Influence of abiotic factors on CO₂-gas exchange of *Pinus pallasiana*, *Juniperus excelsa* and *Arbutus andrachne*

S Korsakova^{1,*}, Y Plugatar², A Pashtetsky¹, and O Ilnitsky¹

¹The Nikitsky Botanical Gardens – National Scientific Center of the RAS, Laboratory of Phytomonitoring, 52 Nikitsky spusk st., Nikita, Yalta, 298648, Russian Federation

²The Nikitsky Botanical Gardens – National Scientific Center of the RAS, Department of Natural Ecosystems, 52 Nikitsky spusk st., Nikita, Yalta, 298648, Russian Federation

Abstract. The complex interactions among environmental factors as incident light, temperature and soil water content create the need for used physiology-based models which describe plants performance under current and changing climatic conditions. In the present work the net photosynthetic rate of *Pinus pallasiana* D. Don, *Juniperus excelsa* M.Bieb. and *Arbutus andrachne* L. was modeled as a function of light irradiance using the modified rectangular hyperbola model, which is capable of describing the photoinhibition by the non-rectangular hyperbola function. A comparative assessment of the adaptive response of the photosynthetic apparatus plants on the effect of abiotic factors and their strategies in maintaining an optimal water balance in accordance with environmental conditions has been performed. The parameters of light curves of photosynthesis under conditions of full sunlight, moderate shading and drought are determined. In relation to light, *Pinus pallasiana* is characterized by wider ecological amplitude compared to *Juniperus excelsa* and *Arbutus andrachne*. Inefficient use of low-intensity of photosynthetically active radiation by immature plants *Pinus pallasiana* and *Juniperus excelsa* indicates poor shade tolerance and inability to resume in shade-type forests. Due to the low plasticity to changes in the light regime, *Arbutus andrachne* L. may experience a significant lack of light in strong shading. *Arbutus andrachne* has the highest ability to actively rearrange water regime in accordance with its external moisture supply, which causes the highest drought resistance, and *Juniperus excelsa* has a slightly lower capacity. Tolerance to hydrothermal stress in *Pinus pallasiana* is significantly lower than in *Arbutus andrachne* and *Juniperus excelsa*.

1 Introduction

Plants in the ecosystems of the southern Russia in areas of insufficient moisture in summer are often subjected to the stress of severe and prolonged drought [1]. Such conditions are

* Corresponding author: korsakova2002@mail.ru

especially critical for vegetative plants that are in the initial stages of development, as they sharply reduce their survival rate and slow down growth during this period [2]. Drought affects the plant in two ways, causing both dehydration and overheating [3].

Under changing environmental conditions, plants must have a positive carbon balance between the level of CO₂ assimilation during photosynthesis and its loss during respiration in order to survive [4]. The photosynthetic capacity depends on the light intensity level, as well as the physiological and morphological features of the leaf [5]. It is known that with a decrease in the level of light intensities in the growing area, the intensity of photosynthesis decreases [6], which in turn should lead to a decrease in plant growth and a decrease in the accumulation of dry biomass [4]. Therefore, the optimal ecological conditions of plant growth are partially determined by their species-specific physiological response to the complex impact of environmental factors [2]. This reaction manifests itself in a coordinated adaptation between hydrothermal stress and lighting, that is, optimization of the processes of life and productivity [7]. In relation to the impact of a particular factor, each species has its own ecological valence and its own ecological spectrum, which was formed in the course of evolution [8]. Understanding these characteristics gives you the ability to simulate plant response to different climatic conditions.

In accordance with the expected climate change scenarios, which predict a general increase in temperature and long periods of drought for the southern regions of Russia [9-10], plants should have sufficient plasticity to adapt to these new conditions. Strategies for plant acclimatization in response to various environmental conditions include changes in photosynthesis and metabolism [11].

Complex interactive responses to environmental influences determine the need to develop physiological models that can predict the response of plants to climate changes and assess their adaptive capabilities. Photosynthesis models are the most effective tool for describing the combined and interrelated effects of climate and environmental conditions on the physiological productivity of plants [12]. They allow us to determine the characteristics of optimal ecological niches for photosynthetic activity and plant productivity, and contribute to decision-making in the framework of adaptive nature management [13]. These models include empirically estimated parameters that may be related to general environmental factors, which makes it possible to predict photosynthetic responses of plants to various environmental shifts [2, 14].

Pinus pallasiana D. Don (Pinaceae), *Juniperus excelsa* M.Bieb. (Cupressaceae) and *Arbutus andrachne* L. (Ericaceae) are native species and the main components of forest communities in the Mountainous Crimea. Due to their high decorative properties, these species are widely used in landscaping the Southern Coast of the Crimea, the Black Sea Coast of the Caucasus, and the Mediterranean [15].

Crimean pine or Pallas pine (species series *Nigrae*) is naturally found in the mountains of the Crimea, in the Northern part of the Black Sea Coast of the Caucasus, in the Balkans and in Asia Minor. It is the main breed for forest cultivation and reconstruction of derived stands in all natural zones of the Crimea, in the conditions of forest-steppe and steppe of Ukraine, Russia, the North Caucasus and even Central Asia [15]. However, in recent years, there has been an increase in negative trends in the drying of artificial forest stands of *Pinus pallasiana* in the Crimea, and one of the reasons for the decline in the vital state and death of stands may be related to global climate change [16].

The range of *Juniperus excelsa* covers the islands of the Greek archipelago, Western Transcaucasia, Asia Minor and Western Asia, Iran, the Black Sea Coast of the Caucasus, and the Crimea [17]. *Arbutus andrachne* is distributed in the Eastern Mediterranean, Asia Minor, Western Transcaucasia, and the Southern Coast of the Crimea [17]. These species are characterized by low seed viability and weak natural regeneration [18-21], included in Red books of the Russian Federation [22] and the Republic of the Crimea [23]. *Juniperus*

excelsa is characterized as a light-loving and very drought-tolerant species, but its immature individuals are sensitive to moisture, light, and temperature conditions [24].

