Jožica Gričar

Effect of Temperature on Radial Growth of Beech and Pine Saplings in the First and Second Year of the Experiment: a Comparison

Utjecaj temperature na radijalni rast mladica bukve i bora u prvoj i drugoj godini pokusa: usporedba

ABSTRACT • *The aim of the study was to monitor the seasonal dynamics of radial growth in one to two-year old saplings of European beech (<u>Fagus sylvatica</u> L.) and Scots pine (<u>Pinus sylvestris</u> L.) under three different temperature regimes: greenhouse (G), cooling chamber (C) and outdoors (K). The research was conducted over two growing seasons, 2010 and 2011, in order to compare the effect of different environmental conditions on the radial growth of saplings in the first and second year of the treatment. The results showed that the patterns of the radial growth of beech saplings exposed to different temperature conditions were similar, especially in 2010. An increase in radial diameter was observed generally one month later in 2010 than in 2011, probably due to transplant shock in 2010. In pines, on the other hand, such delays were not recorded; however, the growth ring patterns of saplings exposed to different treatments differed in the studied growing seasons. In both years, the wood increment of beech was narrowest in G and widest in C. In 2010, xylem growth rings of pines were widest in Gand and narrowest in C, whereas in 2011 they were widest in K. Two-year xylem increments of beech saplings were lowest in G, but similar in C and K. In the case of pine, the two-year xylem increment was widest in K and narrowest in C. Comparison of xylem growth ring widths of pine and beech saplings in 2010 and 2011 under different regimes showed that widths in 2010 were wider in pines under all three regimes, whereas in 2011 increments of pines were narrower than those of beech only in C. Our findings indicate different phenotypic plasticity of pine and beech saplings under different temperature regimes, in terms of radial growth. It is also clear that a continuation of such experiments over many growing seasons is necessary to capture the short- and long-term growth response of trees in changing environmental conditions.*

Key words: <u>*Fagus sylvatica*</u>, <u>*Pinus sylvestris*</u>, *xylem increment, juvenile period, temperature*

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SAŽETAK • *Cilj ovog istraživanja bio je praćenje sezonske dinamike radijalnog rasta jednogodišnjih mladica bukve (Fagus sylvatica L.) i bora (Pinus sylvestris L.) u tri različita temperaturna režima: stakleniku (G), rashladnoj komori (C) i na otvorenome (K). Istraživanje je provedeno tijekom vegetacije u 2010. i 2011. godini. Uspoređuje se dinamika radijalnog rasta u te dvije godine i raspravlja o utjecaju različitih ekoloških uvjeta na rast mladica u prvoj i drugoj godini eksperimenta. Rezultati su pokazali da su trendovi radijalnog rasta bukovih stabala izloženih različitim temperaturama međusobno slični, osobito u 2010. godini. Povećanje radijalnog promjera primijećeno je uglavnom mjesec dana kasnije u 2010. nego u 2011. godini, najvjerojatnije zbog transplantacijskog šoka u 2010. Za borove, nasuprot tome, takva kašnjenja nisu primijećena, ali postojale su razlike u dinamici radijalnog rasta mladica izloženih različitim tretmanima u dvije promatrane godine. U obje godine prirast drva bukve bio je najuži u G i najširi u C. Prirast drva bora bio je u 2010. najširi u G i najuži u C, a u 2011. godini prirast drva bora bio je najširi u K. Dvogodišnji prirast drva bukovih mladica bio je najuži u G, a međusobno sličan u C i K. Dvogodišnji prirast drva bora bio je najširi u K i najuži u C. Usporedba širina godova drva borovih i bukovih mladica u 2010. i 2011. godini pri različitim temperaturnim režimima pokazuje da su u 2010. u svim tretmanima godovi širi u bora, ali su u 2011. samo u C godovi bora bili uži nego u bukve. Rezultati upućuju na različitu fenotipsku plastičnost borovih i bukovih mladica u različitim temperaturnim režimima s obzirom na radijalni rast. Također se pokazalo da je potrebno nastaviti te eksperimente tijekom niza vegetacijskih razdoblja kako bi se otkrile kratkoročne i dugoročne reakcije rasta stabala u promjenjivim uvjetima okoliša.*

