Comparison of Scotch Pine (*Pinus sylvestris* L.) Origins in terms of Photosynthetic Gas Exchange and Chemical Properties

Fatma Merve Nacakci ,* and Süleyman Gülcü

This study was conducted to address the urgent need for identifying drought-tolerant varieties of *Pinus sylvestris* L. (Scotch pine) in response to the increasing impact of global climate change on forest ecosystems. The aim was to evaluate the physiological and biochemical responses of Scotch pine provenances grown in the Lakes Region of Türkiye in terms of photosynthetic gas exchange and selected stress-related chemical traits. Samples from different origins were analyzed to assess parameters such as adaptation to drought stress, water use efficiency, stomatal conductance, and photosynthesis rate. The data, obtained from long-term provenance trials established in 2000 in Aydoğmuş (Isparta) and Kemer (Burdur), revealed how these traits vary depending on origin and site conditions. Among the provenances, Çatacık, Akyazı, and Mesudiye displayed higher photosynthesis rates, stomatal conductance, and transpiration. Additionally, the accumulation of proline and hydrogen peroxide appeared to play a key role in drought adaptation, with Çatacık and Akyazı showing better performance under arid conditions. The findings provide valuable insights for selecting appropriate Scotch pine provenances for afforestation in arid and semiarid environments and contribute to the development of climate-resilient forest management strategies.

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*Contact information: Department of Forest Engineering, Faculty of Forestry, Isparta University of Applied Sciences, 32260, Isparta, Turkiye; *Corresponding author: mervenacakci@isparta.edu.tr*

INTRODUCTION

Pinus sylvestris L. is the most widely distributed conifer species in the world, extending from northern Spain and Scotland to Russia, Mongolia, and large parts of the Northern Hemisphere, including Turkey and the Caucasus (Boratynski 1991; Yaltırık 1988; Eckenwalder 2009; Farjon 2010; Koparan *et. al.* 2024). It grows in both pure and mixed forests, occupying a broad altitudinal range from sea level in northern Europe to approximately 2700 meters in Turkey, and latitudinally up to the 70th parallel.

Economically, *P. sylvestris* plays a key role in European forestry, making up about 20% of commercial forest areas and a major portion of timber production in northern countries. However, its natural distribution is limited by low temperatures in the north and summer drought combined with high temperatures in the south (Carlisle and Brown 1968; Castro *et al.* 2004; Mendoza *et al*. 2009). Growth reductions of up to 50% due to cold and 37% due to drought stress have been reported (Magnani *et al.* 2009).

Regarding drought, precipitation and a lack of water come to mind first. For a region to be called an "arid zone," it is necessary that there is a lack of precipitation and a lack of water in that region; this phenomenon should be permanent (Uluocak 1974). Natural plant populations located in arid regions may have the ability to adapt to these conditions more as a result of thousands of years of natural selection with the stress of drought. On the other hand, forest tree populations of foreign provenance can undergo effective selection during an administration period due to the effects of newly brought habitat conditions (such as drought), and as a result, they can develop adaptation abilities (stress theory) according to these conditions (Zobel and Antos 1987). The drought resistance of a tree species' provenance is often closely related to the degree of drought in its natural habitat, and this relationship—shaped by past natural selection—has important implications for future seed transfer and breeding programs (Dirik 2000; Çalıkoğlu 2002; Kulaç 2010).

In the context of global climate change, which is expected to shift species distributions and reduce genetic diversity in forest ecosystems (IPCC 2007), the selection of drought- and heat-tolerant provenances has become increasingly critical for sustainable forestry. According to Morgenstern (1996) and Schmidtling (1993), provenance trials offer a long-term basis for evaluating the adaptability of forest tree populations under changing environmental conditions and for guiding reforestation efforts.

Under conditions of extreme drought, plant stomata tend to close, resulting in reduced cell growth and developmental activity. Water deficiency stress causes functional disruptions in chloroplasts and accelerates stomatal closure, which in turn suppresses photosynthesis (Machado *et al.* 2009; Endres *et al.* 2010; Sales *et al.* 2012; Medeiros *et al.* 2013; Ribeiro *et al.* 2013; Silva *et al.* 2013; Júnior *et al.* 2019). Under prolonged water stress, although initial stomatal closure helps prevent dehydration, it also limits CO_2 uptake, leading to a decline in both photosynthesis and respiration (Opik and Rofle 2005; Inman-Bamber *et al.* 2012; Sales *et al.* 2012; Medeiros *et al.* 2013). Several studies have confirmed that stomatal conductance and transpiration rates decrease in hot and arid climates due to stomatal closure, occasionally resulting in leaf senescence and a subsequent decline in photosynthetic efficiency (Yin *et al.* 2005; Guo *et al.* 2006; Wikberg and Ogren 2007; Ma *et al.* 2014; Medrano *et al.* 2015; Pliura *et al.* 2018).