Much attention in the scientific literature when studying *Pinus pallasiana*, *Juniperus excelsa* and *Arbutus andrachne* is given to those factors that limit such processes as seed production [19-20] or germination [18], age dynamics [16]. However, their physiological response to environmental influences and climate factors limiting photosynthesis remains the least studied to the present day, and only a few papers have been devoted to it [25-26].

These studies are a necessary basis for obtaining an objective assessment of the stability of stands in warmer and drier environmental conditions predicted by global warming scenarios for the Crimea [9-10], and developing an environmentally sound system for protecting and maintaining bioecological potential.

The objective of this study was to compare the features of the adaptive response of the photosynthetic apparatus of *Pinus pallasiana*, *Juniperus excelsa*, and *Arbutus andrachne* to the effects of abiotic stressors: drought, high temperatures, and changes in the light regime.

2 Materials and methods

The study was carried out in the Nikitsky Botanical Gardens – National Scientific Center on the Southern coast of the Crimea (44°31' N, 34°15' E). The climate of the Southern Coast of Crimea (SCC) is subtropical Mediterranean type, characterized by hot, dry summers and mild wet winters. The average annual air temperature is 12.6°C and the mean annual rainfall amounts to 592 mm [17].

Studies were conducted during several periods of active vegetation in 2017, 2018 (April-October) and 2020 (June-July) on seedlings (8-12 years old) of *Pinus pallasiana*, *Juniperus excelsa* and *Arbutus andrachne* growing on the experimental site and in the conditions of the growing experience (in 15-liter vessels filled with the soil of the experimental site).

The soil of the experimental site is dark brown, medium-loamy, medium-gravelly on a gravelly-stony limestone eluvium. The lowest moisture content (LMC) ranges from 21.6 to 25.2%, the wilting humidity – 9.9-11.1%.

The intensity of CO₂-gas exchange of leaves was determined with 3-fold repetition on well-developed intact leaves of the upper part of the shoot with an interval of 15-20 minutes. An automatic 4-channel open-type system for monitoring CO₂ gas exchange and leaf transpiration "PTM-48A photosynthesis monitor" (Bioinstruments S.R.L., Moldova) was used for measurements [27]. The measurements were carried out at a natural CO₂ concentration in the air of about 0.04 %. The leaf chamber was oriented so that its elements did not obscure the leaf. Temperature (°C) and humidity (%), photosynthetically active radiation (PAR) were recorded using sensors of the RTH-48 Weather module, soil moisture (%) and leaf temperature (°C) were measured by sensors of the PTM-48A system and the PM-11z phytomonitor (Bioinstruments S.R.L., Moldova) [14].

The values of net photosynthetic rate (P_N , $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), total respiration rate (R_{total} , $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), dark respiration rate (R_D , $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) and photorespiration rate (R_{PR} , $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) were used to characterize the CO₂-gas exchange of the leaf in the PAR range from 0 to 2000 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$. When studying the dependence of P_N on light intensity, experimental measurements were made on sunny, mostly clear days. The studied plants grew in favorable hydrothermal conditions: the daytime air temperature varied within 18-31°C, relative humidity – 45-70%, soil moisture – 60-100% Field Capacity (FC). The maximum measured value of the PAR in full light conditions varied in the range from 1350 to 1900 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$, and in moderate shading conditions in the greenhouse it varied in the range of 400-800 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$. In conditions of moderate drought, soil moisture was from 35 to 55 % FC.

A modified model of a rectangular hyperbola describing photoinhibition of the process by a non-rectangular hyperbola (1) was chosen for a comparative assessment of the physiological differences of plants in relation to the light factor [28]:

$$P_N = \varphi_{(I_0 - I_{comp})} \frac{1 - \beta I}{1 + \gamma I} (I - I_{comp}), \quad (1)$$

where P_N is the net photosynthetic rate, $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$; I is photosynthetically active radiation (PAR), $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$; I_{comp} is the light compensation point – the light intensity at which the total CO_2 -gas exchange ($P_N/I_{(x,t)}$) is zero, $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$; $\varphi_{(I_0 - I_{comp})}$ – the quantum yield of photosynthesis (the tangent of the angle of inclination of the light curve was calculated as a derivative of P_N at point I) $I = I_0 - I_{comp}$, $\mu\text{mol CO}_2 \mu\text{mol photons}^{-1}$; β and γ are correction coefficients that do not depend on the intensity of solar radiation [28], $\text{m}^2 \text{ s } \mu\text{mol photons}^{-1}$, and β is a correction coefficient for the tendency to decrease P_N when the PAR exceed the light saturation point due to photoinhibition and is similar to the convexity parameter [28].

The maximum gross photosynthetic rate (P_{gmax}), dark respiration rate (R_D), light saturation point (I_{sat}) and a number of other additional parameters were calculated from equation (1) [29].

When studying the influence of abiotic factors on the processes of leaf gas exchange, plants were exposed to environmental conditions that mimic the hot summer of the Southern Coast of the Crimea and conditions of water scarcity. Soil moisture in the vessels with control plants was maintained at a level corresponding to the moisture content of 60-90% FC.

For a comparative assessment of photosynthetic activity of plants under optimum conditions and under the influence of abiotic stressors we calculated the rate of use of PAR during photosynthesis – the number $\mu\text{mol CO}_2 \text{ mmol}^{-1} \text{ photons}$ (Kr) and the economic ratio of photosynthetic ability, or the coefficient of photosynthetic efficiency (K_{eff}), which is the ratio of gross photosynthetic rate to dark respiration rate ($K_{eff} \approx (P_N + R_D)/R_D$) and describes the maximum possible efficiency of gas exchange [30].

