2100.

As known, water is the fundamental compound for plant growth, development, and all physiological processes such as photosynthesis and carbon assimilation (Yildiz et al., 2014; Soba et al., 2020; Wang et al., 2020; Demir et al., 2021; Uncumusaoğlu and Mutlu, 2021). Under increased summer temperature and lack of water in the soil, plant species are negatively affected by these situations (Varol et al., 2022a, b). However, some plants tolerate different stress levels, and when the stress level is severe enough or exceed the tolerance range, it may cause a severe injury to plants and kill them (Laxa et al., 2019). When plants are exposed to drought, their first mechanism is to close their stomata (Martínez-Vilalta et al., 2017) which results in reduced gas exchange (Koç, 2021b; Koç and Nzokou, 2022) and some changes in photosynthetic pigments (chl a, chl b and carotenes concentration) in their leaf (Jatav et al., 2021). In general, stomatal closure adversely affects the CO_2 uptake, resulting in decreased CO_2 assimilation and photosynthesis that the plant growth and development are hindered (Koç, 2019; Yigit et al., 2021; Koç 2021b, c). Also, plant leaf gas exchange parameters under the changing temperature and soil moisture situation vary based on the age and type of species, intensity and frequency of the drought, and plant adaptation ability.

In contrast, the rate of net photosynthesis and stomatal conductance reflects intrinsic water use efficiency in the plant leaf level using the Li-Cor gas exchange instrument (Lambers et al., 2010). The volume of water used to produce a unit of fixed carbon through photosynthesis in plants is called water use efficiency, and it may vary under drought stress (Maier et al., 2019). Water use efficiency is calculated by the rate of net photosynthesis and transpiration. Water use efficiency and intrinsic water use efficiency are key traits to expose the plant's physiological adaptation to droughty conditions. A stricter stomatal control stimulates to improve short-term (intrinsic water use efficiency (Comstock, 2002) and water use efficiency in a long period (de Miguel et al., 2012). These two traits evaluate plants' adaptation status in different environmental conditions, such as arid and semi-arid regions. In addition, plants use intercellular CO_2 (*Ci*) rather than ambient CO_2 in the air (*Ca*) (Landsberg and Sands, 2011), which stomatal behavior in photosynthesis research provide beneficial knowledge of *C*i and *Ci*/*Ca* under various conditions.

This study aimed to investigate how leaf gas exchange parameters (net photosynthetic rate (*Anet*, μmol m^{-2} s^{-1}), stomatal conductance (*gs*, mmol H_2O m^{-2} s^{-1}), and transpiration rate (*E*, mmol m^{-2} s^{-1}), intercellular CO_2 (*Ci*, μmol mol^{-1}), internal (*Ci*) to ambient CO_2 (Ca) concentration ratio (*Ci*/*Ca*, μmol mol^{-1}), intrinsic water use efficiency (*iWUE*=*Anet*/*gs*) and water use efficiency (*WUE=Anet/E*) change in *A. fraseri* seedlings under different drought conditions. The measurements were done twice in the hottest month of the year to determine how drought stress might affect the seedlings in terms of gas exchange parameters. It is hypothesized that increasing irrigation would increase *Anet*, *gs*, *E* while decreasing *WUE* and *iWUE* in *A. fraseri* seedlings. It was expected that increasing drought stress would cause a decrease in *Anet*, *gs*, and *E* while increasing *WUE* and *iWUE*. The obtained results could provide information to both the scientific world and the producers about the tree growth and development that may occur due to gas changes in *A. fraseri* seedlings under different irrigation regimes in summer.

Material and Methods

Study Design

A randomized complete block design was used with five irrigation levels, two measurement times, four hoop houses (blocking), and 16 plants for each treatment (considered as replication). A total of 560 containerized plants (plug+2) were obtained in 2008 for a different study and planted in this block design.

This experiment was conducted in a semi-automatically controlled four hoop houses, covered by a single layer of clear plastic at the Tree Research Center (lat. 42.65° N, long. 84.42°W) in Michigan State University, USA. Each hoop house was split into five sections and assigned one of the five irrigation treatments. About 1 m waterproof barriers (oriented strand board covered with plastic cover) were vertically inserted into the ground to avoid sideways movement of soil moisture between sections. The hoop houses were designed as open at both ends and 15-20 cm from the soil level on the other sides to permit free airflow and prevent increases in temperatures due to the greenhouse effect. This setup helps avoid higher temperature differences in the hoop houses than outside. For instance, the temperatures inside the hoop house were only 1-2°C higher than the outside temperature in the middle of hot days (June-September). The minimum and maximum air temperatures measured between June - September were 7°C and 30°C, while the minimum and maximum air temperatures were 16 - 26 and 16 - 24°C on August 11 and August 27, 2013 (the hottest month of the year), respectively (Figure 1).

