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Growth Rates of *Lymantria dispar* Larvae and *Quercus robur* Seedlings at Elevated CO₂ Concentration and *Phytophthora plurivora* Infection

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Abstract: Interactions between plants, insects and pathogens are complex and not sufficiently understood in the context of climate change. In this study, the impact of a root pathogen on a leaf-eating insect hosted by a tree species at elevated CO_2 concentration is reported for the first time. The combined and isolated effects of CO₂ and infection by the root pathogen *Phytophthora plurivora* on English oak (Quercus robur) seedlings were used to assess growth rates of plants and of gypsy moth (Lymantria dispar) larvae. For this purpose, two Q. robur provenances (Belgrade and Sombor) were used. At ambient CO_2 concentration, the relative growth rates of larvae consuming leaves of plants infected by *P. plurivora* was higher than those consuming non-infected plants. However, at elevated CO₂ concentration (1000 ppm) higher relative growth rates were detected in the larvae consuming the leaves of non-infected plants. At ambient CO_2 concentration, lower growth rates were recorded in *L. dispar* larvae hosted in *Q. robur* from Belgrade in comparison to larvae hosted in Q. robur from Sombor. However, at elevated CO₂ concentration, similar growth rates irrespective of the provenance were observed. Defoliation by the gypsy moth did not influence the growth of plants while P. plurivora infection significantly reduced tree height in seedlings from Belgrade. The results confirm that a rise of CO₂ concentration in the atmosphere modifies the existing interactions between P. plurivora, Q. robur, and L. dispar. Moreover, the influence of the tree provenances on both herbivore and plant performance at elevated CO₂ concentrations suggests a potential for increasing forest resilience through breeding.

Keywords: *Lymantria dispar; Phytophthora plurivora; Quercus robur;* three-way interaction; climate change

1. Introduction

In recent decades, climate change has had a significant impact on all living organisms on Earth, including forests [1]. Climate change is mainly characterized by global warming and rising CO_2 levels. In turn, rising CO_2 may affect physiological processes of trees through the photosynthesis process [2]. Plants use sunlight and water to convert surplus CO_2 into oxygen and carbohydrates, which form plant tissues, thereby increasing overall forest productivity [3]. By duplicating CO_2 concentration



levels, plants increase photosynthetic and water use efficiency by 30-50% [4]. However, CO₂ levels have risen from 280 ppm in the pre-industrial age, to around 368 ppm in 2000. The most rapid increase of CO₂ concentration was recorded during the second half of the 20th century and the beginning of the 21st century, and according to the Intergovernmental Panel on Climate Change [5] the projected concentration of CO₂ in 2100 will range from 540 to 970 ppm. Previous studies on the effects of elevated CO₂ levels in the atmosphere on different forest tree species, and indirectly on their herbivores were conducted at CO₂ concentrations of 500–700 ppm, under the most probable scenarios of CO₂ increase by the end of the 21st century [6]. Pessimistic scenarios, which predict an increase in CO₂ levels to up to 900–1000 ppm in the atmosphere by the end of the 21st century [6], have not yet been tested.

Three-way interactions, including plants, pests and pathogens, depend mainly on the environmental conditions [7]. Expected climate change, especially extreme events such as severe drought or imbalanced precipitation, can influence plants indirectly by augmenting or diminishing the impact of pathogens and herbivores. Some pest populations have already responded to climate change by increasing their abundance and distribution [8–11]. Changes in insect phenology have also been observed [12,13]. Insect outbreaks are expected to last longer and be more frequent [14,15]. Elevated CO₂ levels can also have a significant impact on relations between hosts and pathogens [16–19], as well as between plants and herbivores [7,20–22]. Changes caused by elevated CO₂ concentration can influence insects directly, as evidenced by numerous studies [2,23–25]. Moreover, the effects of pathogens [26–28] or leaf eating insects [29] in plants is most often assessed individually and not taking into account their interaction, which can result in a decreased [30] or an increased synergistic activity [31] influencing plant health. Increased levels of tree damage after combined attack by several pathogens, compared to damage resulting from separate infections, have been previously recorded [32]. According to the recent review by Eberl et al. [33], few studies have assessed the effects of foliar pathogens and endophytes on the performance of herbivorous insects.