Leaf water potential is a key indicator of plant water status, reflecting the tension that drives water movement from the leaf to the atmosphere. It is widely used in studies to assess the effects of drought on plants (Bergonci *et al.* 2000). Midday xylem water potential is often employed as a sensitive measure of water stress (Naor 2000; Intrigliolo and Castel 2006). Drought stress leads to the overproduction of reactive oxygen species (ROS), which plants counteract through metabolic adjustments involving antioxidants (Alscher *et al.* 1997; Shigeoka *et al.* 2002; Krasensky and Jonak 2012; Lee and Park 2012; Bhargava and Sawant 2013). Prolonged exposure to drought can cause lipid peroxidation, DNA damage, and even cell death (Cruz de Carvalho 2008; Hossain *et al.* 2015; Ozturk 2015). Malondialdehyde (MDA) content is widely used to assess the extent of lipid peroxidation and oxidative damage in plant tissues (Smirnoff 1995; Ozden 2009). Several studies have confirmed that MDA levels increase under water stress, while stress-resistant species show relatively lower MDA accumulation (Pastori and Trippi 1992; Sairam *et al.* 1998; Terzi and Kadioglu 2006). To mitigate drought effects, plants accumulate osmoprotectants such as proline, glycine, and betaine (Turkan 2008). Multiple studies have reported elevated proline levels during drought (Akca and Yazıcı 1999; Opik and Rofle 2005; Güler *et al.* 2012; Terzi *et al.* 2015; Altuntas *et al.* 2019), and higher proline accumulation in stress-

resistant species (Ashraf and Foolad 2007). Hydrogen peroxide (H_2O_2), a signaling reactive oxygen species (ROS) molecule, plays a central role in plant responses to both abiotic and biotic stress factors (Demiralay *et al.* 2013). Notably, H_2O_2 can also induce proline accumulation (Yang *et al.* 2009), indicating a synergistic relationship between osmolyte production and ROS signaling (Altuntas *et al.* 2019).

For the reasons explained, measurements and observations were made regarding some gas exchange properties, midday xylem water potentials, lipid peroxidation, proline, and hydrogen peroxide content of *P. sylvestris*. Such work was done in the origin trials established in Aydoğmuş and Kemer using these characteristics. By such an approach, the effects of drought stress can be understood more clearly, and the adaptation of *P. sylvestris* to trial areas can also be observed. In this context, considering the natural distribution areas of *P. sylvestris* in Turkey, the present work attempted to determine the origins that can be used for the afforestation of arid and semiarid areas within the same climatic zone. Thus, this study aims to obtain results that will guide practitioners in terms of new approaches in both current and future forest formation studies and eliminate the lack of scientific knowledge in this field.

EXPERIMENTAL

Materials

The research material was collected from *P. sylvestris*, which was established in the year 2000 on the borders of the Aydoğmuş (Isparta) (38˚ 36' N, 30˚ 24' E) and Kemer (Burdur) (37˚ 35' N, 30˚ 06' E) districts located in the Lakes region (Fig. 1).