The resulting data array was analyzed using information and mathematical criteria in the MS Excel2010 and Statistica10 software packages. The least squares and robust locally weighted regression methods were used to model and smooth the data (Statistica10). All calculations were performed at a given significance level $p < 0.05$.

3 Results and discussion

Photosynthetic light response curves describe the dependence of the net photosynthetic rate on the intensity of the PAR. They reflect the photosynthetic phenotype of plants: they provide information about the maximum photosynthetic capacity, quantum yield, light compensation point, and the efficiency of using solar radiation by leaves. Analysis of the photosynthetic light response curves provides an important potential ecological and physiological characteristic of this species, which allows us to obtain valuable information about the physiological differences of plants in relation to the light factor, their adaptation to the light environment. Table 1 shows the average values of the measured maximum values of PAR, photosynthesis and leaf respiration of the studied plant species, obtained during the registration of the light curve.

Juniperus excelsa was characterized by the highest photosynthetic ability under comfortable external growing conditions (favorable temperature, absence of water deficit and shading). The intensity of net photosynthetic rate in this species is on average 11-15% higher than the needles of *Pinus pallasiana* and *Arbutus andrachne* leaves (table 1). The

light saturation curve of photosynthesis reached a plateau in *Juniperus excelsa* at a PAR of more than 1000 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ (more than 50-60% of total light intensity). Light saturation of photosynthesis in *Pinus pallasiana* and *Arbutus andrachne* was observed at 850-900 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$. Dark respiration rate in full light conditions in *Pinus pallasiana* and *Juniperus excelsa* leaves was almost twice higher than in *Arbutus andrachne*, indicating their need for more light to compensate for CO_2 .

Under moderate shading conditions, net photosynthetic rates decreased on average by 24% in *Pinus pallasiana*, 19% in *Juniperus excelsa*, 16% in *Arbutus andrachne*, and dark respiration rates by 6-11%, which can be regarded as a direct reaction to a decrease in assimilate formation due to a reduction in the arrival of PAR.

With a moderate water deficit, the decrease in net photosynthetic rate did not exceed 3-5%, and the increase in respiration intensity associated with an increase in energy costs for the synthesis of osmotic that protect proteins from dehydration was 11-13% in *Pinus pallasiana* and *Arbutus andrachne* and 22% in *Juniperus excelsa*, which is one of the ways plants adapt to drought.

The use of PAR during photosynthesis in the formed leaves of all the studied species has significantly increased with the deterioration of lighting conditions. The *Kr* values for moderate shading increased by 89% in *Juniperus excelsa*, 64% in *Pinus pallasiana*, and 55% in *Arbutus andrachne*. Compared to optimal conditions, there were different trends in the use of PAR and when exposed to moderate droughts. *Kr* values for *Pinus pallasiana* decreased by 15%, for *Juniperus excelsa*, on the contrary, increased by 21%, and for *Arbutus andrachne* they remained unchanged.

Table 1. Values (average of maximum) of photosynthetically active radiation, photosynthesis and respiration in leaf of the studied plants when measuring light curves.

Parameters	Environmental condition	<i>Pinus pallasiana</i>	<i>Juniperus excelsa</i>	<i>Arbutus andrachne</i>
PAR ($\mu\text{mol photons m}^{-2} \text{ s}^{-1}$)	1 ^a	1445±78	1528±65	1405±54
	2 ^b	790±224	725±232	776±98
	3 ^c	1530±124	1249±112	1344±103
P_N ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)	1 ^a	15.4±1.1	17.2±0.8	14.6±0.7
	2 ^b	11.7±1.9	14.0±1.8	12.2±1.1
	3 ^c	14.7±1.8	16.7±1.3	14.1±1.0
R_D ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)	1 ^a	1.6±0.3	1.8±0.3	0.9±0.2
	2 ^b	1.5±0.2	1.6±0.2	0.8±0.1
	3 ^c	1.8±0.2	2.0±0.3	0.8±0.1
P_{gmax} ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)	1 ^a	16.8±1.2	18.9±1.0	15.3±0.9
	2 ^b	13.2±2.0	15.6±2.0	12.9±1.0
	3 ^c	16.6±1.7	18.7±1.2	14.9±1.0
<i>Kr</i> ($\mu\text{mol CO}_2 \text{ mmol photons}^{-1}$)	1 ^a	11.8±1.1	12.4±1.1	11.0±0.5
	2 ^b	19.4±8.8	23.4±6.0	17.0±2.1
	3 ^c	10.8±0.3	15.0±0.9	11.1±0.5
<i>Keff</i>	1 ^a	11.2±2.0	11.1±1.6	19.2±3.8
	2 ^b	9.5±2.6	9.9±1.4	16.8±1.7
	3 ^c	9.3±1.8	9.7±1.4	20.6±3.3
PAR – photosynthetically active radiation; P_N , P_{gmax} and R_D – maximum of net photosynthetic rate, gross photosynthetic rate and dark respiration rate; <i>Kr</i> – indicator of the PAR use in photosynthesis; <i>Keff</i> – photosynthetic efficiency coefficient, dimensionless; ± – standard deviation; a – full sunlight, b – moderate shading, c – combined treatment of full sunlight and moderate drought.				

The variation in the values of the photosynthesis efficiency coefficients (K_{eff}), which characterize the maximum possible efficiency of gas exchange and reflect the physiological state of this species in these habitat conditions, also significantly differed both in size and dynamics. The K_{eff} indicator is species-specific and very sensitive to environmental factors [30]. Analysis of the calculations showed that the highest photosynthesis efficiency from the analyzed plant species is characterized by *Arbutus andrachne*, which has this value almost twice higher than that of *Pinus pallasiana* and *Juniperus excelsa*. In comparison with full sunlight, with moderate shading, K_{pe} decreased in all species by 11-15%. Under moderate drought conditions, photosynthesis efficiency decreased by 20% in *Pinus pallasiana*, 14% in *Juniperus excelsa*, and 7% in *Arbutus andrachne*. Differences in K_r and K_{eff} indicators under different lighting conditions and moderate droughts were statistically significant with a 95% probability.