Oak stands are important components of temperate and subtropical ecosystems in the Northern Hemisphere. Moreover, natural or artificial regeneration of oaks is threatened by numerous factors [34] which include the performance of the oak species and the environmental conditions [34,35]. Oak seedlings are especially vulnerable during the first years after establishment or germination [36-38], when plant survival is very dependent to attacks by pests and pathogens [39–41]. English oak (Quercus robur L.), an ecologically and economically important species in temperate and sub-Mediterranean forests, is threatened by *Phytophthora* root rot [42–45]. *Phytophthora plurivora* has been reported by Jung and Burgess to cause significant damage to English oak [42,43]. This oomycete is considered one of the most aggressive pathogens threatening oak trees in different ecosystems, along with several different Phytophthora species such as P. quercina Jung [42,46] and P. cinnamomi Rands [47]. Moreover, according to Milanović et al. [48], English oak is a very suitable host species for the development of gypsy moth larvae (Lymantria dispar L.). The gypsy moth is the most dangerous herbivore in broadleaved forests in the northern hemisphere [49]. Moreover, gypsy moth is considered to be the main pest of cork oak (Quercus suber L.) in the Mediterranean basin [50,51]. Interactions between plants, pests, and pathogens are complex and poorly understood in the context of climate change [46,52,53]. Furthermore, very little is known about how elevated CO_2 affects pests and pathogens inhabiting the same host [54]. According to Juroszek et al. [55], there are no data available on the impact of a root pathogen on a leaf eating insect when the host plant is subjected to elevated CO₂ levels.

Due to the lack of data about the influence of elevated CO_2 concentration on insect-pathogen interactions mediated by a tree species, our study aimed to assess: (i) the impact of *P. plurivora* and CO_2 concentration on gypsy moth larvae, mediated by *Q. robur* seedlings; (ii) the effect of *L. dispar* and *P. plurivora* on the performance of *Q. robur* seedlings at ambient and elevated CO_2 concentrations; and (iii) the influence of plant provenance on the performance of both gypsy moth and *Q. robur* seedlings at ambient and elevated CO_2 concentrations; and (iii) the influence of plant provenance on the performance of both gypsy moth and *Q. robur* seedlings at ambient and elevated CO_2 levels.

2. Materials and Methods

2.1. Plant Material

One-year-old English oak seedlings were used. The acorns were collected from two locations in Serbia, one in the vicinity of Belgrade (44°43′55″ N, 20°09′22″ E) and the second in the vicinity of Sombor (45°50′03″ N, 19°01′17″ E). Forty eight plants per provenance were used. The seedlings were grown in a mixed substrate of peat (Pindstrup, Pindstrup Mosebrug A/S, Denmark) and perlite (Agroperlite, Termika, Serbia) at a ratio of 70:30 inside PVC bags (KESA, Pejkovac, Serbia) with a volume of 750 cm³. Bags were bored four times (holes of 5 mm diameter) to allow drainage. On 1 April 2018, at the beginning of the experiment, plants were approximately 12 cm tall. During the whole experiment, plants were grown at 23 ± 1 °C.