Plant Material

Plant materials were initially obtained from a commercial nursery in 2008 and planted for another study (Kulaç et al., 2012). In 2008, the seedlings were planted in four rows of seven individuals, each with 0.6-m spacing (28 plants total per section) for their study. In that study, plants were manually fertilized with ammonium sulfate (at the rate of 56 kg/ha) at the beginning of the growing season first two years. After that study was done, the plants were continued to be irrigated at the same rate (0, 0.62, 1.25, 2.5, 3.75 cm/week) between June to September and were not subjected to any other treatment until the current study started (in 2013). In addition to weed control by hand, glyphosate herbicide (at the rate of 35.84 kg/ha) was applied using a CO_2–power back sprayer each year.

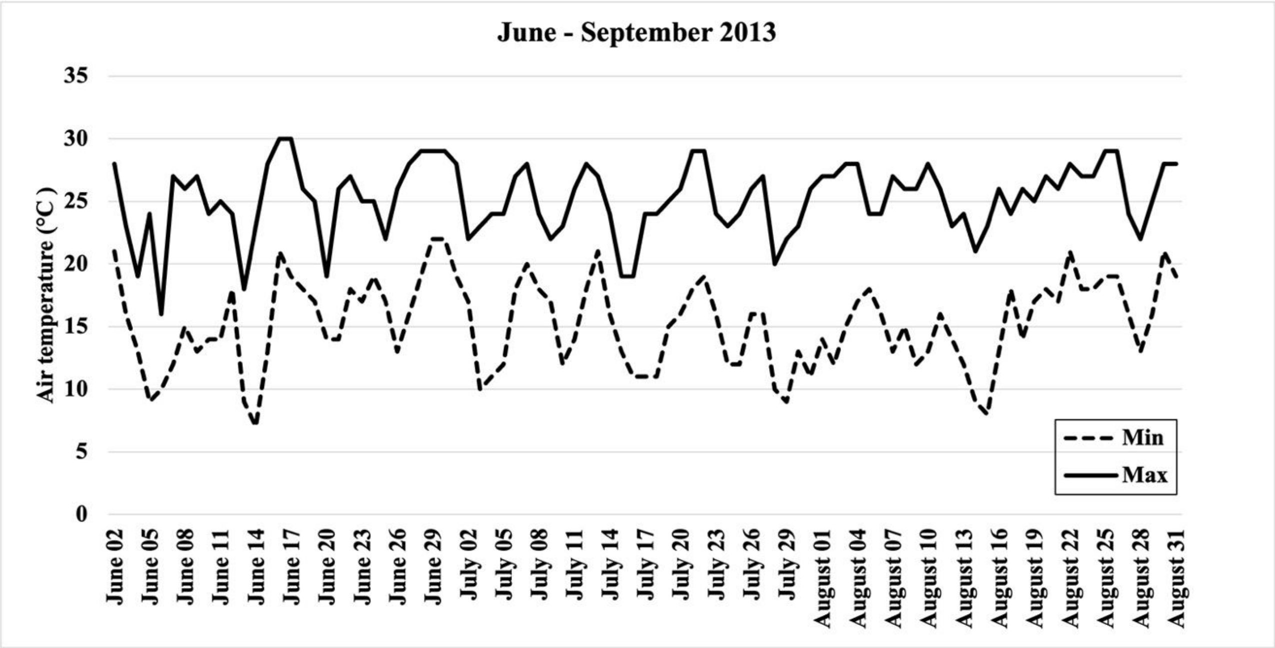

Figure 1. The outside temperature changes during June to September 2013.

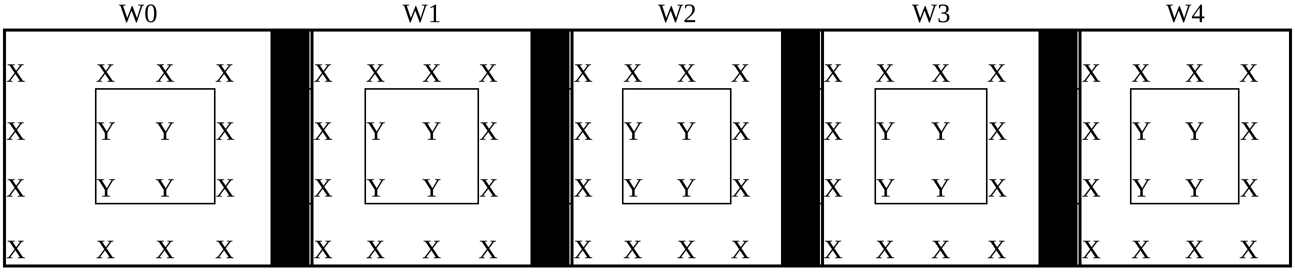

Figure 2. The layout of a single hoop house. Each seedling is represented by X and Y, and 3 out of 4 seedlings in the center of each section (Y) are subjected to gas exchange measurements.

