RESEARCH PAPER

CO$_2$ EXCHANGE OF SEEDLINGS OF *RHIZOPHORA APICULATA BL.* IN ARTIFICIAL AND NATURAL MANGROVE FORESTS OF SOUTHERN VIETNAM

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ABSTRACT. Mangrove forests are an important part of tropical coastal ecosystems. Until recently, these forests were intensively exterminated. Currently, the issue of mangrove conservation is being discussed at a number of symposiums due to their significant role in reducing the effects of greenhouse gas emissions. However, there has recently been uncertainty in estimation of CO$_2$ fluxes in mangrove forests due to a lack of field research.

The results of studies of photosynthesis at the leaf level in-situ in seedlings of *Rhizophora apiculata* Blume, 1827 of both natural and artificial origin are presented. The studies were carried out on a mangrove plantation growing in Can Gio Mangrove Biosphere Reserve, which is 50 kilometres from Ho Chi Minh City (South Vietnam). CO$_2$ gas exchange during photosynthesis was measured using a gas analysing system called the LI-6800 (USA).

Photosynthetically active radiation (PAR) is the main factor affecting the photosynthesis of the studied seedlings. Artificial seedlings that were grown in open areas had higher productivity and greater photosynthetic rates. It has been determined that the measured photosynthesis are scattered over three clearly marked zones, which correspond to the measurements of photosynthesis made in the pre-noon, noon and afternoon hours. The water reserves used up before noon were not fully replenished in the afternoon by the seedlings. Based on the results obtained, it has been suggested that the main inhibitory factor affecting the photosynthesis of *R. apiculata* (if PAR is not taken into account) is a violation of the water balance of the leaves. The optimum air temperature for photosynthesis processes in seedlings is (35 ± 2) °C. The intensity of photosynthesis also increases with an increase in the concentration of CO$_2$ in the air. The increases of photosynthesis continue until the concentration of CO$_2$ reaches ~1000 µmol·mol^{-1} and then do not increase. We associate this circumstance with the maximum possibilities of the photosynthetic apparatus of the leaf of the studied plant.

The obtained research results will contribute to a better theoretical understanding of the productivity of plants of this species in the respective ecosystems, and will also allow us to move from photosynthesis at the leaf level to photosynthesis at the planting level. The work's mathematical models can be used to model changes in *R. apiculata* photosynthesis from the point of view of climate change.

KEYWORDS: *Rhizophora apiculata*, air temperature, CO$_2$ concentration, diurnal dynamics, the intensity of photosynthesis, light response curve

INTRODUCTION

Mangrove forests are one of the unique forest ecosystems. They are an important part of tropical coastal ecosystems. Mangroves play important ecological roles as well as serving as a source of income (Donato et al. 2011; Hogarth 2007; Hogarth 2008; Simard et al. 2019; Saintilan et al. 2020).

However, the degradation of mangrove ecosystems is currently being observed (Alongi 2002; Valiela et al. 2001; Nguyen 2000). This is a result of economic activity, which primarily entails the clearing of these forests (Luong 2014), as well as ongoing global warming (Desherevskaya et al. 2013), which causes sea levels to rise, flooding of mangrove forests,

and the drying up of specific mangrove ecotopes (FAO 2007; Simard et al. 2019).

Scientists are therefore undoubtedly interested in studying mangrove ecosystems. Studying the physiological properties of mangroves is one of the main foci of this type of research. The studies pertaining to their gas exchange are the most relevant of these (Clough 1997). Nevertheless, despite having enough knowledge in this area of research, many unanswered questions still exist. In particular, this applies to the mangroves of Vietnam.

Our estimates place *Rhizophora apiculata* Blume, 1827 as one of the most common tree species in the mangrove forests of South Vietnam. This species is widely used in reforestation

activities (Hogarth 2007). Forming grandiose plantations due to its stilted roots, *R. apiculata* plays an important role in the ecology of mangrove forests (Thongjoo et al. 2018; Wenfang et al. 2020). Of undoubted interest is the fact that *R. apiculata* belongs to plants with C4 photosynthesis, which allows the plant to better adapt when growing in conditions of high temperatures and lack of water (Ehleringer and Björkman 1977; Slack and Hatch 1967). Therefore, it is not accidental that many researchers pay attention to this species (Christensen 1978; Ong et al. 1995).