2.2. Experimental Design

Two different approaches were used (Figure 1). First, to assess the impact of *P. plurivora* and CO_2 concentration on gypsy moth larvae, mediated by *Q. robur* seedlings, plants were divided into four groups as seen in Figure 1a. Twelve plants each, half from Belgrade and half from Sombor were treated as (i) ambient CO_2 concentration + non-inoculated (control), (ii) ambient CO_2 concentration + inoculated with *P. plurivora*, (iii) elevated CO_2 concentration (1000 ppm) + non-inoculated, and (iv) elevated CO_2 concentration (1000 ppm) + inoculated with *P. plurivora*. One larva was weighed and used per seedling, 48 in total. Second, to assess the effect of *L. dispar* infestation and *P. plurivora* infection on the performance of *Q. robur* seedlings at ambient and elevated CO_2 concentrations, plants were divided into six groups (Figure 1b). Fourteen plants each, half from Belgrade and half from Sombor, were treated as (i) ambient CO_2 concentration + no additional treatment (control), (ii) elevated CO_2 concentration (1000 ppm) + no additional treatment (control), (ii) elevated CO_2 concentration (1000 ppm) + no additional treatment (control), (ii) + inoculated with *P. plurivora*, (iv) elevated CO_2 concentration (1000 ppm) + no additional treatment (control), (ii) + inoculated with *P. plurivora*, (iv) elevated CO_2 concentration (1000 ppm) + no additional treatment, (iii) ambient CO_2 concentration + inoculated with *P. plurivora*, (iv) elevated CO_2 concentration (1000 ppm) + no additional treatment, (iii) ambient CO_2 concentration + *L. dispar* infestation, and (vi) elevated CO_2 concentration (1000 ppm) + *L. dispar* infestation.





Phytophthora plurivora inoculation

Plant height

L. dispar infestation

Number of leaves

Plant height

Reisolation

Incubation under elevated CO_2 concentration was conducted in a CO_2 incubator (Reach-In CO_2 Incubator, 3950, Thermo Fisher Scientific, Marietta, OH, USA) and lasted two months and a half, i.e., starting 30 days before inoculation and ending 30 days after insect infestation (Figure 1c). Within each group of treatments, plants were arranged at random.

2.3. Soil Infestation Test

The inoculum was prepared according to Jung et al. [42], where 500 cm³ of fine vermiculite and 40 cm³ of millet (*Panicum miliaceum* L.) seeds were placed into one-liter Erlenmeyer flasks. A liquid medium was prepared with 200 mL/L of V8 juice (Biotta, Swiss), 3 g/L of CaCO₃ and 800 mL/L of distilled water [42]. Then, 350 mL of this liquid medium was poured into each flask. After mixing, the substrate was sterilized for 20 min at 120°C. A selected *P. plurivora* strain (GenBank access code KF234706), isolated from a declining *Q. robur* tree and stored at the Faculty of Forestry in Belgrade, was grown in V8-agar medium (200 mL/L of V8 juice (Biotta, Swiss), 20 g/L of agar (Torlak, Serbia), 3 g/L of CaCO3 and 800 mL/L of distilled water). Three to five days after incubation at 22–25 °C in the dark, 10 pieces of agar with mycelium of ca. 1×1 cm in size were excised with a scalpel from the growing edge of the colony and placed inside the Erlenmeyer flasks containing the sterilized substrate. Incubation lasted four weeks at 22–25 °C in the dark. Before inoculation, the inoculum was washed in sterile distilled water to remove sugar and minimize potential bacterial growth.

Inoculation was conducted on 1 May 2018 (Figure 1c) by using a standardized soil infestation method [42]. Approximately 20 cm³ of inoculum was placed into previously prepared holes, one per plant, and subsequently covered with peat. The inoculated plants were immediately flooded for 72 h, and then the water was removed.

At the end of the experiment, ten inoculated seedlings were selected at random and *P. plurivora* was successfully reisolated. For this purpose, necrotic and non-necrotic fine roots were abundantly washed with tap water, cut into 6–8 mm segments (15 segments per seedling), dried on filter paper then separately plated on PARPNH media [42]. Plates were incubated at 22 °C in the dark.