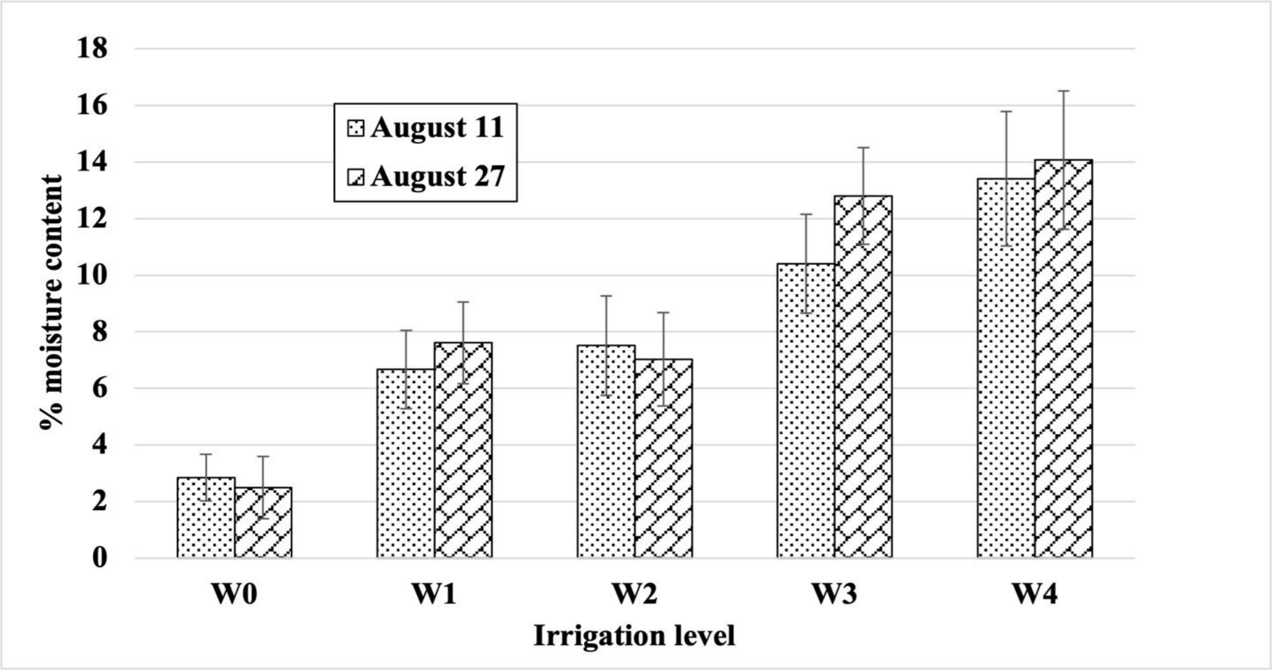

Figure 3. Soil moisture content (%) change (± std. dev.) on August 11 and August 27, 2013.