Our previous studies on mature *R. apiculata* trees showed that photosynthesis depression in these trees began to appear at noon and persisted until the end of the day (Đô Phong Lửu et al. 2021). Based on this, we hypothesized that the parameters characterizing the photosynthetic abilities of *R. apiculata* should differ at different times of the day. We found no studies to support or refute our hypothesis. We also assumed that plants growing in various environments should have varying values for these characteristics.

The proposed hypothesis, which was to investigate the daily change of the indicators of the photosynthetic capacity of *R. apiculata* seedlings of artificial and natural origin, determined the goal of the study.

The following tasks were established in accordance with the study's goal: 1) to obtain daily dynamics of the intensity of photosynthesis for seedlings of artificial and natural origin; 2) to model the response curves of photosynthesis to light according to the Michaelis-Munten equation (1); 3) to obtain the dependence of photosynthesis on temperature and CO_2 concentration in the air; 4) to analyze the obtained results.

The results of our research of the photosynthetic exchange of CO_2 at the leaf level in-situ of seedlings of *R. apiculata* of natural and artificial origin are presented in this article. These results can be used to recalculate photosynthesis at the leaf level, down to the planting level. Also, the results will help in predicting how plants of this species will grow in the future in relation to climatic changes around the world. The results of the study will be helpful in creating reforestation strategies.

MATERIALS AND METHODS

Study site, plant material and growing conditions

The research was carried out in July 2020 in a mangrove plantation located in the Can Gio Biosphere Reserve, located 50 km from Ho Chi Minh City (10°28´36´´N, 106°54´17´´E) (South Vietnam). As the test subject, 5-year-old seedlings of *Rhizophora apiculata* Blume, 1827, both of artificial and natural origin, were selected.

Artificial seedlings grew in an open area and were intended for reforestation activities (Fig. 1a). The number of studied seedlings n = 27, their average height h = 57 cm (Standard Deviation, SD = 7 cm), the average number of leaves per seedling N = 35 (SD = 16).

Natural seedlings grew along the edge of the water channel on its northern side (Fig. 1b). The seedlings were formed as a result of the germination of floating fruits that were washed ashore. At noon, the seedlings were shaded by the trees and shrubs growing behind them. Seedling parameters: n = 14, h = 88 cm (SD = 8 cm), N = 10 (SD = 5). Twice a day, both sites were flooded with water as a result of sea tides.

Measurement of photosynthetic gas exchange and experimental design

Photosynthesis processes were considered from the standpoint of CO_2 gas exchange. The rate of photosynthesis (photosynthesis) was measured using a Portable Photosynthesis System LI-6800 (Li-Cor Inc., USA). For artificial illumination of the investigated part of the sheet, a 3 × 3 cm light source was used, supplied by the LI-6800 manufacturer as an addition to the device. The emission spectrum of the light source consists of red (λ = 660 nm) and blue (λ = 453 nm) colours. When using it, the object was illuminated with light, consisting of red and blue colours in a ratio of 9: 1. During measurements under natural light, photosynthetically active radiation (PAR) was measured using a sensor located in the LI-6800 measuring chamber.

During measurements, the required microclimate parameters were set in the LI-6800 measuring chamber – object illumination, air temperature and humidity, CO_2 concentration.

For the study, we used the formed intact leaves, as a rule, located on the penultimate node of the shoot. The measurements were carried out in the middle part of the leaf, bounded by the frame of the LI-6800 measuring chamber with an aperture of 3x3 cm. Current measurements of photosynthesis were carried out on 2–4 randomly selected seedlings. To construct the diurnal graphical dependencies, the average values of the measured values were used.

Studies of the dependence of photosynthesis on temperature were carried out on artificial seedlings. During measurements, the following microclimate parameters were set in the LI-6800 measuring chamber: illumination

Fig. 1. Studied seedlings of *R. apiculata* of artificial (a) and natural (b) origins

1000 μmol·m^{-2}·s^{-1}, CO$_2$ concentration 400 μmol·mol^{-1}, humidity ~ 60%. The measurements were carried out in an automatic mode in the temperature range from 24 to 46 °C.