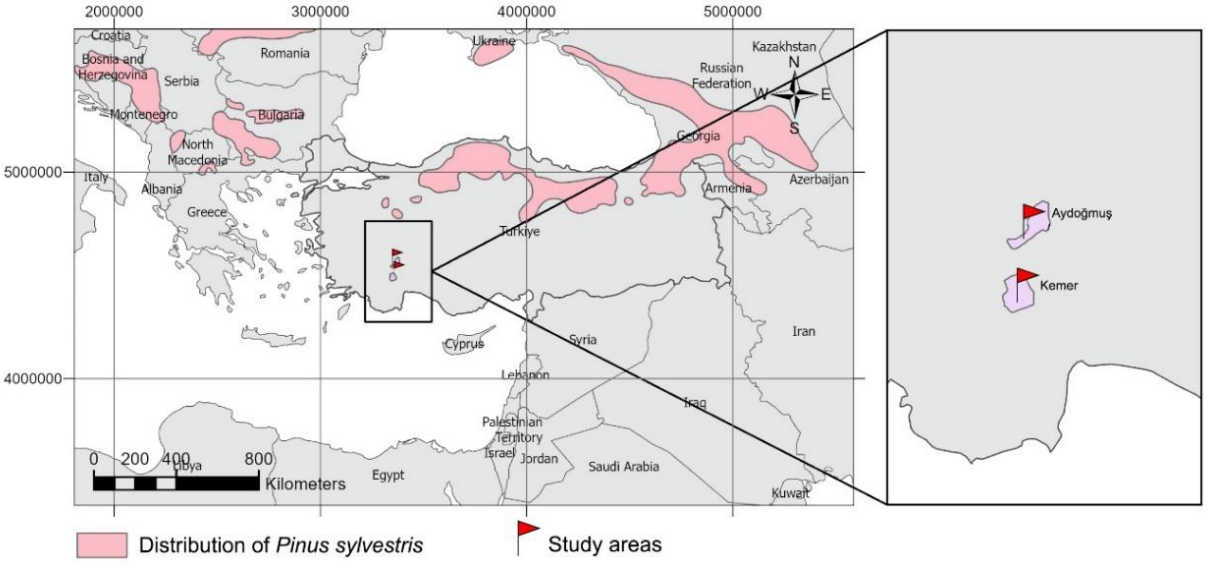

Fig. 1. Map of study areas

The altitude of the Aydogmus trial area is 1103 m, and its slope exposure is southwest. The altitude of the Kemer trial area is 1180 m. The slope exposure of the field is southwest. These two experimental areas were established by Gezer *et al*. in 2000; a trial was established with seedlings from a total of 30 *P. sylvestris* provenances, including 27 belonging to Turkey and 3 belonging to foreign seed sources. The trials were established in three iterative ways under the "Coincidence Plots Trial Pattern". The location and order of the provenances in the iterations were determined following the coincidence rules, and each provenance was represented by 30 seedlings in the iterations. A total of 2700 seedlings (30 provenances* 3 iterations* 30 seedlings) were planted in two trial areas.

To date, seedlings planted in the Aydoğmuş and Kemer trial areas have been evaluated many times during different periods, and their scientific results have been published (Gezer *et al*. 2002; Gulcu and Bilir 2015; Gulcu and Bilir 2017; Nacakci and Gulcu, 2022). To date, several important morphological and genetic characteristics have been compared in terms of their provenances and outcomes, which are appropriate for the region in line with suggestions made about the provenance and similar growing environments. In this context, in the scientific evaluations conducted to date, provenances 3, 5, 12, 18, 21, 22, 23, 27, 29, and 34 appeared among the top ten provenances (Gezer *et al*. 2002; Gulcu and Bilir 2015; Gulcu and Bilir 2017). Therefore, as a result of the evaluations conducted thus far in this study, 10 provenances that stand out and are listed in Table 1 have been identified as materials.

Table 1. Geographic Origins and Sources of Seeds Used in the Study

Provenance Number	Provenance Name	Latitude (N)	Altitude (m)
3	Senkaya- Aydere	40°38´	2050
5	V.Köprü-Ovacık-Kunduz	41°10´	1200
12**	Akdağmadeni-Aktaş	39°41´	910
18	Koyulhisar-Ortakent	40°23´	1950
21	Çatacık-Değirmendere	39°58´	1550
22	Vezirköprü-Gölköy	41°10´	1300
23	Mesudiye-Arpaalan	40°22´	1650
27	Sarıkamış-Merkez	40°18´	2350
29	Akyazı-Dokurcun	40°37´	1450
34**	Erzurum-Merkez	39°54´	1570

**Seed orchard

The soil in both experimental sites has a clay texture. To determine the precipitation regime, climate classification, and vegetation type of the study areas, Erinç's "Precipitation Effectiveness Index" formula was used (Erinç 1965). Based on the calculations, the climate classification of Aydoğmuş was identified as semi-arid, and its vegetation type was characterized as steppe. Similarly, Kemer was also classified as having a semi-arid climate and steppe-type vegetation.

Gas Exchange Measurements

Within the scope of the research, plant gas exchange, xylem water potential, malondialdehyde, proline, and hydrogen peroxide contents were measured. Photosynthetic gas exchange measurements were taken over two years. In the middle of the vegetation period (July), gas exchange measurements were carried out in the trial areas. A LI-COR

6400 XT (Portable Photosynthesis system) model device was used to measure one healthy unit selected from each provenance at each repetition. Gas exchange measurements were conducted on a total of 60 individuals, with one individual per replication for each of the 10 provenances in both sites. For each measured tree, parameters such as the net photosynthesis rate (*P*n), stomatal conductivity (*g*s), transpiration rate (*E*), vapor pressure deficit due to leaf temperature (*V*pdL), and water utilization rate (*P*n/*E*), known as the carbon dioxide (CO_2) assimilation rate, were measured in a branch detected in the same direction. All checks and calibrations of a portable photosynthesis device (LI-COR A.Ş., Lincoln, Nebraska) were performed before the device was placed on land. The parametric values of the device, according to the state of the land and the tree and the basis of the request of the values in the literature (1200 µmol (photons) m^{-2} s^{-1}, temperature 25 °C, 400 µmol m^{-2} s^{-1} CO_2, 500 µmol m^{-2} s^{-1} air flow), are set.

Mid-Day Xylem Potential and Chemical Measurements

To determine the mid-day xylem water potential, the pressure chamber technique and the pressure chamber device developed by Scholander *et al*. (1965) were used. A tree was selected from each repetition for each provenance, and measurements were made in the middle of the day (12.00 to 14.00) in the time period when the plant water tension was highest in the conifers belonging to that tree. For each of the lipid peroxidation, proline, and hydrogen peroxide analyses, 0.1 g of needle leaf tissue was used. The degree of lipid peroxidation was determined as described by Heath and Packer (1968). The samples were measured at wavelengths of 532 and 600 nm. The proline content was measured according to the methods of Bates *et al*. (1973). The samples were measured at a wavelength of 520 nm. The hydrogen peroxide content was determined according to the method of Velikova *et al*. (2000), and the samples were measured at a wavelength of 390 nm. Xylem water potential and chemical measurements were assessed for one year.