The analysis of the light dependences of the gas exchange of the leaves of the studied plants confirmed the conclusions made on the basis of the measurements. *Juniperus excelsa* had the highest rates of photochemical reactions. Its values were slightly lower in *Pinus pallasiana* and *Arbutus andrachne*. The response to the effects of moderate shading and drought in all species was manifested in a steady trend of decreasing the intensity of gas exchange (table 2, figure 1). The values of the obtained determination coefficients indicate that the variation of net photosynthetic rate by 98-99% in the P_N/I dependence model is explained by a change in the intensity of the PAR (table 2).

Table 2. Average values of parameters photosynthetic light response curves in the studied plants under different environmental conditions.

Parameters	Environmental condition	<i>Pinus pallasiana</i>	<i>Juniperus excelsa</i>	<i>Arbutus andrachne</i>
P_{gmax} ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)	1 ^a	15.8±1.0	18.5±0.8	14.7±0.6
	2 ^b	13.2±2.7	15.7±2.2	12.7±1.2
	3 ^c	15.6±1.8	17.5±1.2	14.5±1.0
$\varphi(I_0)$ ($\mu\text{mol CO}_2 \mu\text{mol photons}^{-1}$)	1 ^a	0.06±0.01	0.07±0.01	0.06±0.01
	2 ^b	0.08±0.01	0.08±0.02	0.07±0.01
	3 ^c	0.06±0.02	0.07±0.01	0.06±0.01
$\varphi(I_0 - I_{comp})$ ($\mu\text{mol CO}_2 \mu\text{mol photons}^{-1}$)	1 ^a	0.06±0.01	0.07±0.01	0.06±0.01
	2 ^b	0.08±0.01	0.08±0.01	0.07±0.01
	3 ^c	0.06±0.02	0.07±0.01	0.06±0.01
$\varphi(I_{comp})$ ($\mu\text{mol CO}_2 \mu\text{mol photons}^{-1}$)	1 ^a	0.05±0.01	0.06±0.01	0.06±0.01
	2 ^b	0.07±0.01	0.07±0.01	0.06±0.01
	3 ^c	0.06±0.01	0.06±0.01	0.06±0.01
R_D ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)	1 ^a	1.2±0.2	1.3±0.2	0.6±0.1
	2 ^b	1.2±0.1	1.4±0.3	0.5±0.1
	3 ^c	1.3±0.2	1.5±0.2	0.6±0.1
I_{comp} ($\mu\text{mol photons m}^{-2} \text{ s}^{-1}$)	1 ^a	21.5±3.6	20.5±2.9	10.3±2.0
	2 ^b	15.5±2.8	17.5±3.0	8.4±2.1
	3 ^c	24.0±5.6	22.5±2.7	9.2±1.3
I_k ($\mu\text{mol photons m}^{-2} \text{ s}^{-1}$)	1 ^a	277±39	278±42	229±19
	2 ^b	165±31	199±23	191±13
	3 ^c	290±95	259±59	224±13
I_{sat} ($\mu\text{mol photons m}^{-2} \text{ s}^{-1}$)	1 ^a	1092±185	1587±304	1149±146
	2 ^b	713±141	776±207	647±108
	3 ^c	929±175	927±70	1169±413
β ($\text{m}^2 \text{ s } \mu\text{mol photons}^{-1}$)	1 ^a	0.0003±0.0001	0.0001±0.0001	0.0002±0.0001
	2 ^b	0.0005±0.0003	0.0004±0.0002	0.0005±0.0001
	3 ^c	0.0004±0.0001	0.0003±0.0001	0.0003±0.0001
γ ($\text{m}^2 \text{ s } \mu\text{mol photons}^{-1}$)	1 ^a	0.0018±0.0005	0.0024±0.0006	0.0026±0.0005
	2 ^b	0.0033±0.0019	0.0023±0.0009	0.0021±0.0004
	3 ^c	0.0019±0.0017	0.0020±0.0011	0.0025±0.0007
I_{max} ($\mu\text{mol photons m}^{-2} \text{ s}^{-1}$)	1 ^a	915±107	1150±135	896±55
	2 ^b	591±61	682±132	593±71
	3 ^c	805±106	827±43	856±159
R^2 (%)	1 ^a	98.8±0.4	99.0±0.1	98.7±0.5
	2 ^b	98.8±0.3	98.5±0.7	98.6±0.6
	3 ^c	98.0±1.2	98.9±0.2	98.8±0.4
<p>P_{gmax} – maximum gross photosynthetic rate; $\varphi(I_0)$, $\varphi(I_0 - I_{comp})$, $\varphi(I_{comp})$ – quantum yield of photosynthesis for different light intensities; R_D – dark respiration rate; I_{comp} – light compensation point; I_k – light constant; I_{sat} – light saturation point; β and γ – coefficients; I_{max} – light saturation point beyond which there is no significant increase in P_N; R^2 – determination coefficient; means±SDs includes the values from 2–4 leaves for 6–8 different days;</p> <p>a – full sunlight, b – moderate shading, c – combined treatment of full sunlight and moderate drought.</p>				

The parameter of the substrate light constant I_K equal to the value of the light intensity at the intersection of the maximum photosynthetic rate with the line of the initial slope of the light curve ($I_K = P_{gmax}/\varphi(I_0)$), is one of the oldest and most used in the description of

light dependencies. The value of the I_K parameter can be used to assess the adaptive properties of the species, since it characterizes light conditions when photosynthesis is limited by dark reactions, under which protective mechanisms begin to act. The adaptation of photophysical and photochemical stages to changes in the light regime determines the nature of dark reactions of photosynthesis. A low I_K value often indicates inefficient use of high PAR, rather than efficient use of low ones, and vice versa [31].