Studies of the dependence of photosynthesis on CO$_2$ concentration were also carried out on artificial seedlings. During measurements, the following microclimate parameters were set in the LI-6800 measuring chamber: illumination 1000 μmol·m^{-2}·s^{-1}, temperature 30 °C, humidity ~ 70%. The measurements were carried out in an automatic mode in the CO$_2$ concentration range from 350 to 1000 μmol·mol^{-1} with a step of 50 μmol·mol^{-1}.

The work used meteorological data obtained from a meteorological station located on the territory of the reserve.

Diurnal curves of photosynthesis and PAR

The data for plotting the diurnal dynamics of photosynthesis and PAR were obtained over two days: July 4, 2020, from 15:00 to 19:00 and July 27, 2020, from 05:00 to 14:30. The total solar radiation these days differed by 6% (the cloudiness on July 4, 2020, in the first half of the day was slightly higher). The average air temperature during the daylight hours on July 4, 2020, was 34 °C, and on July 27, 2020 – 36 °C.

The measurements were carried out with an interval of ~20 min with the following microclimate parameters in the LI-6800 measuring chamber: CO$_2$ content 400 μmol·mol^{-1}, humidity ~65%, temperature ~32 °C.

In order to conduct a more detailed analysis of the obtained dependences, daily measurements were divided into three time periods: pre-noon time – from 06:00 to 09:30, noon – from 09:30 to 15:30 and afternoon – from 15:30 to 18:30.

The total values of PAR and CO$_2$ gas exchange were calculated for a full day, as well as in the pre-noon time – from 00:00 to 12:00 and in the afternoon – from 12:00 to 24:00.

Light-response curves

The Michaelis–Munten equation served as the foundation for the mathematical explanation of the photosynthetic light response curves (Michaelis and Menten 1913). We used this equation in a modified form (Kaipiainen 2009):

$$A = A_m \times Q / (Q + K_M) + A_d \qquad (1)$$

where A is the intensity of photosynthesis, μmol·m^{-2}·s^{-1};
A_m – is the maximum intensity of photosynthesis, μmol·m^{-2}·s^{-1};
Q – PAR, μmol·m^{-2}·s^{-1}; A_d - respiration rate at $Q = 0$, μmol·m^{-2}·s^{-1};

K_M – Michaelis constant (K_M is numerically equal to PAR, at which the intensity of photosynthesis is half of the maximum $A = 0.5A_m$). K_m values are often used by researchers when comparing the physiological characteristics of plants (Hieke et al. 2002). According to (1), the light compensation point (*LCP*) was determined, μmol·m^{-2}·s^{-1}, which shows at what intensity of PAR photosynthesis becomes zero.

To assess the efficiency of photosynthesis, we propose to use the slope of the tangent *a* (italic font) to the function curve of (1) at the point corresponding to K_M. From a physical point of view, this coefficient reflects the rate of change in the intensity of photosynthesis with a change in PAR by one unit.

Statistical analysis

Data processing was carried out using the MS Excel "Descriptive statistics" package ($p < 0.05$). The degrees of association of the studied datasets were determined using Pearson's correlation coefficients, *r*. To determine the statistical significance of the coefficient *r*, *p*-values were calculated. *P*-values were calculated using the T.TEST function and corresponded to a paired Student's t-test with a two-tailed distribution at a significance level of α = 0.05. The parameters of equation (1) were selected using the MS Excel package "Parameters of the solution search" (the limiting number of iterations is 100, the relative error is 0.00001, the permissible deviation is 5%, the convergence is 0.0001). The slope *a* of the tangent, the coefficients of the equation for this tangent, as well as the extremum points of the graphical dependencies, were determined using differentiation methods. The total values of the investigated quantities were determined by the integration method. Graphing was carried out using the MS Excel environment.

RESULTS

Diurnal dynamics of photosynthesis and PAR

Fig. 2 shows the daily dynamics of the intensity of photosynthesis and PAR, obtained as a result of measurements on seedlings of artificial origin.