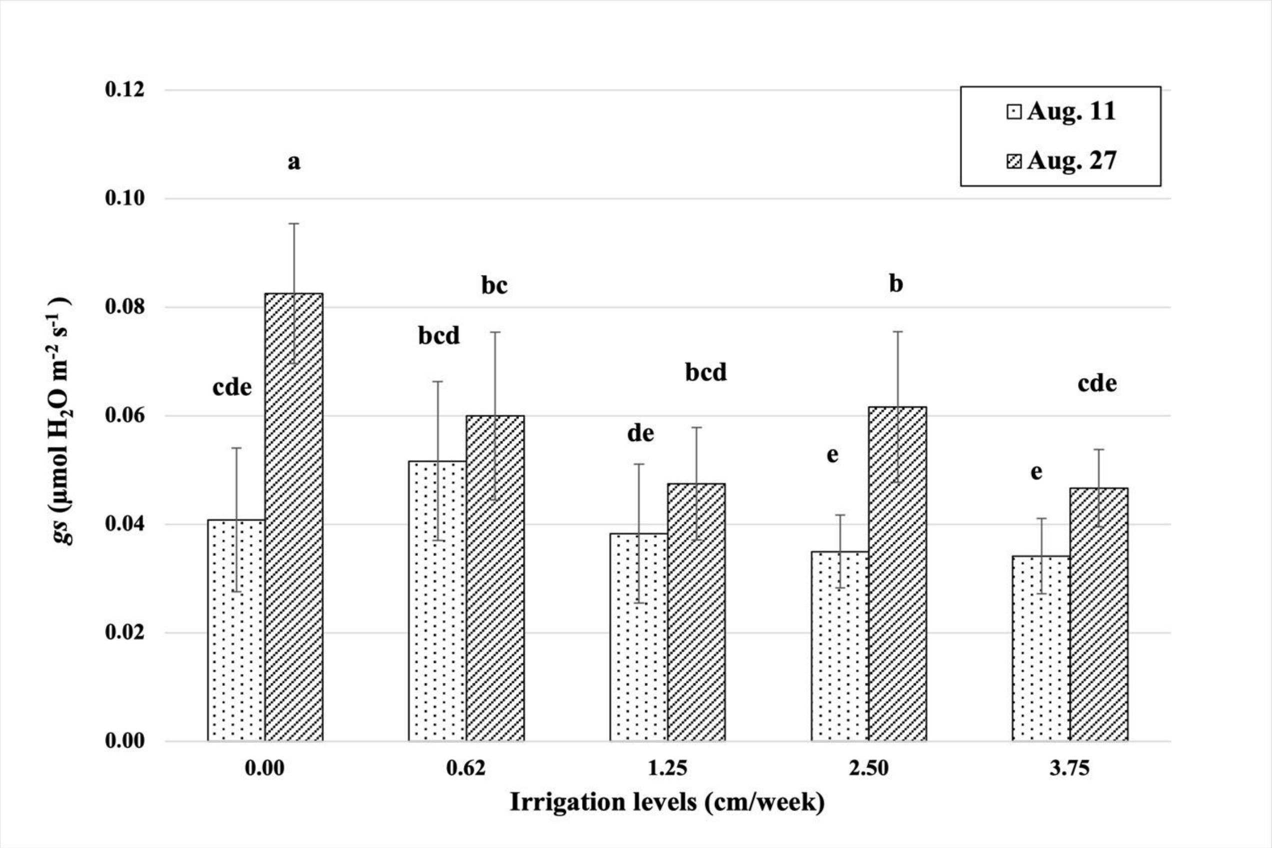

Figure 4. The mean values (±SE) and Tukey's test results separation of *gs* (µmol H_2O m^{-2} s^{-1}) rate in terms of the interaction of irrigation level and time.