Statistical Analysis

Photosynthetic and chemical changes were statistically determined using an analysis of variance (ANOVA). The acquired data were analyzed at a 95% confidence level using the IBM SPSS Statistics 22 application. Significant differences between the average of all data were identified after each multiple comparison was assessed separately. For each property examined, the Tukey test was employed to compare leaf samples if the ANOVA was deemed significant.

RESULTS AND DISCUSSION

Gas Exchange Traits

As a result of the measurements carried out, the three provenances with the highest average photosynthesis rates were the Çatacık, Akyazı, and Mesudiye in Aydoğmuş and the Çatacık, Sarıkamış, and Gölköy provenances in Kemer (Table 2). In terms of stomatal conductivity, the provenances with the highest average stomatal conductivity were determined to be Çatacık, Mesudiye, and Akyazı in Aydoğmuş; the Çatacık, Gölköy, and Sarıkamış provenances were determined at Kemer. In terms of transpiration rates, Çatacık, Mesudiye, and Akyazı are among the top three in Aydoğmuş, and in Kemer, the provenances of Gölköy, Çatacık, and Sarıkamış. The provenances with the greatest vapor pressure deficit due to leaf temperature are Kunduz, Sarıkamış, and Şenkaya in Aydoğmuş

and Mesudiye, Erzurum, and Sarıkamış in Kemer. The three provenances with the highest average water use efficiency were Akyazı, Gölköy, and Mesudiye in Aydoğmuş and Şenkaya, Kunduz, and Çatacık in Kemer. The results of the multiple variance analysis performed in terms of these characteristics are given in Table 3.

Midday Xylem Water Potential and Biochemical Properties

According to the results of multiple variance analysis performed in terms of midday xylem water potential and some biochemical properties, the differences between both provenances and trial areas were statistically significant (Table 2).

Accordingly, the provenances with the highest average water potential were Kunduz, Şenkaya, and Gölköy in Aydoğmuş, respectively, and Sarıkamış, Kunduz, and Mesudiye in Kemer (Table 2). In terms of the amount of MDA, Çatacık, Akyazı, and Gölköy in Aydoğmuş and Mesudiye, Erzurum, and Akdağmadeni provenances in Kemer were in the first three places. When the amounts of proline contained in the provenances were examined, it was revealed that the Akyazı, Gölköy, and Mesudiye provenances in Aydoğmuş and the leaves of the Çatacık, Mesudiye, and Koyulhisar provenances in Kemer contained more proline. When the provenances were compared according to the amount of hydrogen peroxide, the provenances of Kunduz, Akyazı, and Gölköy in Aydoğmuş and Sarıkamış, Mesudiye, and Çatacık in Kemer presented relatively high amounts of H_2O_2. The results of the multiple variance analysis performed in terms of these characteristics are given in Table 3.