Fig. 3 shows the daily dynamics of the intensity of photosynthesis and PAR, obtained as a result of measurements on seedlings of natural origin.

The indicators characterizing the degree of association *r* between the intensity of photosynthesis *A* and PAR, as well as the values of total PAR and CO$_2$ gas exchange for daily dynamics of the intensity of photosynthesis and PAR of seedlings of artificial and natural origin, are summarized in Table 1.
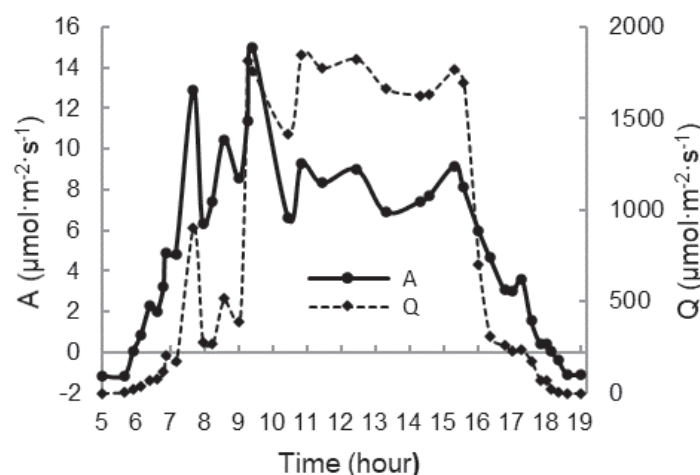

Fig. 2. Daily dynamics of the intensity of photosynthesis – A, and PAR – Q, of artificial seedlings
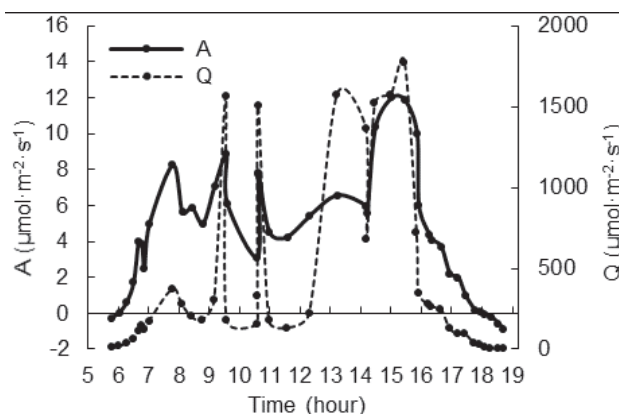
Fig. 3. Daily dynamics of the intensity of photosynthesis – *A*, and PAR – *Q*, seedlings of natural origin

Table 1. Indicators characterizing daily dynamics of photosynthesis and PAR in seedlings of artificial and natural origin

Index	Seedlings of artificial origin Seedlings of natural origin			
	Whole day	Pre-noon time	Noontime	Afternoon time
r / *p*	0.78 / 4.7E-06 0.78 / 2.1E-05	0.85 / 0.012 0.96 / 0.002	0.50 / 5.0E-09 0.77 / 0.006	0.87 / 0.044 0.90 / 0.006
Total PAR, mol·m^{-2}	46.9±2.4 24.2±1.3	24.2±1.3 5.8±0.3		22.8±1.2 18.4±1.0
Total gas exchange CO$_2$, mol·m^{-2}	0.304±0.016 0.241±0.013	0.154±0.008 0.103±0.006		0.151±0.008 0.138±0.007

Light-response curves

Fig. 4 shows the values of photosynthesis depending on PAR, measured on seedlings of artificial (Fig. 4a) and natural (Fig. 4b) origin. The figures also show the curves approximating these values, constructed according to (1) for the values obtained in the pre-noon (curves 1) and in the afternoon (curves 2) and tangents to these curves at the points corresponding to the K_M values.

The indicators characterizing the photosynthetic characteristics of seedlings obtained according to (1), as well as the R^2 values for the curves plotted and the number of measurements n, are summarized in Table 2.