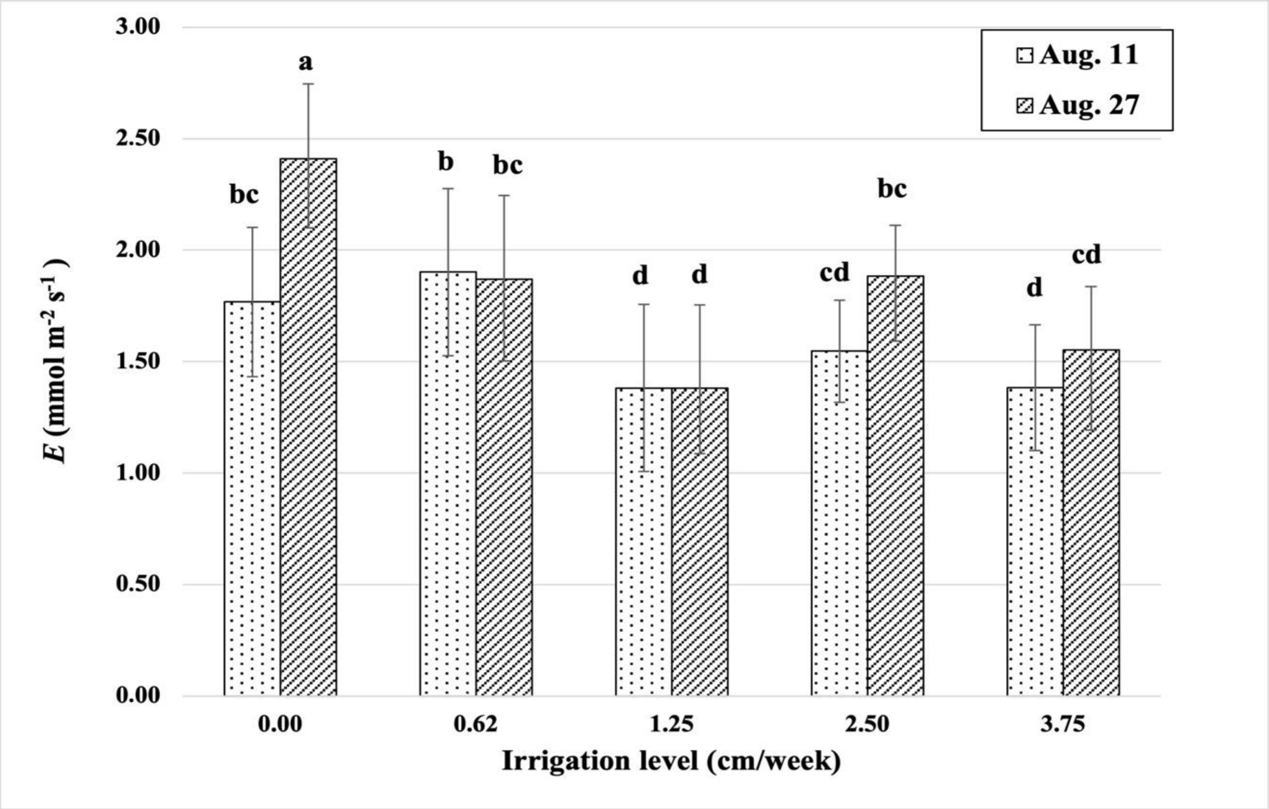

Figure 5. The mean values (±SE) and Tukey's test results separation of *E* (mmol m^{-2} s^{-1}) rate under irrigation and time interaction.

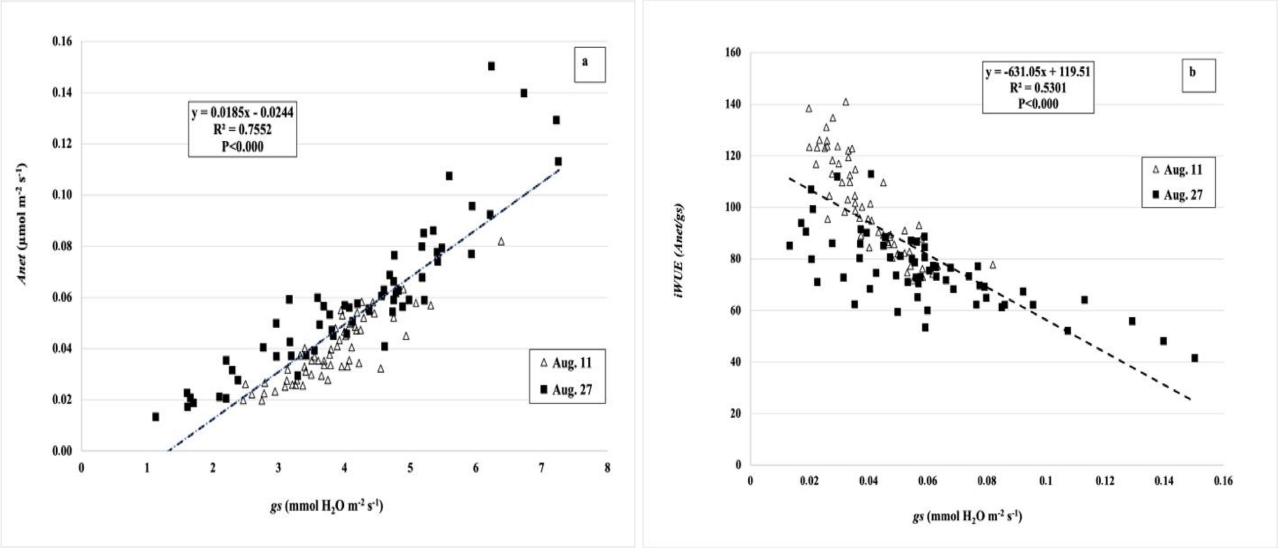

Figure 6. Relationships between *gs* and *Anet* (a) and *gs* and *iWUE* (b) in *Abies fraseri* plants.

Table 1. Degrees of freedom (df), F values of analysis of variance for *Anet*, *gs*, *E*, i*WUE*, *WUE*, *Ci*, and *Ci/Ca* among five irrigation levels and two measurement times.

Source of variation	df	Anet	gs	E	iWUE	WUE	Ci	Ci/Ca
Irrigation (I)	4	5.27***	5.52***	11.54***	3.98**	0.80ns	3.25*	3.80**
Time (T)	1	3.85ns	33.91***	8.41**	86.88***	0.24ns	73.01***	80.67***
IxT	4	1.66ns	3.61***	2.60*	2.20ns	0.56ns	1.44ns	1.80ns

Note: * significant at 0.05 level. ** significant at 0.01 level. *** Significant at 0.001 level. ns: not significant.