Ključne riječi: *Fagus sylvatica*, *Pinus sylvestris*, *prirast drva, juvenilno razdoblje, temperatura, svjetlosna mikroskopija*

1 INTRODUCTION
1. UVOD

With its 60 % forest cover, Slovenia is one of the most heavily wooded countries in Europe. The majority of Slovenian forests consist of beech, fir-beech and beech-oak stands (70 %), which are known for their relatively high productive capacity (Gozdnogospodarski *etc.*, 2006; Božič *et al*, 2010). Tree growth responds to short- and long-term environmental variations (e.g., Larcher, 2003). Due to global warming and climate change, growing conditions are expected to change in Slovenia in the coming decades and this will affect the biodiversity and production of its forest ecosystems (Kutnar *et al*, 2009). As a result of increasing climate extremes, which have a strong impact on forest stability and primary production, management risk is increasing due to lower prediction reliability, particularly in marginal and extreme forest ecosystems (e.g., Beniston and Diaz, 2004; Jump and Peñuelas, 2005; IPCC, 2007). At the moment, it is impossible to predict with certainty the long-term extent of the consequences, because the relationship of phenological events and tree productivity to climate is complex and not a simple matter of threshold values and monotonic responses (Jolly *et al*, 2005; Pichler and Oberhuber, 2007; Prislan *et al*, 2013). Changed climatic conditions will undoubtedly alter the onset, intensity and cessation of developmental processes in trees. However, species' response to climate change will be different, which will greatly affect their distribution and competition capacity in mixed stands and natural ecosystems, since tree migration will be influenced in the long-term. In the short-term, on the other hand, the physiological limits of tree growth at the warm and dry distribution limit are most important, since they determine species extirpation (i.e., local extinction) (Alpert and Simms, 2002; UN-ECE, 2008; Kramer *et al*, 2010). In order to adapt to the coming changes, it is necessary to understand the impact of climate change on forest ecosystems and to develop new approaches in forest and woodland management, based on the concept of sustainable management.

Empirical downscaling models developed to predict future climate change scenarios for Slovenia anticipate a 0.5-2.5 °C increase in temperatures in the period 2001-2030, 1-3.5 °C in the period 2031-2060 and 1.5-6.5 °C in the period 2061-2090. Model estimation in the case of precipitation is less reliable, although it is speculated that the amount of precipitation will decrease in summer (up to 12 %) and increase in winter (up to 20 %) (Bergant and Kajfež-Bogataj, 2004; Kajfež-Bogataj, 2007; De Luis *et al*, 2012). In Slovenia, plants are already responding to higher temperatures by their earlier flowering and leaf unfolding (Črepinšek *et al*, 2006; Čufar *et al*, 2012). Since the regional distribution of precipitation varies more than that of temperature, it is necessary to investigate independently the influence of the two climatic variables on the growth responses of trees. To do that, initial tests under stable environmental conditions are needed. Experimentally controlled tests on various tree species have shown that it is possible to influence cambial activity and cell differentiation, which is reflected in the anatomical structure of wood and phloem (e.g., Oribe *et al*, 2001; Gričar *et al*, 2006; Gričar *et al*, 2007; Begum *et al*, 2008; Begum *et al*, 2013; Gričar, 2013). Many such experiments have been performed on seedlings or saplings, allowing simulation of different growing conditions and evaluation of their impact on the growth and adaptivity of young trees (e.g., Rossi *et al*, 2009; De Luis *et al*, 2011). Determining how climate variability can modify both growth rates and the anatomical characteristics of formed tree-rings plays a decisive role in defining the hydraulic and mechanical properties of wood (De Luis *et al*, 2011; Froux *et al*, 2002; de Micco *et al*, 2008; Martinez-Meier *et al*, 2008; Hoffmann *et al*, 2011). The availability of this information may be critically important in evaluating the range of plasticity in species under different envi-

ronmental conditions as a first step in predicting their response to future climatic scenarios (De Luis *et al*, 2011).