Dependence of photosynthesis on temperature and on CO$_2$ concentration

The obtained values of the intensity of photosynthesis for seedlings of artificial origin, as a function of the temperature *T* of the air surrounding the leaf, are approximated by a quadratic equation (*R*^{2}=0.97, n=20):

$$A(T) = -0.0889T^2 + 6.2453T - 100.84 \quad (2)$$

The extremum of this function corresponds to a value of T = 35 °C. Therefore, taking into account measurement errors, the optimal temperature for photosynthesis of *R. apiculata* seedlings is T_{opt} = 35 ± 2 °C.

The dependence of the intensity of photosynthesis of *R. apiculata* on the concentration of CO$_2$ in the air is described by a quadratic equation (*R*^{2}=1.00, *n*=13):

$$A(CO_2) = -8E-06(CO_2)^2 + 0.016(CO_2) - 0.599 \quad (3)$$

DISCUSSION

Effect of PAR on photosynthesis

The following unique patterns can be seen in the diurnal dynamics of the intensity of photosynthesis in seedlings of artificial origin (Fig. 2, Table 1):

1) an increase in photosynthesis to maximum values in the pre-noon time, up to 09:30, in proportion to an increase in PAR (*r* = 0.85);
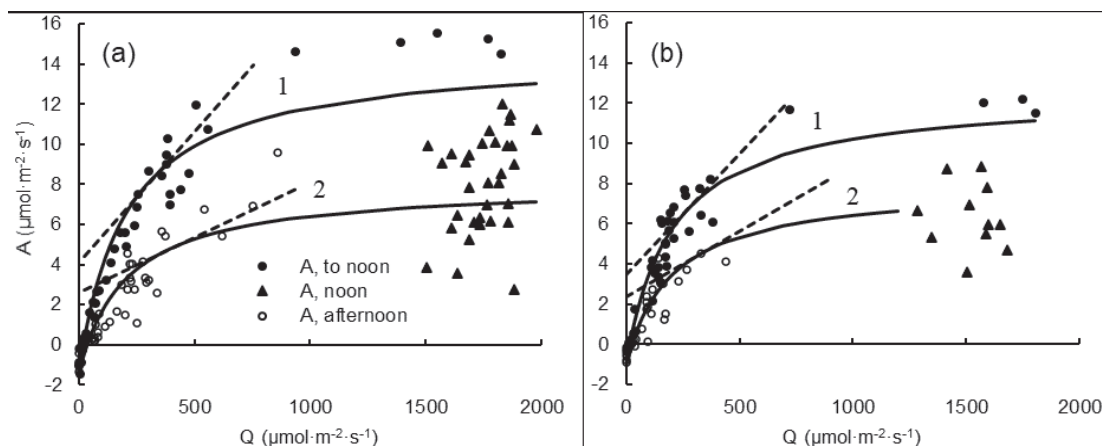

Fig. 4. Dependences of the intensity of photosynthesis – *A*, on PAR – *Q*, obtained on seedlings of artificial (a) and natural (b) origins

Table 2. Indicators characterizing photosynthetic characteristics of seedlings

Index	Seedlings of artificial origin		Seedlings of natural origin	
	Pre-noon time	Afternoon time	Pre-noon time	Afternoon time
R^2	0.97	0.90	0.95	0.89
n	124		94	
A_m, µmol·m^{-2}·s^{-1}	16.0	9.5	13.5	8.9
a	0.013	0.006	0.012	0.007
K_M	202.5	202.7	204.2	204.6
Ad, µmol·m^{-2}·s^{-1}	-1.5		-1.0	
LCP, µmol·m^{-2}·s^{-1}	21.0	38.0	16.3	25.9

2) a decline in photosynthesis from maximum values to values corresponding on average to 8.0 µmol·m^{-2}·s^{-1} (SD = 2.4 µmol·m^{-2}·s^{-1}), and the exit of the photosynthesis curve to a kind of plateau at noon, from 09:30 to 15:30, with a weak dependence of photosynthesis on PAR ($r = 0.50$);

3) a decline in photosynthesis in the afternoon, from 15:30, in proportion to a decrease in PAR ($r = 0.87$);

4) negative values, indicating the processes of respiration occurring in the leaf, at night.