Table 2. The mean values and Tukey's test results of *Anet* (µmol m^{-2} s^{-1}) by the interaction of irrigation and time.

	Irrigation level (I) (cm/week)					
Time (T)	W0 (0.00)	W1 (0.62)	W2 (1.25)	W3 (2.5)	W4 (3.75)	Mean of T
Aug.11	3.96	4.40	3.67	3.65	3.48	3.83
Aug.27	4.89	4.42	3.46	4.34	3.66	4.16
Mean of I	4.42^{a}	4.41^{a}	3.57^{b}	4.00^{ab}	3.57^{b}	

Note: The lowercase letters indicate the significance within the irrigation treatment.

In 2013, when the current study was started, the plants were eight-year-old, and 16 seedlings were in each treatment section. The hoop houses were covered in plastic since 2008. Due to the edge effect, the plants on every four sides (X) were not used (buffer). So, 3 out of 4 seedlings (bold Y) in the center of each treatment section within each hoop house (Figure 2) were subjected to gas exchange measurement in the current study. The average size of these plants was about 52 mm and 98 cm in diameter and height, respectively.

Irrigation Treatment

At the beginning of June 2013, the irrigation system was set up to apply water instantaneously to all four hoop houses, which was the irrigation treatment started for the current study. The irrigation volumes for each irrigation level were 0 (W0), 0.62 (W1), 1.25 (W2), 2.5 (W3), and 3.75 (W4) cm/week, which represent 0, 12, 18, 25, and 38 min of run time daily applied every day.

The plants were irrigated with a fully automatic irrigation system equipped with a drip line (Netafilm Irrigation Inc., Fresno, CA, USA) during the growing season (June to September). The soil moisture and temperature were monitored in each treatment using a digital time domain reflectometry moisture sensor model ACC-SEN-TDR (Acclima Inc., Meridian, ID, USA). Soil moisture and temperature readings were monitored instantly (without being logged) with the help of this system, and the irrigation level automatically adjusted at midday, confirming the clear separation between non-irrigated and irrigated treatments. However, a soil moisture sensor model ACC-SEN-TDR was used to obtain the soil moisture content twice (August 11 and 27, 2013) in this study.

Gas Exchange Parameter Measurements

The Li-Cor portable gas exchange system (Li-Cor Biosciences, Lincoln, NE, USA) has been widely used in the last two decades to provide quick and robust simultaneous measurements of gas exchange parameters and eliminate time delays. This instrument (Li-Cor 6400XT) has a closed system that controls CO_2, relative humidity, IRGA, and light intensity. Using Li-Cor provides information about net photosynthesis, stomatal conductance, and transpiration rate based on a unit area on the leaf or needle leaf. Also, it was calculated water use efficiency and intrinsic water use efficiency, using obtained Li-Cor data.

Three out of four randomly selected plants from each treatment (bold Y in Figure 2) in each hoop house were subjected to gas exchange parameters measurement using Li-Cor needle leaf chamber (LI-6400XT, Lincoln, NE, USA) with an accessory of a light source (red, green, and blue) (640-18A). Then reference CO_2 was set 400 µmol

mol^{-1} s^{-1}, and the airflow rate was maintained at 500 µmol s^{-1}. The photosynthesis photon flux density (PPFD) was set at 1200 µmol s^{-1}. Three random seedlings (different individuals used each time) were selected from each treatment in a single hoop house in each measurement time (August 11 and August 27, 2013). A total of 12 plants (3 plants from each hoop house) were subjected to gas exchange measurement from each treatment in each measurement time. The needle leaves were separated from the shoot and scanned after the gas exchange measurements were done. Projected leaf area was determined using the ImageJ software program. The measured leaf areas were inserted into the system to adjust the values for each previously measured gas exchange parameter.

Anet, *gs*, and *E*, *Ci*, *Ci*/*Ca* gas exchange parameters were instantaneously measured when the LI-6400XT software calculated *iWUE=Anet/gs* and *WUE=Anet/E*.

Statistical Analysis

Data were analyzed using SAS 9.1 software (SAS Institute Inc., Cary, NC, USA). PROC UNIVARIATE function was used to test for normality, and then an analysis of variance (ANOVA) was examined by using PROC MIXED function for all gas exchange parameters. The mean separation of treatment, time, and the interaction of treatment and time were tested by Tukey's adjustment when alpha was 0.05. The regression analysis was used to determine the relations between the parameters of gas exchanges.

Results

Soil Moisture

Soil moisture content did not fluctuate between two measurements within each irrigation regime. Seedlings in the W4 treatment had the highest soil moisture, while non-irrigated seedlings had the lowest values. There was no clear separation between W1-W2 and W3-W4 treatments (Figure 3).