European beech (*Fagus sylvatica*) is the dominant deciduous tree species in Slovenia, so any changes in the quantity and quality of beech wood caused by climate change will have a major economic influence (Kutnar *et al*, 2009; Kutnar and Božič, 2011). Scots pine (*Pinus sylvestris*) is also an economically important species, representing about 4.3 % of the Slovenian timber stock (Westergren *et al*, 2010). Due to its moderate site demands, Scots pine is an ideal species for artificial regeneration and it is able to survive in an environment not optimal for its growth and development (Mátyás *et al*, 2009). The aim of the current study was to monitor the seasonal dynamics of radial growth in one to two-year old saplings of European beech and Scots pine under three different temperature regimes: greenhouse (G), cooling chamber (C) and outdoors (K). The research was conducted over two growing seasons, 2010 and 2011, in order to compare the effect of different environmental conditions on the radial growth of saplings in the first and second year of the treatment.

2 MATERIAL AND METHODS
2. MATERIJAL I METODE

2.1 Tree material and growth conditions
2.1. Materijal mladica i uvjeti rasta

The tree material consisted of Scots pine (*Pinus sylvestris* L.) and European beech (*Fagus sylvatica* L.) saplings. For the experiment, 120 one- to two-year old pine and 90 one- to two-year old beech saplings were bought from Omorika tree nursery (Muta, Slovenia) in November 2010. The stem diameter and height of each sapling were measured immediately. The saplings were then planted in pots and 30 beech and 40 pine saplings were placed in each of the three different temperature regimes: greenhouse (G), cooling chamber (C) and outdoors (K) (Fig. 1).

Pine and beech saplings intended for controls (K) were placed outside; about 10 m from the greenhouse (G) and cooling chamber (C). Saplings were exposed to natural climatic conditions in Ljubljana in 2010 and 2011. A weather station, which recorded average, maximum and minimum daily air temperature (T) and precipitation, was installed in the immediate vicinity of the plants (Fig. 2a). Saplings in G were generally exposed to higher T than outdoors, although the oscillations in T were similar (Fig. 2b). However, minimum air T in G was much higher and always above 10 °C, while maximum T often exceeded 30 °C. Saplings in C were exposed to lower and more constant T than with G and K, with minimum air T of around 15 °C, maximum T around 20 °C and average T around 17 °C (Fig. 2c).

Water supply was not a limiting factor under any regime. Watering (frequency and amount) in G and C was performed according to the substrate humidity, which was automatically measured by Decagon EC-5 probes. The humidity of the substrate was maintained above 15 %. The relative air humidity was also constantly monitored and kept between 70 % and 90 %.

2.2 Monitoring radial growth of saplings and histometric analysis
2.2. Praćenje radijalnog rasta mladica i histometričke analize

We monitored the seasonal dynamics of the radial growth of beech and pine saplings in the growing seasons of 2010 and 2011. For this purpose, for better accuracy of data, we marked all sapling stems to ensure that the measurement was always taken at the same point of a stem base. Measurements were taken at two-week intervals with a vernier caliper providing a precision to 0.010 mm. At the end of the experiment, i.e., in winter 2011, 10 beech and 10 pine samplings from each regime were taken from the pots and prepared for further analysis.