Fig. 1. Regression lines net photosynthetic rates (PN) leaves of *Pinus pallasiana*, *Juniperus excelsa* and *Arbutus andrachne* under full sunlight (1, 3, 5) and combined treatment of full sunlight and moderate drought (2, 4, 6).

The highest ranges of changes in the light constant (I_K), indicating a wider ecological amplitude relative to light, were observed in *Pinus pallasiana* (by 40%). In *Juniperus excelsa* and *Arbutus andrachne*, they were 1.5-2 times smaller. Under moderate drought conditions, changes in I_K did not exceed 2-7%. Analysis of the values of I_{comp} , I_K , $\phi(I_0)$, $\phi(I_0-I_{comp})$, R_D and their changes at different levels of insolation indicates a high photophilicity of *Pinus pallasiana* and *Juniperus excelsa* and the effective use of high-intensity PAR by plants. Variations in the values of the light compensation point in different lighting conditions allow us to conclude that *Pinus pallasiana* is better adapted to shading than *Juniperus excelsa*. High I_{comp} values (15.5-17.5 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$) indicate inefficient use of low-intensity PAR, low shade tolerance, and inability to renew in shade-type forests by immature *Pinus pallasiana* and *Juniperus excelsa* plants.

The lack of a clear downward trend in light of the constants in the shading and its high magnitude, and the tangent of the slope of the light curve is characterized *Arbutus andrachne* as a photophilous plant with effective use of the intensity of par in full sunlight, mild plasticity to changes in light regime. The values of I_K and their amplitude when

changing lighting conditions indicate a low activity in the use of low light intensities by young *Arbutus andrachne* plants and the probability of oppressive effects of strong shading on them. However, low levels of dark respiration ($0.5\text{--}0.6\text{ }\mu\text{mol CO}_2\text{ m}^{-2}\text{ s}^{-1}$) and low I_{comp} values ($8.4\text{--}10.3\text{ }\mu\text{mol photons m}^{-2}\text{ s}^{-1}$) indicate the ability to absorb CO_2 in low light. The lowest I_{comp} value indicates that in low light, the *Arbutus andrachne* leaf absorbed carbon dioxide, while other species studied were observed to release it.

Long-term continuous recording of the dynamics of the main characteristics CO_2 -gas exchange in leaves under favorable and stressful environmental conditions revealed the degree of expression and genotypic features of the adaptive strategy and stress-tolerant properties of *Pinus pallasiana*, *Juniperus excelsa* and *Arbutus andrachne*.

Studies have shown that under favorable growing conditions with saturating light intensity, the average net photosynthetic rate in light leaves of *Pinus pallasiana* was $12.3\text{ }\mu\text{mol CO}_2\text{ m}^{-2}\text{ s}^{-1}$, in *Juniperus excelsa* – $14.7\text{ }\mu\text{mol CO}_2\text{ m}^{-2}\text{ s}^{-1}$ and in *Arbutus andrachne* – $13.8\text{ }\mu\text{mol CO}_2\text{ m}^{-2}\text{ s}^{-1}$ (table 3). Under the influence of moderate drought, the intensity of photosynthetic CO_2 -gas exchange in *Pinus pallasiana* decreased by 13%, while the functional activity of the photosynthetic apparatus in *Arbutus andrachne* did not change, which is obviously due to the degree of stomatal openness.

Table 3. Characteristics of CO_2 -gas exchange of leaves of the studied plants under optimal conditions and under the influence of moderate drought at saturating light intensity.

Parameters	Environmental condition	<i>Pinus pallasiana</i>	<i>Juniperus excelsa</i>	<i>Arbutus andrachne</i>
P_N ($\mu\text{mol CO}_2\text{ m}^{-2}\text{ s}^{-1}$)	1 ^a	12.3±1.5	14.7±1.2	13.8±2.3
	2 ^b	10.7±1.4	14.2±0.8	13.6±0.6
R_{PR} ($\mu\text{mol CO}_2\text{ m}^{-2}\text{ s}^{-1}$)	1 ^a	0.3±0.1	0.3±0.1	0.4±0.4
	2 ^b	0.4±0.1	0.7±0.5	0.4±0.2
R_D ($\mu\text{mol CO}_2\text{ m}^{-2}\text{ s}^{-1}$)	1 ^a	0.8±0.7	3.0±0.5	1.9±0.7
	2 ^b	0.9±0.6	3.1±0.7	2.0±0.1
R_{total} ($\mu\text{mol CO}_2\text{ m}^{-2}\text{ s}^{-1}$)	1 ^a	1.1±0.7	3.4±0.4	2.3±0.7
	2 ^b	1.2±0.6	3.8±0.4	2.4±0.2
$R_{total}/Pg, \%$	1 ^a	8.2±4.6	18.6±2.3	14.4±3.5
	2 ^b	10.4±4.9	20.9±1.1	15.2±1.6
PAR – photosynthetically active radiation; P_N , P_g , R_{PR} , R_D and R_{total} ($R_{total} = R_{PR} + R_D$) – mean of net photosynthetic rate, gross photosynthetic rate, photo respiration rate, dark respiration rate and total respiration rate; ± – standard deviation; a – full sunlight, b – combined treatment of full sunlight and moderate drought.				

Total light respiration includes photorespiration, Moeler reactions, and dark or mitochondrial respiration [32]. The data obtained by us suggest that all the plants presented in the study have a low intensity of photorespiration and a low intensity of dark respiration. The highest intensity of total respiration was observed in *Juniperus excelsa* with the highest level of light saturation of photosynthesis. An average level of respiration intensity was observed in *Arbutus andrachne*.