Gas Exchange Parameters

The statistical analysis of variance for *Anet*, *gs*, *E*, *iWUE*, *WUE*, *Ci*, and *Ci*/*Ca* under five irrigation treatments and two measurement times are given in Table 1.

Irrigation (I) was significant ($P<0.05$), while time (T) and the interaction of IxT were not significant ($P>0.05$) for *Anet* (Table 1). W0 and W1 treatment statistically had the highest *Anet*, while W2 and W4 had the lowest values (Table 2). The plants under W0 (non-irrigated) on August 27 had the highest *Anet* values, while W2 (1.25cm/week) treatment had the lowest value on August 27 under the IxT combination (Table 2).

As a result, I, T as a single factor, and the interaction of IxT were significant ($P<0.05$) for *gs* (Table 1). When I considered a single factor, plants in W0 treatment statistically had the highest *gs* values while plants in W3 and W4 treatment had the lowest values. Plants showed higher *gs* values on August 27 compared to August 11. Under the interaction of IxT, non-irrigated plants on August 27 had the highest *gs* values, while non-irrigated plants on August 11 had the lowest values (Figure 4). *A. fraseri* plants showed lower *gs* values on August 11 than August 27 under each irrigation level (Figure 4).

The single factors (I and T) and their interaction were statistically significant on *E* ($P>0.05$) (Table 1). Increasing irrigation generally decreased *E* that non-irrigated plants had the highest *E* values while the plants in W2 and W4 treatments had the lowest values (Figure 5). The plants measured on August 27 were higher *E* values than August 11 when the time was a single factor. Under IxT interactions, non-irrigated plants measured on August 27 had the highest mean *E* value, while plants in W3 treatment for both measured days and W4 treatment on August 11 had the lowest *E* values (Figure 5).

The single factors such as I and T were significant ($P<0.05$) on *iWUE* (Table 1). The highest mean *iWUE* value was observed in W4 treatment plants, while the lowest *iWUE* was observed in the W0 treatment plants when I was considered a single factor (Table 3). The highest *iWUE* values were observed on August 11 compared to August 27 when T considered a single factor (Table 3). Even though IxT interaction was not significant ($P>0.05$), the highest mean *iWUE value* was observed in W4 treatment on August 11, while the lowest *iWUE* value was observed in W0 treatment on August 27 (Table 3).

The factors (I and T) and their interaction did not show any statistical differences on *WUE* in plants (Table 1). However, I and T were significant ($P<0.05$) on *Ci* and *Ci*/*Ca* while IxT interaction was not significant on both the same parameters (Table 1). W0 and W1 treatments had the highest *Ci* values (appr. 207 µmol mol^{-1}) statistically, while the W4, W3, and W2 treatments had the lowest values (appr. 195, 193,192 µmol mol^{-1}, respectively).

Plants had higher *Ci* values (182 µmol mol^{-1}) on August 27 than August 11 (160 µmol mol^{-1}). The *Ci*/*Ca* parameter showed similar results, such as *Ci* for I and T. For instance, W0 and W1 treatments had higher *Ci*/*Ca* values (0.58) than W2 (0.54), W3 (0.54), and W4 (0.53) treatments between irrigation. For the time factor, plants showed higher *Ci*/*Ca* values on August 27 (1.82) than August 11 (1.60).

The relationship between *gs* and *Anet*, and *gs* and *iWUE* are given in Figure 6a, b. There was a robust positive correlation between *gs* and *Anet* (Figure 6a), while a negative correlation between *gs* and *iWUE* was observed in *A. fraseri* plants (Figure 6b).

Discussion

Our world has recently faced many disasters such as wildfires (Ertugrul et al., 2021), massive flooding (Kilicoglu et al., 2021), earthquakes, climate change, and pollution (Mutlu and Aydın Uncumusaoglu, 2017; Mutlu and Aydın Uncumusaoglu, 2018; Mutlu, 2019; Emin et al., 2020; Mutlu and Arslan, 2021). Among these factors, air pollution includes heavy metals (Isinkaralar et al., 2022; Key et al., 2022; Koç et al., 2022) and drought (Koç et al., 2021; Koç, 2022; Koç & Nzokou, 2022), which are the most effective on living things, come to the fore. In the recent century, among many other unfavorable environmental factors worldwide, drought stress has become the most critical one due to the importance of plant growth, development, and physiology (Turfan et al., 2019; Sevik et al., 2021). Plant physiological processes, including gas exchanges, are directly or indirectly affected by drought stress (Zhang et al., 2018). The increasing severity of drought stress negatively inhibits gas exchange parameters in conifer species (Koç, 2021b, c). In general, the lack of water in the soil diminishes xylem pressure potential, especially when plants do not have a developed root system. The decrease in xylem pressure potential stimulates stomatal closure to reduce water loss from leaves via stoma, resulting in a decline in *Anet* and *E*, contrary to the present study. A decline occurs in CO_2 assimilation when stomatal aperture is reduced under unfavorable conditions, such as drought stress. The stomatal closure is caused by an increasing abscisic acid and reducing water potential (Hsu et al., 2021) in needle-leaved species (Brodribb and McAdam, 2013). A robust stomatal closure results in a decline in *Anet*, *gs*, and *E* as observed in *Pinus* and *Abies* species (Zweifel et al., 2009; Hart et al., 2020).