For histometric analysis of wood increments at the stem base, about 2 cm long pieces of stems were extracted from each sapling and immediately placed in FEA fixative solution (a mixture of formalin, 50 % ethanol and acetic acid). After one week, the samples were dehydrated in an alcohol series (30 %, 50 % and 70 %) and permanently stored in 70 % ethanol. Using a G.S.L. 1 (© Gärtner and Schweingruber, design and production: Lucchinetti, Schenkung Dapples, Zurich, Switzerland) sliding microtome and disposable blades for universal knives, 20-25 µm thick stem cross-sections were prepared, stained in an aqueous mixture of safranin (Merck, Darmstadt, Germany) (0.04 %) and astra blue (Sigma-Aldrich, Steinheim, Germany) (0.15 %) dyes (Werfvan der *et al*, 2007) and finally mounted in Euparal (Waldeck, Münster, Germany) to produce permanent sections. All necessary observations and measurements of tissues were performed with an im-

Figure 1 Saplings of beech and pine in: a) greenhouse; b) cooling chamber and c) outdoors
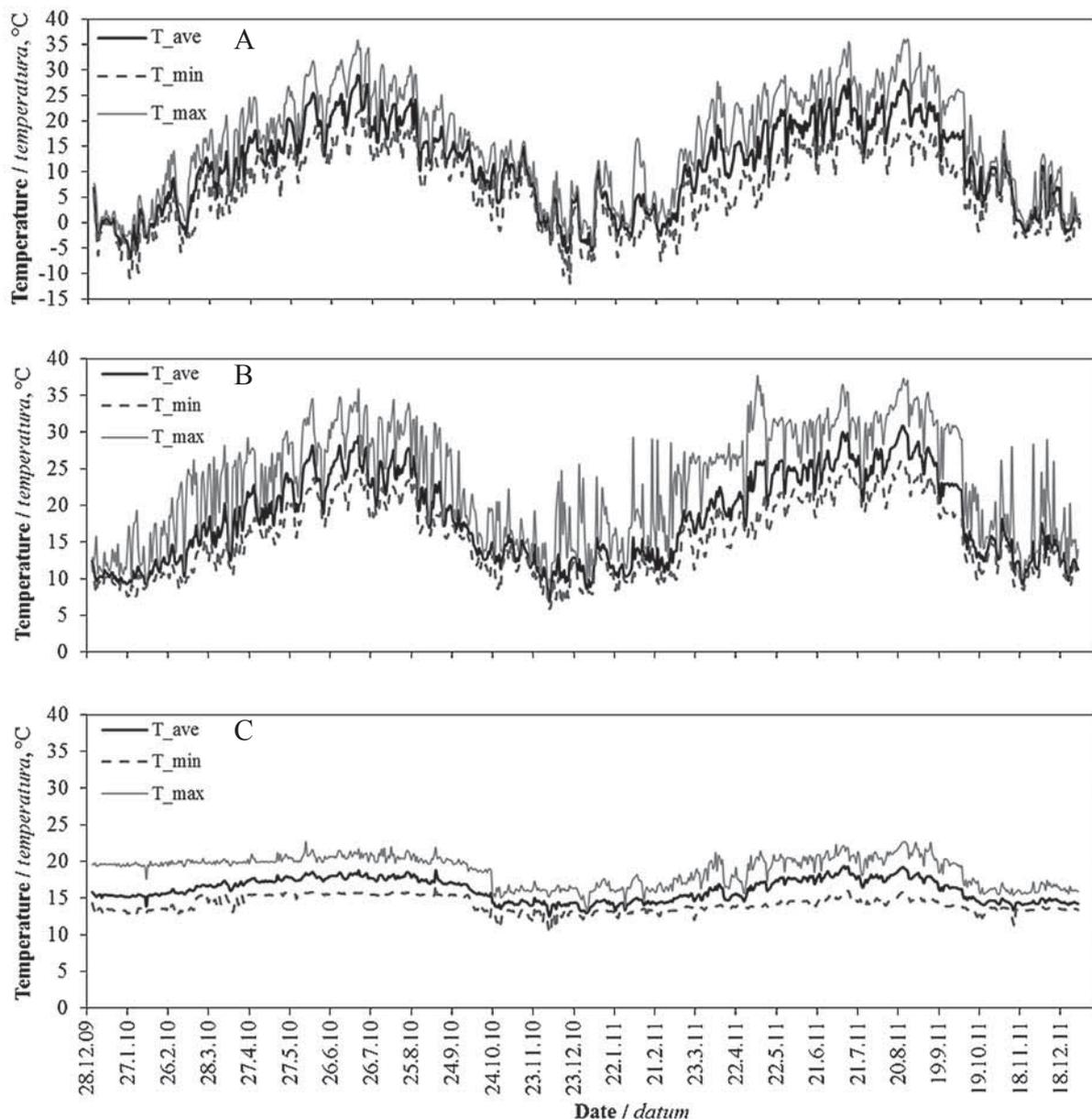**Slika 1.** Mladice bukve i bora: a) u stakleniku, b) u rashladnoj komori i c) na otvorenom prostoru