2.4. Infestation with Gypsy Moth Larvae

In autumn 2017, gypsy moth egg masses were collected from an oak forest in the vicinity of Bor, Serbia (44°03′14″ N, 22°04′ 26″ E). The gypsy moth population in this area was in a stable low density phase. Eggs were kept at 4 °C until spring 2018, where they were exposed at 25 ± 0.1 °C to induce hatching. After hatching, the larvae were fed on gypsy moth artificial diet [56] in Petri dishes (120 × 15 mm) at 23 ± 0.1 °C, relative humidity of 65 ± 1 % and under a light regime of 15:9 (day:night) until they molted to the fourth larval stage. When most of the larvae had molted, they starved for 24 h. Then larvae were weighed (initial weight) and the seedlings infested (Figure 1c). Sex ratios were assumed to be equal within groups of larvae used for each treatment. To check this, the initial weight of larvae was assessed individually, and each group of larvae had a similar weight according to Kolmogorov-Smirnov tests (p > 0.1). To prevent migration of the larvae, the seedlings were isolated inside transparent perforated PVC bags. One gypsy moth larva was used per seedling. After 72 h, the larvae were carefully removed from the seedlings and weighed again (final weight). Growth rates were obtained according to Waldbauer [57]:

$$GR = (final weight - initial weight)/T [mg/day]$$
 (1)

$$RGR = ((final weight - initial weight)/initial weight)/T [mg/mg/day] (2)$$

where GR is the growth rate, RGR is the relative growth rate, and T is the time lapse between initial and final weights in days (i.e., 3 days).

Plant height was measured in all seedlings before inoculation (1 May) and one and half month later (15 June). Growth rate of plants was obtained by the difference of these two measurements and dividing by 1.5 months. The number of leaves was counted in 15 June in all seedlings (Figure 1c).

2.5. Statistical Analysis

To assess the effect of *P. plurivora* and CO₂ concentration, mediated by oak seedlings, on the performance of *L. dispar* larvae, general linear mixed (GLM) models were used. The growth rate (GR) and the relative growth rate (RGR) were dependent variables, the CO₂ concentration (ambient vs. elevated) and *P. plurivora* infection (non-infected vs. infected) were fixed factors, the tree provenance (Belgrade vs. Sombor) was a random factor, and the weight of the larvae before infestation was a covariate. To assess the effect of CO₂ concentration, *L. dispar* infestation and *P. plurivora* infection on the performance of *Q. robur* seedlings, additional GLM were used. The number of leaves, final plant height, and plant growth rate were dependent variables, the CO₂ concentration (ambient vs. elevated) and biotic stressor (control vs. *L. dispar* infestation vs. *P. plurivora* infection) were fixed factors, the tree provenance (Belgrade vs. Sombor) was a random factor, and the initial plant height was a covariate. Normality and homoscedasticity of all the dependent variables were checked by Kolmogorov-Smirnoff and Bartlett's tests. Tukey HSD tests were used to test differences between average values.

To assess if relationships between growth rates of seedlings and initial plant height varied depending on whether trees were at ambient or elevated CO₂ concentrations, non-stressed, defoliated by *L. dispar*, or infested by *P. plurivora*, and from Belgrade or Sombor, homogeneity-of-slopes tests were performed. For this purpose, several general linear models included the 'plant growth rate' as the dependent variable, and the interactions between 'initial plant height' (continuous predictor) and 'CO₂ concentration', 'biotic stressor', or 'provenance' (categorical predictors) variables. All analyses were performed with STATISTICA v. 10 software.

3. Results

3.1. Lymantria dispar Larvae Performance at Elevated CO₂ Concentration Is Impaired Mostly When Trees Are Infected by Phytophthora plurivora

The results of the general linear mixed models showed a significant effect of CO_2 concentration on both growth rate (GR) and relative growth rate (RGR) parameters of the gypsy moth larvae (Table 1). On average, larvae consuming leaves from *Q. robur* plants exposed to ambient CO_2 concentration gained 27.5 mg per day, while larvae consuming leaves from plants exposed to elevated CO_2 concentration gained 3.6 mg per day. On average, the RGR of larvae consuming leaves from plants exposed to ambient and elevated CO_2 concentrations were 0.49 and 0.06 mg mg⁻¹ day⁻¹, respectively. Values of RG and RGR ranged from -5.2 to 41.4 mg day⁻¹ and from -0.14 to 0.86 mg mg⁻¹ day⁻¹, respectively.