The ratio of respiration and photosynthesis (R_{total}/Pg) is an integral indicator of the energy balance of the whole plant, the consistency of the main physiological processes, and characterizes the share of respiratory costs from the total number of photoassimilates during plant functioning [33]. From the results obtained, we can conclude that *Juniperus excelsa* and *Arbutus andrachne* spend a fairly high amount of photoassimilates on respiration. Evaluation of the efficiency of carbon use for plant growth processes showed that the share of fixed carbon, which is realized in net productivity, was 92% in *Pinus pallasiana*, 81% in *Juniperus excelsa*, and 86% in *Arbutus andrachne*. The obtained ratios of photosynthesis and respiration processes reflect the regularities of quantitative organization of the whole

plant under optimal conditions [33-34]. Under conditions of moderate water deficit, the ratio of respiration and photosynthesis in the studied plant species increased by 1-2%. This ratio under stress, as a rule, increases due to an increase in total respiration by the value of R_a (adaptive component of respiration), and this value is more significant in less resistant to this particular stress plant species. The new R_{total}/P_g ratio has the lowest possible value under these conditions [34].

The study of the temperature dependence of photosynthesis in the absence of water stress in conditions of sufficient light intensity showed a variation of the temperature optima P_N in the considered species within a fairly wide range. The analysis of experimental data revealed that the rate of assimilation of carbon dioxide per unit leaf surface of *Juniperus excelsa* accelerated with increasing leaf temperature up to 28-32°C, *Arbutus andrachne* – up to 37-39°C. Under optimal conditions of soil moisture with non-limiting light, the maximum net photosynthetic rate in *Pinus pallasiana* was observed at a leaf temperature of 16-22°C (fig. 2).

Fig. 2. Dependence of net photosynthetic rate (P_N) of *Pinus pallasiana*, *Juniperus excelsa* and *Arbutus andrachne* from leaf temperature under well-watered (solid line) and moderate water deficit (dotted line) conditions.

When the leaf temperature increased above the threshold values, there was a violation of the assimilation balance, increased respiration, and as a result, a decrease in photosynthesis. Under the influence of moderate drought, the temperature optimum zones changed insignificantly (within 2-3°C). However, under conditions of severe hydrothermal stress with soil moisture below 25% of FC, photosynthesis inhibition in the studied plant species was observed at temperatures of 8-10°C below the threshold.

In conditions of insufficient water supply, the ability of plants to regulate the water regime of aboveground parts plays a primary role. A promising approach to study the

mechanisms that ensure plant adaptation to water scarcity is to compare species that differ in drought tolerance.

Determination of the ecological and physiological characteristics of net photosynthetic rate in a wide range of changes in soil moisture allowed us to determine the dependence of the intensity of gas exchange of the studied plant species on soil moisture (fig. 3).

The zone of optimal soil moisture for *Pinus pallasiana* is in the range of 60-80% FC. When the soil moisture was below or above the specified limits, the intensity of photosynthesis decreased. The effect of soil drought on the activity of CO₂ assimilation was already evident in *Pinus pallasiana* when the soil moisture dropped to 55% of the FC. Below 30% FC, there was a negative carbon balance between the level of CO₂ assimilation during photosynthesis and its loss during respiration.

For young *Juniperus excelsa* plants, the optimal soil moisture was 65-100% FC. When humidification was less than 60% of FC, a gradual decrease in CO₂-gas exchange began. Periodic complete inhibition of photosynthesis due to stomatal closure occurred at soil moisture below 20% FC.

Arbutus andrachne was distinguished by its high tolerance to drought and ability to function effectively in a wide range of soil moisture (within 35-100% FC).

Fig. 3. Responses of net photosynthetic rate (P_N) of *Pinus pallasiana*, *Juniperus excelsa*, and *Arbutus andrachne* to water stress treatment.

Analysis of the results showed that the optimum environmental conditions, providing higher net assimilation of CO₂ of young plants *Pinus pallasiana* are the needles temperature from 14 to 23°C when the soil moisture at 60-80% FC under sunlight treatment at 600-400 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ PAR. For *Juniperus excelsa* the optimum environmental condition are needles temperature from 26 to 35°C, soil moisture at 65-100% FC and light

intensity about 700-1900 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ PAR. Optimal growing conditions for *Arbutus andrachne* determined by the leaf temperature in the range 27-39°C, soil moisture at 35-100% FC and PAR at 600-1700 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$.

A negative carbon balance under sufficient soil water content for *Pinus pallasiana* plants occurs when the needles overheat above 42-43°C. For *Juniperus excelsa* and *Arbutus andrachne* plants it was observed periodically at temperatures above 46-47°C. However, under the complex effect of hydrothermal stress as a result of leaf dehydration and overheating, periodic complete inhibition of photosynthesis in the studied plant species occurs already at temperatures 8-10°C below the threshold. With increasing soil drought, a critical loss of soil water content, leading to an almost complete cessation of photosynthesis due to stomata closure, occurs in *Pinus pallasiana* plants when relative water content reduce below 30% of FC, in *Juniperus excelsa* – below 20% of FC, in *Arbutus andrachne* – below 10-15% of FC. Carbon assimilation by young plants of *Pinus pallasiana* onset only when PAR above 15-24 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$, *Juniperus excelsa* – above 17-24 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ and *Arbutus andrachne* – above 8-10 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$.

4 Conclusion

As a result of the research, a comprehensive assessment of the features of regulation of photosynthetic activity of young plants *Pinus pallasiana*, *Juniperus excelsa* and *Arbutus andrachne* under various lighting, temperature and humidity conditions was carried out. The cardinal points of their light curves are determined and quantitative values of optimal and threshold values of environmental factors that limit gas exchange processes are obtained.

It was found that in the absence of stress effects of moisture deficiency and high temperatures, *Juniperus excelsa* has the highest intensity of CO_2 -gas exchange, and *Arbutus andrachne* has the highest efficiency. In relation to light, *Pinus pallasiana* is characterized by wider ecological amplitude compared to *Juniperus excelsa* and *Arbutus andrachne*.