Table 2. Average Values Observed in the Aydoğmuş and Kemer Trial Areas

		Şenkaya	Kunduz	Akdağmadeni	Koyulhisar	Çatacık	Gölköy	Mesudiye	Sarıkamış	Akyazı	Erzurum	Mean
Aydoğmuş												
	***P*n**	0.92±0.21de	0.61±0.1e	1.29±0.34de	1.4±0.62cd	3.49±2.81a	0.83±0.49de	2.56±1.86b	2.15±1.56bc	2.9±1.52ab	2.2±1.3b	1.83
	***g*s**	0.007±0.002def	0.003±0.001f	0.011±0.003cd	0.01±0.003cde	0.021±0.016a	0.005±0.003ef	0.018±0.014ab	0.014±0.01bc	0.018±0.011ab	0.014±0.01bc	0.012
	E	0.148±0.088cd	0.08±0.045d	0.195±0.101bcd	0.199±0.045bc	0.395±0.338a	0.102±0.085cd	0.350±0.303a	0.298±0.247ab	0.324±0.247a	0.288±0.23ab	0.238
	***V*pdl**	1.5894±0.67ab	1.8728±0.66a	1.4808±0.59b	1.3712±0.78b	1.3644±0.38b	1.5074±0.55b	1.3513±0.40b	1.6106±0.33ab	1.3397±0.38b	1.5317±0.32b	1.502
	Pn/E	9.22±6.13c	10.83±5.92abc	7.96±2.81c	8.09±2.99c	10.44±3.64bc	12.93±8.69ab	11.18±5.25abc	8.95±2.67c	13.82±9.7a	11.11±5.33abc	10.453
	Ψmd	-1.83±0.06ab	-1.78±0.03a	-1.88±0.03abc	-1.83±0.15ab	-2.03±0.15c	-1.82±0.1ab	-1.87±0.06abc	-1.98±0.13bc	-1.87±0.06abc	-2.03±0.06c	-1.89
	Mda	5.05±0.6bc	5.99±1.46abc	4.94±0.75c	5.28±0.18bc	6.66±0.73a	6.32±0.61ab	5.69±0.31abc	5.41±0.77abc	6.37±0.66ab	5.38±1.58abc	5.71
	Proline	13.93±2.33bc	11.7±1.13cd	6.67±0.5d	10.56±2.17cd	13.16±1.8bc	20.94±3.38a	19.12±6.67ab	11.05±2.4cd	21.46±4.84a	9.74±1.22cd	13.83
	H_2O_2	60.74±18.77c	129.6±56.7a	66.7±31.4c	109.6±43.7abc	72.22±4.71bc	125.6±44.3ab	74.81±10.42abc	93.33±9.43abc	127.4±61.5ab	100.0±30.3abc	96.0
Kemer												
	***P*n**	2.51±1.6bc	2.76±1.51bc	1.38±0.34d	2.51±1.41bc	3.88±1.48a	2.95±0.8b	2.25±0.66c	3.08±1.49b	1.58±0.59d	1.13±0.6d	2.40
	***g*s**	0.02±0.011b	0.021±0.01b	0.01±0.002c	0.02±0.0102b	0.03±0.006a	0.03±0.007a	0.017±0.003b	0.021±0.01b	0.011±0.002c	0.008±0.005c	0.0179
	E	0.215±0.115cd	0.248±0.100bc	0.174±0.035de	0.245±0.102bc	0.382±0.085a	0.396±0.087a	0.286±0.067b	0.352±0.161a	0.177±0.033de	0.127±0.078e	0.260
	***V*pdl**	1.047±0.105e	1.093±0.157e	1.428±0.124ab	1.106±0.157e	1.211±0.095d	1.338±0.144c	1.456±0.174a	1.443±0.049a	1.357±0.08bc	1.445±0.236a	1.292
	Pn/E	11.38±2.2a	10.58±2.34ab	7.96±0.99de	9.54±2.13bc	10.21±3.64ab	7.44±1.24e	7.93±1.46de	8.68±0.76cd	8.68±2.09cd	9.43±1.77bc	9.180
	Ψmd	-2.42±0.13cde	-2.07±0.06ab	-2.33±0.06cde	-2.5±0.1e	-2.17±0.06abc	-2.5±0.1e	-2.2±0.1abcd	-2.03±0.06a	-2.43±0.06de	-2.32±0.1bcde	-2.30
	MDA	5.12±0.48d	5.69±0.92d	11.01±1.84a	8.92±2.34bc	8.90±0.55bc	10.81±1.63ab	12.19±1.36	5.76±9.95d	8.25±0.96c	11.15±1.39a	8.78
	Proline	8.78±2.83c	7.59±1.37c	13.3±1.0b	15.62±2.62b	21.91±4.07a	7.86±0.88c	15.91±3.22b	14.81±1.57b	8.32±0.95c	11.78±2.19bc	12.59
	H_2O_2	84.07±12.78de	70.0±13.33e	77.41±6.19de	83.7±13.17de	120.74±21.84abc	88.52±29.63de	126.3±15.94ab	128.52±14.82a	95.56±27.54cde	99.63±18.96bcd	97.44

*P*n: Net photosynthesis rate, *g*s: Stomatal conductivity, *E:* Transpiration rate, *V*pdL: Vapor pressure deficit due to leaf temperature, *Pn*/*E:* Water utilization rate, Ψmd: Midday xylem water potential, Mda: Malondialdehyde , H_2O_2: Hydrogen peroxide content
Units: *P*n (μmol m^{-2} s^{-1}), *g*s (mol H_2O m^{-2} s^{-1}), *E* (mmol H_2O m^{-2} s^{-1}), *V*pdl (kPa), MDA (nmol g^{-1}), Prolin (μg g^{-1}), H_2O_2 (mM g^{-1})

Table 3. Results of Multiple Variance Analysis

	Origin	Area	Year	Origin*Area	Origin*Year	Area*Year	Origin*Area*Year
***P*n**	**	**	**	**	**	**	**
***g*s**	**	**	**	**	**	**	**
E	**	**	**	**	**	**	**
***V*pdl**	**	**	**	**	**	**	**
P*n/*E	**	**	**	**	**	**	**
Ψ_{md}	**	**	-	**	-	-	-
MDA	**	**	-	**	-	-	-
Proline	**	*	-	**	-	-	-
H_2O_2	**	ns	-	**	-	-	-

Units: *P*n (μmol m^{-2} s^{-1}), *g*s (mol H_2O m^{-2} s^{-1}), *E* (mmol H2O m^{-2} s^{-1}), *V*pdl (kPa), MDA (nmol g^{-1}), Prolin (μg g^{-1}), H_2O_2 (mM g^{-1})
***P* < 0.01; * *P* <0.05; ns: non-significant

According to the multivariate analysis of variance (MANOVA), all variables showed statistically significant differences at the 0.01 level when evaluated across provenances. When the experimental sites were considered, most variables also showed significant differences at the 0.01 level; however, proline differed at the 0.05 level, and hydrogen peroxide showed no significant difference between sites.

Gas exchange measurements were conducted over two years, while the other traits were measured in a single year, as previously stated. When evaluating year-based differences, statistically significant variation was observed at the 0.01 level. Additionally, significant interactions ($p < 0.01$) were found for provenance × year, site × year, and provenance × site × year combinations. The provenance × site interaction also yielded significant differences at the 0.01 level for all variables.