Table 1. Results of the general linear mixed models to assess the influence of CO_2 concentrations (ambient vs. elevated), infection by *Phytophthora plurivora* (non-infected vs. infected), *Quercus robur* provenance (Belgrade vs. Sombor), and their interactions on the growth rate (mg day⁻¹) and relative growth rate (mg mg⁻¹ day⁻¹) of *Lymantria dispar* larvae. Fixed (F) and random (R) effects were included, and significant *p*-values are indicated in bold.

Source of Variation	Effect	Degrees of Freedom	Growth Rate		Relative Growth Rate	
			F-Ratio	<i>p</i> -Value	F-Ratio	<i>p</i> -Value
CO ₂ concentration (C)	F	1	169.7	<0.001	125.0	<0.001
Phytophthora plurivora infection (I)	F	1	20.6	0.136	2.9	0.343
Provenance (P)	R	1	0.2	0.745	0.4	0.667
$C \times I$	F	1	39.4	< 0.001	41.9	< 0.001
$C \times P$	R	1	18.9	0.006	7.6	0.040
$I \times P$	R	1	0.3	0.616	0.4	0.512
Initial weight of larvae (covariate)	F	1	0.4	0.518	2.7	0.102

At ambient CO₂ concentration, GR of larvae was similar irrespective of plant infection (Figure 2a). However, RGR of larvae was highest in *P. plurivora*-infected seedlings (Figure 2b). At elevated CO₂ concentration, GR and RGR of larvae consuming leaves from infected plants were significantly lower than those of larvae consuming leaves from non-infected plants (Figure 2). The strong and differential decrease of GR and RGR values when larvae fed on infected plant material at elevated CO_2 concentration explained the significant C × I interactions shown in Table 1 (p < 0.001).



Figure 2. Mean growth rates (**a**) and mean relative growth rates (**b**) of *Lymantria dispar* larvae fed on *Quercus robur* seedlings at ambient and elevated CO₂ concentrations, non-infected (control) and infected by *Phytophthora plurivora*. Vertical bars are standard errors and different letters indicate significant differences (p < 0.01) of mean values (n = 12) according to the Tukey HSD test.

GR and RGR of larvae were dependent on the *Q. robur* provenance (Figure 3). However, at elevated CO_2 concentrations, GR and RGR of larvae were similar for the Belgrade and Sombor provenances. Differences in larval performance depending on CO_2 concentrations and tree provenance explain the significant $C \times P$ interactions shown in Table 1 (p < 0.05).



Figure 3. Mean growth rates (**a**) and mean relative growth rates (**b**) of *Lymantria dispar* larvae fed on *Quercus robur* seedlings from Belgrade and Sombor provenances at ambient and elevated CO_2 concentrations. Vertical bars are standard errors and different letters indicate significant differences (*p* < 0.01) of mean values (*n* = 12) according to the Tukey HSD test.

3.2. Quercus robur Growth Is More Influenced by CO₂ Concentration and Tree Provenance Than by *Phytophthora plurivora Infection*

Elevated concentrations of CO₂ significantly influenced *Q. robur* performance in terms of number of leaves (Table 2) and plant height. In June 2018, the average number of leaves and mean height of seedlings exposed to ambient vs. elevated CO₂ concentrations were 5.1 vs. 7.9, and 17.1 vs. 25.0 cm, respectively. Untreated seedlings from Belgrade and Sombor were 15.9 ± 1.1 and 13.1 ± 1.9 cm tall before inoculations and 18.4 ± 2.2 and 17.0 ± 3.9 cm tall in mid-June (mean \pm standard deviation), coinciding with the end of the experiment. At the end of the experiment, neither *L. dispar* nor *P. plurivora* induced significant changes in the number of leaves (Table 2) but in the height of plants (results not shown).