It is interesting to note that the same diurnal dynamic was obtained for the light leaves of *Rhizophora mucronata* Poir. growing in Indian red mangroves (Kumar et al. 2017).

In order to give a more detailed interpretation of the listed patterns, let us turn to the dependences of photosynthesis on PAR (Fig. 4a) and indicators characterizing the photosynthetic characteristics of seedlings (Table 2).

The markers representing the obtained photosynthesis values are distributed in three clearly marked zones: 1 – in the zone corresponding to the photosynthesis values obtained in the pre-noon (markers in the form of circles); 2 – in the zone corresponding to the values obtained at noontime (triangular markers); 3 – in the zone corresponding to the values obtained in the afternoon (markers in the form of open circles) (Fig. 4a).

The curves plotted according to (1) for the photosynthesis values obtained in the pre-noon and afternoon (Fig. 4a) have a high degree of association (Table 2). The K_M coefficients characterizing the physiological characteristics of plants are approximately the same, which is obvious since we examined plants of the same type. However, the maximum intensity of photosynthesis, Am, in seedlings in the pre-noon time was significantly higher than in the afternoon. The same applies to the slopes a. Thus, in artificial seedlings, the efficiency of photosynthesis in the pre-noon time was 2.2 times higher than in the afternoon.

On the other hand, the LCP for these seedlings in the afternoon was 1.8 times higher than that in the pre-noon. That is, in the afternoon, at a PAR of 38.0 µmol·m^{-2}·s^{-1}, the absorption of CO_2 by the leaf was compensated by its release. Such processes are caused by respiration, as a rule, associated with metabolic processes occurring in the leaf. In addition to the foregoing, it should be mentioned that these seedlings' photosynthesis, is sated when the PAR is about 1800 µmol·m^{-2}·s^{-1}, as shown in Fig. 2 and Fig. 4a.

Similar patterns in the dynamics of photosynthesis, indicating its different behaviour in the pre-noon and daytime hours, in similar studies by other researchers, the authors of this work did not reveal. However, it should be noted that the authors of the work (Ball et al. 1997), when conducting similar studies, noted a very large scatter of

data. With the exception of measurements taken around noon, this was not noticed in our research.

The daily dynamics of photosynthesis in seedlings of natural origin (Fig. 3, Table 1), in general, is characterized by the same regularities as in seedlings of artificial origin. Distinctive features of these dynamics are somewhat large values of r obtained before and afternoon (0.96 and 0.90), as well as the presence of a relationship between photosynthesis and PAR at noon ($r = 0.77$).

A similar situation emerges when analyzing the features of photosynthesis of seedlings according to Fig. 4b – the obtained values of photosynthesis are also distributed in the three zones indicated above.

The plotted curves (1) for the values of photosynthesis obtained before and afternoon also have a high degree of association (Table 2). The K_M coefficients are approximately the same. The maximum intensity of photosynthesis, A_m, in seedlings in the pre-noon time is significantly higher than in the afternoon. The same applies to the slopes a. Thus, in seedlings of natural origin, the efficiency of photosynthesis in the pre-noon time was 1.7 times higher than in the afternoon. The LCP for these seedlings in the afternoon was 1.6 times higher than that in the pre-noon time. In the afternoon, LCP was 25.9 µmol·m^{-2}·s^{-1}.

Summarizing what has been said, we can present a comparative analysis of the characteristics of the growth of seedlings of artificial and natural origin.

On the one hand, these seedlings have similar characteristics. Thus, the diurnal dynamics of seedlings are characterized by an increase in photosynthesis in the pre-noon and a decrease in photosynthesis in the afternoon, with strong degrees of connection with PAR (Fig. 2, Fig. 3, Table 1). The obtained values of photosynthesis are distributed in three clearly marked zones, corresponding to the values of photosynthesis obtained in the pre-noon, noon and afternoon (Fig. 4a and Fig. 4b). Photosynthesis values obtained in the pre and afternoon time are described with a high degree of association.