Correlations between Traits

According to the correlation analysis, the photosynthetic rate (P_n) showed a strong and significant positive correlation with stomatal conductance (g_s) and transpiration rate (E), indicating that stomatal opening and water vapor loss directly support photosynthetic activity. The vapor pressure deficit between leaf and air (V_{pdl}) was significantly negatively correlated with P_n, suggesting that increasing evaporative demand limits photosynthesis. Midday leaf water potential (Ψ_{md}) was positively correlated with V_{pdl} and negatively correlated with MDA, a marker of lipid peroxidation, implying that as water loss increases, oxidative stress also intensifies. Biochemical stress indicators such as proline and hydrogen peroxide (H_2O_2) were moderately and positively correlated with each other, indicating that proline accumulation may be triggered by elevated oxidative stress. Additionally, the significant positive correlation between proline and *P*n/*E* suggests a possible link between proline accumulation and water use efficiency. Overall, these results highlight the interrelationships among physiological and biochemical traits under drought conditions and contribute to our understanding of adaptive responses in stressed environments.

Table 4. Correlations between Traits

	*P*n	*g*s	*E*	*V*pdl	*P*n/*E*	Ψ_{md}	MDA	Proline	H_2O_2
***P*n**	1								
***g*s**	**,964****	1							
E	**,923****	**,895****	1						
***V*pdl**	**-,604****	**-,677****	-,377	1					
P*n/*E	,110	-,033	-,034	-,087	1				
Ψ_{md}	-,285	-,405	-,157	**,554***	,375	1			
MDA	,082	,179	,075	-,123	-,407	**-,664****	1		
Proline	,236	,152	,203	-,015	**,516***	,277	,120	1	
H_2O_2	,019	-,032	-,014	,282	,261	,180	,161	**,471***	1

** $P<0.01$, * $P<0.05$

Physiological Responses to Drought Stress

In the case of extreme drought, the stomata on the leaves of plants become smaller, and the growth and development of cells slow. Stress due to a lack of water leads to various problems in the chloroplasts of plants and leads to the closure of stomata. This also reduces the rate of photosynthesis (Farquhar and Sharkey 1982; Dubey 1996; Deltoro *et al*. 1998; Bosabalidis and Kofidis 2002; Machado *et al*. 2009; Endres *et al*. 2010; Sales *et al*. 2012; Medeiros *et al*. 2013; Ribeiro *et al*. 2013; Silva *et al*. 2013; Júnior *et al*. 2019). A decrease in soil moisture decreases the water potential during times of water stress, which slows the stomatal conductivity and photosynthesis rate (Epron and Dreyer 1993; Lawlor and Cornic, 2002; Michelozzi *et al*. 2008; Güler *et al*. 2012; Xiang *et al*. 2013; Priwitzer *et al*. 2014). In some studies, stomatal shrinkage and CO_2 uptake decrease due to water stress, and the photosynthesis rate and respiration rate decrease due to water stress (Opik and Rofle 2005). Since the plant reacts quickly to excessive water loss by preventing leaf dehydration, it becomes harmful when it takes a long time, as the closure of the stomata initially interferes with the flow of CO_2, although it is advantageous (Machado *et al*. 2009; Inman-Bamber *et al*. 2012; Sales *et al*. 2012; Medeiros *et al*. 2013). In some scientific studies, it has been determined that plants close their stomata in hot and arid environments, and accordingly, the stomatal conductivity and the rate of transpiration decrease, even when leaf fall occurs; accordingly, there is a decrease in the rate of photosynthesis (Gratani *et al*. 2000; Li *et al*. 2004; Reddy *et al*. 2004; Yin *et al*. 2005; Guo *et al*. 2006; Wikberg and Ogren 2007; Ma *et al*. 2014; Medrano *et al*. 2015; Pliura *et al*. 2018). The Kemer trial area is located farther south than the Aydoğmuş trial area and is slightly more arid. However, the average pigment values (chlorophyll a, chlorophyll b, total chlorophyll) were found to be significantly higher in the Kemer trial area, and the average photosynthesis rates and stomatal conductivities of the provenances were greater in Kemer. This situation can be explained by the fact that the degree of drought experienced in the area is not at a level that negatively affects the stomatal conductivity and photosynthesis rates of the provenances, although the Kemer trial area is drier than Aydoğmuş. In addition, the high rate of photosynthesis in the Kemer trial area may also have been caused by the overabundance of individuals in the first years of the trial and, accordingly, the fact that individuals who continue their lives have grown more freely and received better sun. Due to excessive sun exposure at the crown of the hill, trees experience higher levels of light and temperature, which lead to an increased vapor pressure deficit and consequently enhance transpiration. Therefore, if the stomata are open, the stomatal conductivity and transpiration rate of the plant increases

(Goudiaby *et al*. 2011). In this study, the photosynthesis rate, stomatal conductivity, and transpiration rate were greater in Catacık, Akyazı, and Mesudiye in the Aydoğmuş trial area and in Çatacık, Sarıkamış, and Gölköy provenances in Kemer.