Table 2. Results of the general linear mixed models to assess the influence of CO_2 concentrations (ambient vs. elevated), biotic stressor (control vs. infection by *Phytophthora plurivora* vs. defoliation by *Lymantria dispar*), acorn provenance (Belgrade vs. Sombor) and their interactions on the number of leaves and plant growth rate (cm month⁻¹) of *Quercus robur* seedlings. Fixed (F) and random (R) effects were included, and significant *p*-values are indicated in bold.

Source of Variation	Effect	Degrees of Freedom	Number of Leaves		Plant Growth Rate	
			F-Ratio	<i>p</i> -Value	F-Ratio	<i>p</i> -Value
CO_2 concentration (C)	F	1	156.5	<0.001	9.6	0.012
Biotic stressor (S)	F	1	4.8	0.173	0.1	0.887
Provenance (P)	R	1	1.6	0.724	1.4	0.376
$C \times S$	F	1	2.3	0.096	1.9	0.155
$C \times P$	R	1	0.0	0.861	12.8	< 0.001
$S \times P$	R	1	1.3	0.272	4.8	0.009
Initial plant height (covariate)	F	1	0.8	0.368	29.4	<0.001

During treatments, plant growth was significantly influenced by CO_2 exposure (Table 2), as the growth rates were 150.3 % higher in seedlings exposed to elevated CO_2 than in seedlings exposed to ambient CO_2 . At ambient CO_2 concentrations, both provenances grew similarly (Figure 4a). However, at elevated CO_2 exposure, plants from Belgrade grew relatively more in terms of height than those of Sombor (Figure 4a) (significant C × P interaction in Table 2). Plant growth rates also changed differently within each provenance in response to biotic stress (Figure 4b). In particular, only in plants from Belgrade, was height growth significantly reduced by *P. plurivora* (Figure 4b) (significant S × P interaction in Table 2).

Depending on the CO₂ concentration (Figure 5a) and the biotic stressor (Figure 5b), plant growth rates related differently to initial plant height, as indicated by the significant 'initial plant height' × 'CO₂ concentration' and 'initial plant height' × 'biotic stressor' interactions of the homogeneity-of-slopes tests (p < 0.001). At ambient CO₂ concentrations, taller plants grew more; however, at elevated concentrations, taller plants grew less (Figure 5a). When infested by *L. dispar*, taller plants plant grew more (i.e., recovered better), but when infected by *P. plurivora* taller plants grew less (i.e., were more affected) (Figure 5b). When analysing only defoliated seedlings, the influence of initial plant height on plant growth rates was highest for the plants from Belgrade (Figure 5c).



Figure 4. Growth rates of one-year-old *Quercus robur* seedlings from Belgrade and Sombor provenances at ambient and elevated CO₂ concentrations (**a**) and different biotic stress treatments (control vs. *Lymantria dispar* infestation vs. infection by *Phytophthora plurivora*) (**b**). Vertical bars are standard errors and different letters indicate significant differences (p < 0.01) of mean values (n = 14) according to the Tukey HSD test.



Figure 5. Relationships between plant growth rate and initial plant height of one-year-old *Quercus robur* seedlings at ambient (empty circles) and elevated (red circles) CO₂ concentrations (n = 24) (**a**), different biotic stress treatments (control, empty circles vs. *Lymantria dispar* infestation, orange circles vs. infection by *Phytophthora plurivora*, brown squares) (n = 28) (**b**), and provenances (Belgrade, black circles vs. Sombor, green circles) after *L. dispar* infestation (n = 14) (**c**). The *p* values refer to the 'initial plant height' × categorical variable interactions, and were obtained from homogeneity-of-slopes tests.