Figure 2 Average, maximum and minimum daily air temperatures during the experiments: outdoors (A), in the greenhouse (B) and in the cooling chamber (C)
Slika 2. Prosječne, maksimalne i minimalne dnevne temperature za vrijeme pokusa na otvorenom prostoru (A), u stakleniku (B) i u rashladnoj komori (C)

age analysis system consisting of an Olympus BX51 (Tokyo, Japan) light microscope, a PIXElink, PL-A66Z digital camera and NIS-Elements Basic Research V.2.3 image analysis program (Tokyo, Japan). We measured the widths of xylem increments for 2010 and 2011. Measurements were taken at four locations on the cross-sections and then averaged.

Data processing, graph preparation and statistical analysis were done in Microsoft Excel and Statgraphics programs. The one-way ANOVA test was used to compare growth characteristics of pine and beech saplings among regimes. In addition, Fisher's least significant difference (LSD) procedure was used for pairwise comparisons of treatment groups to discriminate among the means. Leven's test was used to assess the equality of variances in the samples. Student's t-test

was used to compare the widths of xylem increments for 2010 and 2011 under a specific regime.

3 RESULTS
3. REZULTATI

The seasonal dynamics of radial growth of beech saplings were fairly similar in 2010 and 2011 under specific regimes, while they differed greatly with pine (Fig. 3, 4). In general, an increase in radial diameter was detected in beech at the beginning of May in 2010 under all regimes. Two weeks later, they had already reached maximum weekly growth, which slowly started to decline in mid-June (Fig. 3a). Beech saplings in C and G had a two-week radial diameter increase of more than 0.3 mm during this period, while K had an in-
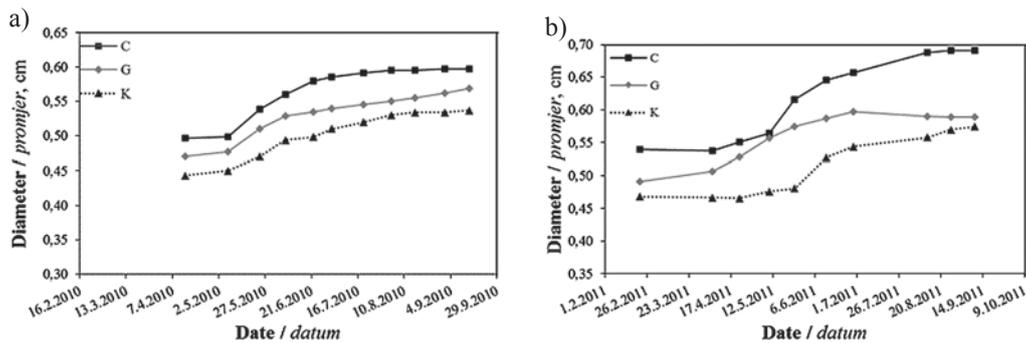
F. sylvatica

a)

b)