Notably, the decrease in the effectiveness of water use is caused by a decrease in stomatal conductivity and an increase in the rate of transpiration due to high temperature (Kellomäki and Wang 2001; Zhang *et al*. 2005). Owing to the lack of water in hot and dry environments, lower water use efficiency has been observed in many plant species (Klein *et al*. 2001; Llorens *et al*. 2003; Liang *et al*. 2006; Pliura *et al*. 2018). Some researchers have noted that the efficiency of water use, which is the ratio of these two variables, also decreases due to a decrease in the rate of photosynthesis and the rate of transpiration under arid conditions (Sinclair *et al*. 1984; Larcher 2003). Similar results were obtained in this study, and the water use efficiency of provenances with high photosynthesis rates, stomatal conductivities, and transpiration rates were greater. Variations in water use efficiency may vary depending on environmental factors and may vary from provenance to provenance. For example, in a study conducted in an Anatolian Chestnut, individuals in the Mediterranean ecotype who are adapted to drought presented lower water use efficiency than individuals who are adapted to the humid environment in the east (Lauteri *et al*. 1997, 2004). Stomatal conductivity depends on many environmental factors, but most importantly, it is highly influenced by factors such as vapor pressure deficit, soil water, and soil and air temperature (Miller and Schultz 1987; Schäfer *et al*. 2000). Leaf temperature, vapor pressure deficit, and air temperature variability play active roles in leaves during the day because of their water potential, stomatal conductance, and transpiration effects (Conard *et al*. 1997). The provenances Kunduz and Şenkaya in Aydoğmuş and Mesudiye and Erzurum in Kemer were among the top three in terms of V_{pdl}. The leaf vapor pressure deficit was greater in the Aydoğmuş trial area. This, in turn, can explain why other photosynthetic properties are more common in Kemer. The rate of photosynthesis in photosynthesis measurements varies depending on the time of day when the measurements are performed (Yang *et al*. 2002; Goudiaby *et al*. 2011). The measurements carried out in the trial areas revealed that the stomata were open between 09.00 and 11.00 am in the morning and closed after this time. For this reason, a decrease in photosynthesis rates was observed in the measurements taken in the trial areas since the stomata were closed after 12:00.

Chemical Responses to Drought Stress

The leaf water potential reflects the water tension in the leaf that directs the flow of water from the plant to the atmosphere and is widely used in studies on the effects of water stress on plants (Bergonci *et al*. 2000). Many researchers have also used the mid-day xylem water potential to determine water stress in plants (Naor 2000; Intrigliolo and Castel 2006). Water potential of leaves affects the stomatal conductivity and transpiration level of plants (Conard *et al*. 1997; Endres *et al*. 2010; Silva *et al*. 2013). In many studies, a negative relationship has been found between deceleration of water potential (an increase in water stress) and proline (Lansac *et al*. 1994; Kandemir 2002; Yang *et al*. 2007). In this study, no direct relationship was found between midday xylem water potential and proline. Serrano *et al*. (2005) reported that the soil water content of Holy Oak and Akcakes is closely related to the midday xylem water potential and predawn plant water potential and varies in direct proportion. Vieira *et al*. (2014) determined that the leaf water potential increases in direct proportion to the increase in the water supply as a result of different irrigation practices in sugarcane and that the product obtained at low leaf potential

experiences more stress. Demir (2019) also reported that water potential values decrease as water stress increases in a study conducted on larch. In this study, all the provenances tested had greater average midday xylem water potential in the Aydoğmuş trial area than in the Kemer trial area. This can be explained by the fact that individuals in Aydoğmuş are exposed to less water stress. In Aydoğmuş, the highest average value was found in the Kunduz provenance, and in Kemer, the highest average xylem water potential was found in the Sarıkamış provenance. The beaver and Sarıkamış provenances are less affected by water stress in the areas where they are found than other provenances are.

Plants change their metabolism in various ways, including through the use of antioxidants, to eliminate excess reactive oxygen species (ROS) (Krasensky and Jonak 2012). Drought and stress increase the production of ROS (Bowler *et al*. 1992; Foyer *et al*. 1994; Alscher *et al*. 1997; Shigeoka *et al*. 2002; Lee and Park 2012; Bhargava and Sawant 2013). Prolonged drought stress results in increased ROS production, and lipid peroxidation occurs as a result of excessive accumulation of ROS, and DNA degradation or even cell loss may occur (Cruz de Carvalho 2008; Hossain *et al*. 2015; Ozturk 2015). One of the methods used to calculate the extent of destruction in plant cells is the determination of lipid peroxidation. The amount of malondialdehyde (MDA) present in plants is considered important for understanding lipid peroxidation and oxidative damage (Smirnoff 1995; Ozden 2009). In some studies, the MDA content has been shown to increase in species under water stress, and lipid peroxidation is lower in those that are resistant to stress (Pastori and Trippi 1992; Sairam *et al*. 1998; Terzi and Kadioglu 2006). According to the measurements and meteorological data carried out, it is believed that the MDA is greater in the Kemer trial area since there are fewer droughts in Aydoğmuş than in Kemer, and less water stress occurs.