4. Discussion

In our study, gypsy moth larvae grew less when consuming leaves from plants exposed to elevated CO₂ concentrations than when consuming leaves from plants exposed to ambient CO₂ concentrations. Wang et al. [25] determined that the GR of gypsy moth larvae feeding on a mixed diet of Mongolian oak (*Quercus mongolica* Fisch.), poplar (*Populus pseudo-simonii* Kitag.), and birch (*Betula platyphylla* Sukaczev), was 44% lower at elevated CO₂ than at ambient CO₂ concentrations. Based on our results, elevated CO₂ concentration induced approximately 80% reduction in the GR of larvae. Hättenschwiler and Schafellner [24] investigated gypsy moth larvae on mature trees in natural stands under elevated CO₂ concentrations (530 ppm). Although results from experiments using seedlings and adult trees are not comparable, they found that the RGR of larvae consuming *Quercus petraea* (Matt.) Liebl. leaves

at elevated CO₂ was reduced by 30% compared to the RGR of larvae consuming leaves of trees at ambient CO₂ concentrations (370 ppm). In our study, RGR was reduced by circa 80% when gypsy moth larvae consumed *Q. robur* leaves grown at elevated CO₂ concentration. However, RGR of larvae consuming leaves of common hornbeam (*Carpinus betulus* L.) at elevated CO₂ levels increased by 29%, while those consuming leaves of common beech (*Fagus sylvatica* L.) did not show any increase [24]. In summary, this shows that the effects of elevated CO₂ on larval performance are tree specific. This was confirmed by Traw et al. [2], who monitored feeding by gypsy moth larvae on yellow birch (*Betula allegheniensis* Britt.) and gray birch (*Betula populifolia* Marsh.) at normal (350 ppm) and elevated (700 ppm) CO₂ levels. Their results indicated that elevated CO₂ concentration does not affect gypsy moth larvae feeding on the leaves of gray birch, while the mass of the females decreased when feeding on the leaves of yellow birch.

The nutritional value of plant tissues is expected to be altered by climate change. Going one step further, we obtained that an increased concentration of CO₂ clearly alters the growth rates of *Q. robur* and modifies the plants' behavior to L. dispar and P. plurivora. If the concentration of CO2 is doubled, the content of phenols in a plant increases, and simultaneously the thickness of the leaves is reduced [58,59]. Roth et al. [59] monitored the effect of elevated CO₂ on American aspen (*Populus tremuloides* Michx.) and sugar maple (Acer saccharum Marshall) on the feeding and development of the forest tent caterpillar (Malacosoma disstria Hübner), and reported that the responses of host trees to climate change follow different patterns. Watt et al. [60] found negligible changes in nitrogen and phenolic contents in European beech (Fagus sylvatica L.) and sycamore maple (Acer pseudoplatanus L.) leaves at elevated CO₂ concentration, and reported that the development of winter moths (Operophtera brumata L.) feeding on those leaves was not significantly affected [61]. In contrast, in loblolly pine (*Pinus taeda* L.) increased herbivory was observed in young needles grown at elevated CO₂ levels, compared to those grown at ambient conditions, and this was explained by changes in the carbon to nitrogen ratio [62]. The response of five species of sucking insects feeding on European beech and on sycamore maple grown at elevated concentrations of CO₂ was monitored in the United Kingdom, but no significant differences were found in the insects' performance compared to populations grown at ambient CO_2 levels [63,64]. In contrast, Awmack et al. [65] reported increased mortality and a reduced level of immunity in aphid populations at elevated CO₂ concentrations. In summary, the effect of elevated CO₂ is specific to each insect-plant system and can be positive, negative, or indifferent [2,24,25,66–68]. However, in the future any effect of CO_2 concentration on a tree-insect interaction should be considered. The significance of the gypsy moth as a pest is expected to increase in the future along with the distribution areas of the main host species due to climate change [69,70]. Predictions are mainly based on the effects expected from changes in temperature and precipitation values around Europe on host tree species and pests [8,11,71,72]. These predictions do not take into account that environmental changes, particularly elevated CO₂ levels, may alter interactions between trees and pests [73]. Our findings reveal the need to include altered interactions between trees and pests in prediction models.