Slope coefficients a obtained for seedlings during the pre-noon and during the afternoon are identical (Table 2). Accordingly, the efficiency of photosynthesis during pre-noon and during the afternoon is approximately the same; and during pre-noon, it is higher than during the afternoon. K_M coefficients for seedlings are approximately the same. LCP for seedlings in the afternoon was higher than that during the pre-noon.

On the other hand, the seedlings under consideration also have distinctive characteristics. So, at noon, photosynthesis in seedlings of artificial origin was more stochastic, while in seedlings of natural origin, there is a connection between photosynthesis and PAR. Further,

the maximum values of photosynthesis, A_m, for seedlings of artificial origin, both during pre-noon and afternoon, were significantly higher than those of seedlings of natural origin. This is primarily due to different lighting conditions of seedlings: the total PAR for artificial seedlings was 46.9 ± 2.4 mol·m^{-2} (in the first and second half of the day it was 23.5 ± 1.3 mol·m^{-2}), while for seedlings natural origin - 24.2 ± 1.3 mol·m^{-2} (in the first half of the day it was 5.8 ± 0.3 mol·m^{-2}, in the second - 18.4 ± 1.0 mol·m^{-2}) (Table 1).

Accordingly, the total CO_2 gas exchange for artificial seedlings was 0.304 ± 0.016 mol·m^{-2} (in the first and second half of the day it was the same and amounted to 0.153 ± 0.008 mol m^{-2}), whereas, for seedlings of natural origin, the total CO_2 exchange was 0.241 ± 0.013 mol·m^{-2} (in the first half of the day it was 0.103 ± 0.006, in the second – 0.138 ± 0.007 mol·m^{-2}) (Table 1).

The saturation of photosynthesis for these seedlings (Fig. 3 and Fig. 4b) occurs when PAR equals about 1500 μmol·m^{-2}·s^{-1}.

It should be noted here that the saturation values of photosynthesis obtained by us, both for artificial seedlings and for seedlings of natural origin, are fundamentally different from those presented in (Ball et al. 1997) that was amounting to about 400 μmol·m^{-2}·s^{-1}.

Thus, seedlings of artificial origin had higher productivity, and this was determined, first of all, by the amount of PAR supplied to the plants. Higher metabolic processes occurring in the leaves of seedlings of artificial origin are also indicated by higher values of *LCP* and A_d (Table 2).

Naturally, the considered physiological parameters affected the morphological characteristics of the seedlings. Thus, the average number of leaves on a seedling of artificial origin is N = 35 (SD = 16), while on a seedling of natural origin - N = 10 (SD = 5). However, such a significant difference in the number of leaves on seedlings was to some extent compensated by the height – seedlings of natural origin were 1.5 times higher.

Effect of temperature and CO2 concentration on photosynthesis

Analysis (2) showed that the optimal air temperature for photosynthesis of *R. apiculata* is T_{opt} = 35 ± 2 °C. It can be noted here that our similar studies on an adult tree *R. apiculata* of natural origin gave the same result (Đô Phong Lưu et al. 2021). According to (Ball et al. 1997), this figure is approximately 38 °C. However, the authors noted a large scatter of data and, unfortunately, do not indicate the amount of error in the determined value. In another work (Okimoto et al. 2013), two values of this temperature are given: 33 °C and 26 °C. Because the authors used similar equipment to carry out their studies, taking into account the error, we can say that the first temperature coincides with T_{opt}. Thus, the deviation of the air temperature from T_{opt}, both to a lower and to a higher side, causes a decrease in photosynthesis in *R. apiculata*. This circumstance is confirmed, for example, by studies (Sage and Kubien 2007; Kristine et al. 2022), which studied the temperature responses of various tropical plants, including those with C4 photosynthesis.

The average air temperature during measurements at noon was 37.2 °C (SD = 1.0 °C). However, such temperatures could cause a decrease in photosynthesis by only 0.1%. On the other hand, we did not measure the temperature of the leaves, which, as a result of exposure to direct solar radiation (Fig. 1a and Fig. 2), could be quite high. High leaf temperatures inhibit photosynthesis. In addition, plants

could experience a water shortage. For example, our studies related to the moisture content of leaves in relation to their absolutely dry weight on an adult *R. apiculata* tree showed that from 08:50 to 15:20 the leaves were losing 34% of moisture.