Based on the results of the study of CO_2 -gas exchange, we can conclude that *Pinus pallasiana* and *Juniperus excelsa* are heliophytes with their characteristic efficient use of high-intensity of PAR. Variations in the values of the light compensation point in different lighting conditions indicate a better adaptation to shading of *Pinus pallasiana* than *Juniperus excelsa*. High values of the light compensation point indicate that the immature plants *Pinus pallasiana* and *Juniperus excelsa* do not effectively use low PAR intensities, weak shade tolerance, and inability to renew in shade-type forests.

Features of CO_2 assimilation during photosynthesis allow us to conclude that *Arbutus andrachne* is a light-loving plant with a weakly expressed plasticity to changes in the light regime and may experience a significant lack of light under strong shading. However, the low level of dark respiration and low values of the light compensation point indicate the ability to absorb CO_2 in low light.

Under optimal conditions, the share of fixed carbon that is realized in net productivity is 92% for *Pinus pallasiana*, 81% for *Juniperus excelsa*, and 86% for *Arbutus andrachne*. During the period of increasing soil moisture deficit, there is a natural decrease in the intensity of leaf gas exchange. Comparison of the results obtained between the species showed a significant variability in their sensitivity to temperature and water stress. *Arbutus andrachne* has the highest ability to actively rearrange the water regime in accordance with its external moisture supply, while *Juniperus excelsa* has a slightly lower capacity. Tolerance to hydrothermal stress in *Pinus pallasiana* is significantly lower than in *Arbutus andrachne* and *Juniperus excelsa*.

References

1. Plugatar Y V, Klymenko Z K, Ulanovskaya I V, Zykova V K and Plugatar S A 2019 Prospects for the use of the Crimean flora resources in the floriculture *Acta Horticulturae* **1240** 65–8 doi: 10.17660/ActaHortic.2019.1240.10
2. Calama R, Puértolas J, Madrigal G and Pardos M 2013 Modeling the environmental response of leaf net photosynthesis in *Pinus pinea* L. natural regeneration *Ecological Modelling* **251** 9–21 doi: 10.1016/j.ecolmodel.2012.11.029
3. Korsakova S P, Plugatar Yu V, Ilnitsky O A and Kleiman E I 2018 Water relation features of *Nerium oleander* L. under progressive soil drought stress *South of Russia: ecology, development* [Yug Rossii: ekologiya, razvitiye – in Russian] **13(1)** 101–115 doi: 10.18470/1992-1098-2018-1-101-115
4. Ivanov L A, Ivanova L A., Migalina S V, Yudina P K, Drobyshev Yu I, Tserenkhand G, Tsoog S and Gunin P D 2016 Photosynthesis adaptation of the desert-steppe shrub *Caragana bungei* Ledeb. to larch forest conditions at mountainous slopes in mongolian *Khangai Arid Ecosystems* [Aridnyye ekosistemy – in Russian] **6(3)** 195–205 doi: 10.1134/S2079096116030070
5. Liu J, Wang X, Rong Z, Gao Yu, Zhang G, Wang W, Ge L, Mao Ya, Guo Z, Wang Q and Zhao Ch 2019 Modified non-rectangular hyperbola equation with plant height for photosynthetic light-response curves of *Potentilla anserina* and *Elymus nutans* at various growth phases in the Heihe River Basin, Northwest China *J.of Arid Land* **11** 764–73 doi: 10.1007/s40333-019-0003-z
6. Pons T L and Poorter H 2014 The effect of irradiance on the carbon balance and tissue characteristics of five herbaceous species differing in shade-tolerance *Frontiers in Plant Science* **5(12)** 1–14 doi: 10.3389/fpls.2014.00012
7. Sack L 2004 Responses of temperate woody seedlings to shade and drought: do trade-off limits potential niche differentiation? *Oikos* **107** 107–27 doi: 10.1111/j.0030-1299.2004.13184.x
8. Mirkin B M and Naumova L G 2015 Conception of plant community: History and modern state of art *Biol. Bull. Rev.* **5** 493–504 doi: 10.1134/S2079086415050059
9. Efimov V V, Volodin E M and Anisimov A E 2015 Modeling of the Black Sea region climate changes in the XXI century *Physical Oceanography* **2** 3–13 doi: 10.22449/1573-160X-2015-2-3-13
10. IPCC 2013 Climate Change 2013: The Physical Science Basis: Summary for Policymakers, Technical Summary and Frequently Asked Questions: Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change ed T F Stocker, D Qin, G-K Plattner et al (Cambridge University Press) p 1535 doi:10.1017/CBO9781107415324
11. Herrmann H A, Schwartz J-M and Johnson G N 2019 Metabolic acclimation – a key to enhancing photosynthesis in changing environments? *Journal of Experimental Botany* **70(12,1)** 3043–56 doi: 10.1093/jxb/erz157
12. Johnson I R, Thornley J H M, Frantz J M and Bugbee B 2010 A model of canopy photosynthesis incorporating protein distribution through the canopy and its acclimation to light, temperature and CO₂ *Ann. Bot.* **106(5)** 735–49 doi: 10.1093/aob/mcq183
13. Zavala M A 2004 Integration of drought tolerance mechanisms in Mediterranean sclerophylls: a functional interpretation of leaf gas exchange simulators *Ecological Modelling* **76(3-4)** 211–26 doi: 10.1016/j.ecolmodel.2003.11.013