Despite researchers paying increased attention to climate change, knowledge about the consequences of climate change on species interactions across trophic levels is insufficient [55,74]. Elevated CO_2 levels can alter plant defense processes and also pest and pathogen aggressiveness [54]. Elevated CO_2 in combination with plant infection can change plant metabolism substantially and thereby also plant growth and phenology. In turn, this can have significant consequences on the insect performance [75].

In our study, larvae consuming leaves of *P. plurivora* infected seedlings at ambient CO₂ concentration showed higher RGR compared to those consuming leaves of healthy seedlings. This is in concordance with Milanović et al. [76], who obtained similar results with red oak (*Quercus rubra* L.), where an increase of 25% of RGR in larvae consuming leaves of *P. plurivora*-infected trees under natural conditions was observed. According to Milanović et al. [76], the larvae consuming leaves from healthy trees needed more time to complete their fourth stage. Comparison of results should be done with caution because of differences in the tree species used and in the timing of the disease development.

10 of 14

In the present study, infestation started 15 days after inoculation, during the pathogenesis stage, and leaves were apparently not affected by the pathogen; in the previous study [76], leaf infestation occurred in a *P. plurivora*-symptomatic tree, infected for a long time, with a delayed leaf phenology in comparison to healthy trees. Additional experiments taking into account the period of infection occurring before insect infestation will provide interesting results.

Another aspect of our research was related to the effect of plant provenance on gypsy moth performance. According to Solla et al. [77] (also in [78]), variability of the chemical composition of plant tissues between and within populations of holm oak (*Quercus ilex* L.) determines the herbivore's impact [79] and consequently its performance. Significant differences in larval weight gain depending on holm oak provenances were observed [77]. Similarly, our results showed higher GR and RGR values when larvae fed on plants from Sombor in comparison to Belgrade. At elevated CO_2 concentration, this difference did not occur but plant growth rates were provenance-dependent. Irrespective of the CO_2 concentration, *Q. robur* seedlings from Belgrade were more susceptible to *P. plurivora* (in terms of growth impact) than seedlings from Sombor. Our results are relevant in respect of the influence of CO_2 concentrations on forests in the future and should encourage tree breeding with a focus on climate change.

This is the first report on the effects of ambient and elevated CO_2 levels on the growth rates of *Q. robur* seedlings. Broadmeadow and Jackson [80] determined that the leaf mass of *Q. petraea* was 39% greater if plants were at elevated CO_2 concentration. Research by Norby et al. [81] showed an 85% increase in the growth of white oak (*Quercus alba* L.) seedlings if plants were grown at elevated CO_2 concentration (690 ppm). In addition, a study by Johnson and Riegler [82] showed that elevated CO_2 concentration increased the height of *Eucalyptus globulus* Labill. plants compared to those grown at ambient CO_2 levels.

5. Conclusions

The pessimistic scenario that predicts an increase of CO_2 levels in the atmosphere of up to 900–1000 ppm by the end of the 21st century was used for the first time in this study to assess growth rates of plants and insects interacting each other. Elevated CO_2 had a negative effect on gypsy moth larval performance and a positive effect on plant height growth. At 1000 ppm CO_2 , *L. dispar* larvae consuming leaves of *P. plurivora*-infected *Q. robur* seedlings showed a significantly lower performance compared to those consuming the leaves of non-infected *Q. robur* seedlings. Several relationships between the root rot pathogen and the leaf-eating insect were dependent on the host plant, indicating that changing climatic conditions can easily influence three-way interactions. Particularly relevant was the influence of the plant provenance on both herbivore and tree performance, which suggests a potential for increasing forest resilience to climate change through breeding.

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