Figure 3 Seasonal dynamics of radial growth of beech saplings in 2010 (a) and 2011 (b) growing seasons.
C = cooling chamber, G = greenhouse, K = outdoors
Slika 3. Sezonska dinamika radijalnog rasta bukovih mladica tijekom vegetacije u 2010. godini (a) i u
2011. godini (b), C – rashladna komora, G – staklenik, K – otvoreni prostor

crease of 0.25 mm. Radial growth stopped under all three regimes at the same time, at the end of August. In 2011, an increase in radial diameter of beech saplings was observed in mid-March in G, in the first half of April in C and in the second half of April in K (Fig. 3b). The most intense period of radial growth occurred in April in G, in the middle of May in C and at the end of May/beginning of June with the saplings exposed to natural conditions (K). In all three cases, the period of maximum radial growth occurred about one month after the onset of radial growth. During the most intense period of radial growth, the highest values were recorded in saplings in C (0.5 mm) and the lowest in those in G (0.28 mm). Radial growth of G saplings finished earliest (at the beginning of July), and at the end of August in C and K.

With pine saplings, radial growth started earliest in G (mid-April) in both years, followed by C saplings (end of April) and lastly those outdoors (K), at the beginning of May (Fig. 4). The peak of radial growth in 2010 was first reached in K (end of May/beginning of June) and only at the beginning of July in G and C. The two-week radial growth in 2010 was very low and did not exceed 0.4 mm. Radial growth stopped first in C at the end of July and a month later also in the other two regimes. In 2011, the seasonal dynamics of radial growth of pine saplings was different (Fig. 4b). The

peak of radial growth occurred in all three regimes at the same time, at the end of June/beginning of July. However, the two-week increment was widest in K pines (up to 1 mm), whereas in G and C it was around 0.25 mm. Radial growth ceased at the end of August in C and K and in the middle of September in G.

With beech, wood increment was narrowest in both years in G (282.01 ± 94.52 μm in 2010; 371.40 ± 242.31 μm in 2011) and widest in C (380.89 ± 134.98 μm in 2010; 755.00 ± 182.93 μm in 2011) (Fig. 5). Xylem increments in 2010 were in general very narrow (less than 400 μm) under all three regimes. In 2011, the annual increments in C and K substantially increased (by about 100 %), while in G, increments increased by about a quarter (Fig. 7, Table 1).

In 2010, xylem growth rings of pines were widest in G (912.45 ± 206.69 μm) and narrowest in C (636.09 ± 136.21 μm) (Fig. 6). In 2011, the radial growth patterns of pine saplings exposed to given environmental conditions changed. With the exception of K pines, increments were smaller than in 2010 (Fig. 6b). Xylem widths in 2011 were double in K compared to the other two regimes (K =1242.63 ± 329.92 μm; G = 586.89 ± 329.92 μm; C = 572.74 ± 148.95 μm). The increment widths in G were significantly reduced in 2011, increased in K and only slightly decreased in C (Table 1). The xylem rings were thus narrowest in C in both years (Fig. 7).
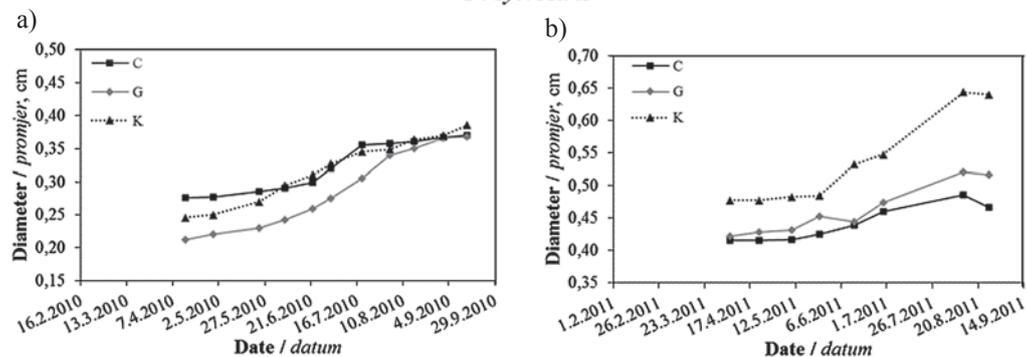
P. sylvestris

a)

b)