Plants adapt their metabolism to environmental conditions *via* osmotic regulators such as proline, glycine, and betaine under extreme seasonal conditions in their habitats (Turkan 2008). The most basic task of proline is to protect cells from osmotic damage by providing osmotic adjustment and to protect plants against various environmental stresses by destroying ROS species formed under stress (Szabados and Savouré 2010; Hayat *et al*. 2012; Roychoudhury *et al*. 2015). Proline accumulation occurs in the case of extreme drought and aims to minimize damage to enzymes by acting as a defense against damage that may occur on membranes (Iyer and Caplan 1998; Kishor *et al*. 2005; Tanner 2008; Szabados and Savoure 2010; Moustakas *et al*. 2011; Singh *et al*. 2015; Yavas *et al*. 2016). For these reasons, proline is used to determine the physiological state of plants (Yılmaz 2013; Kishor and Sreenivasulu 2014). Some researchers have reported that the amount of proline increases during drought under water stress (Lansac *et al*. 1994; Akca and Yazıcı 1999; Opik and Rofle 2005; Yang *et al*. 2007; Kulac 2010; Güler *et al*. 2012; Terzi *et al*. 2015; Altuntas *et al*. 2019). A study conducted on various plant species revealed that the amount of proline was greater in species that were resistant to stress than in sensitive species (Ashraf and Foolad 2007).

The highest average amount of proline in the Aydoğmuş trial area was found in Akyazı, and the highest average value was found in the Catacık provenance in Kemer. These results suggest that Akyazı and Catacık provenances can withstand drought more than other provenances can. Altuntas *et al*. (2020) determined that proline application, given at low levels, is an application that increases the amount of photosynthesis in the leaf. Therefore, if the conditions are suitable, the application of proline in nurseries in the process of growing seedlings, especially in arid and semiarid areas, may be recommended.

Moreover, hydrogen peroxide (H_2O_2), a type of ROS, plays a central and important role in the response of plants to both abiotic and biotic stresses (Demiralay *et al*. 2013). Various scientific studies have reported that H_2O_2 plays a role in the adaptation of Cistus albidus to summer drought (Jubany-Marí *et al*. 2009) and salt stress in corn (Azevedo Neto *et al*. 2005) and increases the soluble sugar content of melon fruits (Ozaki *et al*. 2009). Yang *et al*. (2009) concluded that H_2O_2 triggers the accumulation of proline, a compatible solute, in corn seedlings. In this study, a relationship between H_2O_2 and proline was found. Altuntas *et al*. (2019) reported that there might be an interaction between osmolytes and H_2O_2, which modulates genes involved in proline and polyamine metabolism to increase drought tolerance. In studies conducted on various plant species, it has also been reported that the external application of H_2O_2 increases antioxidant activity, reduces lipid peroxidation, and accordingly increases the tolerance of plants to stresses such as temperature, frost, and salt stress (Uchida *et al*. 2002; Azevedo Neto *et al*. 2005; Wahid *et al*. 2007). Ishibashi *et al*. (2011) reported that the addition of H_2O_2 alleviates the effects of drought stress, maintains the relative water content in the leaf, delays the closure of stomata, and reduces the reduction in the photosynthesis rate by alleviating the effects of drought stress.

CONCLUSIONS

1. The study highlighted the significance of proline and hydrogen peroxide (H_2O_2) accumulation in Scotch pine (*Pinus sylvestris* L.) for drought stress adaptation. The Çatacık and Akyazı provenances demonstrated higher resistance to arid conditions, making them suitable for afforestation in such environments.
2. The Çatacık, Akyazı, and Mesudiye provenances exhibited superior photosynthetic gas exchange traits, including higher photosynthesis rates, stomatal conductance, and transpiration values. These characteristics contributed to their improved water use efficiency, an essential factor for survival in drought-prone regions.
3. Provenances differed significantly in terms of midday xylem water potential and biochemical markers. The Kunduz, Şenkaya, and Gölköy provenances in Aydoğmuş, and Sarıkamış, Kunduz, and Mesudiye in Kemer showed higher water potential values, indicating better water retention capacity under drought stress.
4. Malondialdehyde (MDA) accumulation, an indicator of lipid peroxidation and oxidative stresses, varied across provenances. The Çatacık and Akyazı provenances exhibited higher MDA levels, suggesting their enhanced stress response mechanisms.
5. Given the increasing threat of climate change and prolonged drought periods, selecting drought-resistant provenances is important for forestry practices. The study suggests using Çatacık and Akyazı as seed sources for Aydoğmuş-like environments and Mesudiye and Çatacık for Kemer-like regions.

6. Continuous monitoring of the provenance trials is necessary to refine afforestation strategies. Reassessing physiological and biochemical traits over extended periods will provide valuable insights into Scotch pine's long-term adaptation to changing climatic conditions.

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