14. Pashtetsky A, Plugatar Y V, Ilnitsky O and Korsakova S 2019 Using of phytomonitoring data for eco-physiological evaluation of the environmental factors limiting development of ornamental plants *Acta Horticulture* **1263** 199–206 doi: 10.17660/ActaHortic.2019.1263.25
15. Plugatar Yu V *Crimean forests: Monograph* [Lesa Kryma: Monografiya – in Russian] (Simferopol: IT "ARIAL") p 385
16. Koba V P, Khromov A F and Sakhno T M 2020 State and ecological structure of populations of *Pinus pallasiana* D. Don of the lower belt of the southern macroslope of the main ridge of the Crimean mountains Scientific Notes of V.I. Vernadsky Crimean Federal University *Biology. Chemistry* [Uchenyye zapiski Krymskogo federal'nogo universiteta imeni V.I. Vernadskogo. Biologiya. Khimiya – in Russian] **6 (72,2)** 75–84 doi: 10.37279/2413-1725-2020-6-2-75-84
17. Plugatar Yu V, Bagrikova N A, Belich T V, Kostin S Yu, Krainyuk E S, Maslov I I, Sadogurskiy S E, Sadogurskaya S A and Sarkina I S 2018 “Cape Martian” Nature Reserve [Prirodnyy zapovednik “Mys Mart’yan” – in Russian] (Simferopol: "ARIAL") p 104
18. Melia N, Gabedava L, Barblishvili T and Jgenti L 2012 Reproductive biology studies towards the conservation of two rare species of Colchic flora, *Arbutus andrachne* and *Osmanthus decorus* *Turk. J. Bot.* **36** 55–62 doi:10.3906/bot-1008-42
19. Shevchenko S 2017 Reproduction and propagation of some rare species of the Crimean flora *Agriculture and Forestry* **63(4)** 99–106 doi: 10.17707/AgricultForest.63.4.11
20. Karapatzak E K, Varsamis G, Koutseri I, Takos I and Merou T 2019 The effect of pollen performance on low seed fertility in a Greek population of *Juniperus excelsa* *J. For. Sci.* **65** 356–67 doi/10.17221/42/2019-JFS
21. Korsakova S P, Sarkina I S and Bagrikova N A 2019 Pollination biology of *Juniperus excelsa* and *J. deltoides* (Cupressaceae) in the South Coast of the Crimea *The Botanical journal* [Botanicheskii Zhurnal – in Russian] **104(10)** 1574–87 doi: 10.1134/S0006813619100077
22. *Red Book of Russian Federation (plants and fungi)* [Krasnaya kniga Rossiyskoy Federatsii (rasteniya i griby) – in Russian] 2008 ed L V Bardunov, V S Novikov (Moscow: KMK Scientific Press Ltd) p 855
23. *Red book of the Republic of Crimea: plants, algae and fungi* [Krasnaya kniga Respubliki Krym (rasteniya, vodorosli i griby) – in Russian] 2015 eds A V Yena and A V Fateryga (Simferopol: "ARIAL") p 480
24. Kirichok E I 2016 Ontogenesis of Grecian juniper (*Juniperus excelsa* M. Bieb) in sparse forests of the black sea coast of the Crimea and the Caucasus *Russian Journal of Ecosystem Ecology* [Rossiyskiy zhurnal ekologii ekosistem – in Russian] **1(3)** doi: 10.21685/2500-0578-2016-3-4
25. Ilnitsky O, Plugatar Yu and Pashtetsky A 2020 Features of Water Exchange of *Pinus nigra* subsp. *pallasiana* in Conditions of Southern Coast of Crimea *Advances in Social Science, Education and Humanities Research* **393** doi: 10.2991/assehr.k.200113.145
26. Ilnitsky O A, Plugatar Yu V and Pashtetsky A V 2020 Dynamics of the Rate of Photosynthesis in *Juniperus excelsa* M. Bieb and Environmental Factors during Growing Seasons in the Conditions of the Southern Coast of Crimea *Russian Agricultural Sciences* **46(3)** 218–22 doi: 10.3103/S1068367420030052
27. Balaur N S, Vorontsov V A, Kleiman E I and Ton Yu D 2009 Novel technique for component monitoring of CO₂ exchange in plants *Plant Physiology* **56(3)** 466–70 doi: 10.1134/S1021443709030170

28. Ye Z-P 2007 A new model for relationship between irradiance and the rate of photosynthesis in *Oryza sativa* *Photosynthetica* **45(4)** 637–40 doi: 10.1007/s11099-007-0110-5
29. Korsakova S P, Plugatar Yu V, Ilnitsky O A and Karpukhin M 2019 A research on models of the photosynthetic light response curves on the example of evergreen types of plants *Agronomy Research* **17(2)** 518–39 doi: 10.15159/AR.19.065
30. Bolondinskii V K and Vilikainen L M 2017 A study of CO₂ gas exchange in Karelian birch under low solar radiation conditions in plantations with different levels of soil fertility *Transactions of the Karelian Research Centre of the Russian Academy of Sciences* [Trudy Karel'skogo nauchnogo tsentra Rossiyskoy akademii nauk – in Russian] **5** 52–65 doi: 10.17076/eb518
31. Jodłowska S and Śliwińska S 2014 Effects of light intensity and temperature on the photosynthetic irradiance response curves and chlorophyll fluorescence in three picocyanobacterial strains of *Synechococcus* *Photosynthetica* **52** 223–32 doi: 10.1007/s11099-014-0024-y
32. Hurry V, Igamberdiev A U, Keerberg O, Parnik T, Atkin O, Zaragoza-Castells J and Gardestrom P 2005 Respiration in Photosynthetic Cells: Gas Exchange Components, Interactions with Photorespiration and the Operation of Mitochondria in the Light *Plant Respiration: From Cell to Ecosystem* ed H Lambers and M Ribas-Carbo **18** pp 43–61 doi: 10.1007/1-4020-3589-6_4
33. Garmash E V 2016 Mitochondrial respiration of the photosynthesizing cell *Russian Journal of Plant Physiology* [Fiziologiya Rastenii – in Russian] **63(1)** 17–30 doi: 10.7868/S001533031506007X
34. Rahmankulova Z F 2019 Physiological aspects of photosynthesis – respiration interrelations cell *Russian Journal of Plant Physiology* [Fiziologiya Rastenii – in Russian] **66(3)** 365–74 doi: 10.1134/S1021443719030117