On the other hand, reducing soil moisture (from 100% [well-watered] to 25% [drought-stressed] water requirement) generally increases *WUE* and *iWUE* in *Pinus brutia* (Koç, 2021b) and *A. concolor* and *A. balsamea* species (Koç and Nzokou, 2022). Conifer species can perform high *iWUE* either due to low stomatal conductivity and/or high *Anet* under the interaction of both (Koç, 2019; Koç, 2021a, b, c; Koç et al., 2021), in line with the current study. A reduction in *gs* in the leaf level can decrease the *E* values; thus, this could positively change *WUE* in plants (Belmecheri et al., 2021), unlike the current study. When the intensity of drought stress increases on trees, water usage is increased due to improved tree growth and development (Liu et al., 2015; Li et al., 2020). Trees with higher *WUE* and *iWUE* rates result in better tree growth and productivity (Xu et al., 2020).

In general, growing the severity of water deficit on trees reduces *Anet*, *gs*, and *E* while increasing *iWUE* to alleviate drought stress effects under arid and semi-arid regions. Stomatal behavior plays a key role in balancing *Anet* and *gs*, and *Anet* and *E* resulting in lower or higher *iWUE* and *WUE* in trees (Urban et al., 2017; Koç and Nzokou, 2022). In this study, a robust balance between *Anet* and *gs* was observed. In general, the reduced *E* and *gs* indicate that trees have a vigorous stomatal control to avoid excessive water loss throughout water deficit conditions, contributing to better drought adaptation. Stomatal behavior also affects Ci and Ci/Ca parameters due to controlling CO_2 in the leaf level (Katul et al., 2010). In general, Ci/Ca increases with soil water content and decreases with water vapor deficit (Tan et al., 2017), contrary to the current study. It is caused by soil moisture not showing clear variation between treatments even though different irrigation regimes were used on seedlings.

It is stated that the tress, which has been exposed to drought stress for a long time, has developed a more expanded root system in the hoop house settings (Koç, 2019; Maier et al., 2019). The root features (root type, length, ratio of the finer root, and root/shoot ratio) and genetic variation are key factors for plant growth, development, and physiology in critical environments (Maier et al., 2019). Therefore, it is thought that they become more advantageous than watered seedlings in gas exchange due to their adaptation to drought and benefiting from deep water thanks to an extended root system. Although irrigation levels differed in the current study, soil moisture did not show much difference between treatments, which could explain similar behavior between the measured individuals in terms of gas exchange parameters. Based on the visual observations made during the measurements, it was observed that the non-irrigated seedlings had a lower height and diameter growth than the others. Although there was no obvious difference between the irrigated seedlings, especially between W1 - W2 and W3 - W4, it was observed that the seedlings from W4 and W3 irrigation regimes had a higher height growth than the seedlings from W2 and W1 treatment.

Conclusion and Suggestions

Water is the source of life not only for humans but also for plants. Water shortage causes many disorders in plants' growth, development, and physiological processes such as photosynthesis. The severity or intensity of water deficit conditions negatively affects tree species. Gas exchange measurement is one of the practical ways to observe drought stress effects on trees. It was expected that increasing drought stress would cause a decrease in *Anet*, *gs*, and *E* while increasing *iWUE*; however, a clear trend was not observed in *A. fraseri*. Non-irrigated or less watered seedlings might have developed a better and deeper root system that alleviates drought stress and has better gas exchange values in *A. fraseri* trees.

A future study should focus on the below-ground to support the present study results because when trees have a well-developed root system, they can avoid drought stress by using a different drought tolerance mechanism, such as osmotic adjustment, protective solutes and enzymes. These studies are necessary to test *Abies* species because they are economically prominent trees for landscape and Christmas trees production in Europe and Türkiye . These studies will provide some knowledge about how irrigation regimes change the *Abies fraseri* species gas exchange patterns, resulting in altered tree growth and development for researchers and growers.

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