It is possible that in different leaves of seedlings, water deficiency manifested itself in different ways with corresponding changes in photosynthesis. At least, this hypothesis can explain the stochastic distribution of the values of photosynthesis in artificial seedlings at noon.

In contrast to this, in seedlings of natural origin, the presence of a connection between photosynthesis and PAR was noted at noon. This is due to the fact that these seedlings in midday time were shadowed by the trees and shrubs growing behind them (Fig. 1b and Fig. 3). As a result, the leaves of these seedlings were exposed to significantly less overheating and so experienced less water deficit.

Based on what has been said, we can make the following assumption. In the studied seedlings, the water consumed during midday time was not completely restored afterwards. This can explain the significantly lower photosynthetic parameters observed in seedlings during the afternoon (Table 2) than during the pre-noon. This assumption is confirmed by the conclusions made in the work (Kumar et al. 2017).

The dependence of the intensity of photosynthesis in *R. apiculata* on the CO_2 concentration in the air is described by equation (3). It follows from this equation that in the range of CO_2 concentrations under consideration, with its increase, photosynthesis naturally increases. Obviously, this circumstance has a positive effect on plant growth. An increase in the growth of *R. apiculata* seedlings at increased CO_2 concentration in the air is noted by (Eong et al. 1997; Kumar et al. 2017).

The analysis of function (3) for extrema shows that the increase in photosynthesis occurs up to the CO_2 concentration in the air, reaching ~1000 μmol·mol^{-1}. Interpolation of the obtained results allows us to make the assumption that at a CO_2 concentration of ~1000 μmol·mol^{-1}, *R. apiculata* photosynthesis reaches maximum values and does ot increase with further increases in CO_2 concentration. This circumstance, first of all, is determined by the maximum capabilities of the photosynthetic apparatus of the leaf of the studied plant.

The presented dependences of photosynthesis on temperature and CO_2 concentration find their confirmation also in a number of works related to the study of the effect of elevated temperature and CO_2 concentration, simulating global warming, on photosynthesis of C4 plants (Alberto et al. 1996; Ghannoum et al. 2000; Read and Morgan 1996; Morgan et al. 1994).

In our case, for example, if we consider the most optimistic forecasts associated with an increase in the concentration of CO_2 in the air in the next decade from 412 ppm to 460 ppm (and this concentration is already observed over cities), then the intensity of photosynthesis in the studied seedlings will increase by about 6%. This trend will be one of the tools for stabilizing the climate on Earth.

CONCLUSIONS

PAR is an obvious determining factor influencing the photosynthesis of *R. apiculatta* seedlings under study. This determines the higher productivity of seedlings of artificial origin growing in open areas compared to seedlings of natural origin. In addition, as a result of the study, we found that the indicators characterizing the photosynthetic

features of seedlings in the pre-noon, noon and afternoon hours are fundamentally different. The best photosynthetic parameters were observed in seedlings in the pre-noon time. The main reason for this was the violation of the water balance of the leaves – the water consumed in the midday time, stored in the leaves during the night, was not fully restored later.

The optimum air temperature for photosynthesis in *R. apiculatta* seedlings is (35 ± 2) °C. With an increase in the concentration of CO_2 in the air, the intensity of *R. apiculatta* photosynthesis naturally increases. The increases of photosynthesis continue up to the concentration of CO_2 ~1000 µmol·mol^{-1} and then does not increase. We associate this circumstance with the maximum possibilities of the photosynthetic apparatus of the leaf of the studied plant.

Our developed mathematical models according to the Michaelis–Munten equation (1), Table 2, describe the dependence of photosynthesis on the PAR of the studied seedlings, as well as mathematical models describing the dependence of the intensity of photosynthesis on air temperature (2) and CO_2 concentration in the air (3), in the future, they will make it possible to move on to a general model describing the dependence of photosynthesis on three main environmental factors: PAR, temperature, and CO_2 concentration. And another important point of our research is the prospect of recalculating photosynthesis at the leaf level to the plantation level, which will ultimately allow us to quantify the CO_2 balance of the plantation. ■

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