Figure 4 Seasonal dynamics of radial growth of pine saplings in 2010 (a) and 2011 (b) growing seasons.
C = cooling chamber, G = greenhouse, K = outdoors
Slika 4. Sezonska dinamika radijalnog rasta borovih mladica tijekom vegetacije u 2010. godini (a) i 2011.
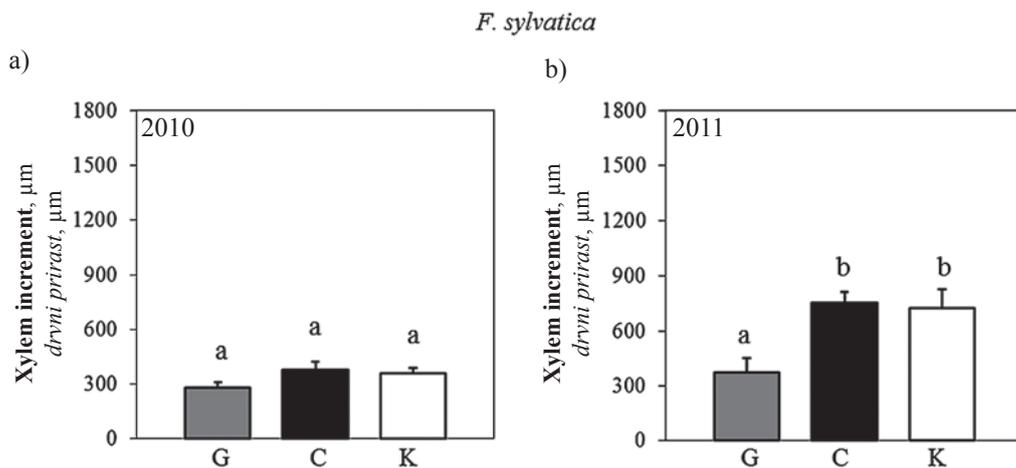godini (b); C – rashladna komora, G – staklenik, K – otvoreni prostor

F. sylvatica

a)

b)

Figure 5 Xylem increment of beech saplings under different regimes during the growing seasons 2010 ($F = 1.89$, $p = 0.1725$) (a) and 2011($F = 7.86$, $p = 0.0025$) (b) (mean ± SE, $n = 10$ independent saplings). Different letters indicate statistically significant differences between regimes (One-way ANOVA). C = cooling chamber, G = greenhouse, K = outdoors
Slika 5. Prirast drva bukovih mladica u različitim režimima tijekom vegetacije u 2010. godini. ($F = 1,89$, $p = 0,1725$) (a) i u 2011. godini (b) ($F = 7,86$, $p = 0,0025$) (srednja vrijednost ± SE, $n = 10$ neovisnih mladica); različita slova označavaju statistički značajne razlike među režimima (One-way ANOVA); C – rashladna komora, G – staklenik, K – otvoreni prostor

The two-year xylem increment of beech saplings was lowest in G (653.41 ± 274.10 μm), but similar in C (1102.73 ± 238.17 μm) and K (1081.12 ± 323.42 μm) (Fig. 8a). Xylem growth rings contributed almost equally to the two-year wood increment in G in 2010, whereas in C and K only about a third (Fig. 8b). In the case of pine, the two-year xylem increment was widest in K (1951.53 ± 414.04 μm) and narrowest in C (1208.83 ± 246.83 μm) (Fig. 9a). Xylem growth rings contributed 60 % to the two-year increment in G in 2010, 50 % in C and 34 % in K (Fig. 9b). Comparison of xylem growth ring widths of pine and beech saplings under different regimes in 2010 and 2011 showed that xylem ring widths of 2010 were wider in pines under all three regimes; even three times under the K regime, while in 2011 only increment widths of pines in C were narrower than those of beech (Fig. 4, 5, Table 1).

Table 1 Comparison of xylem ring widths in 2010 and 2011 in pine and beech saplings under different regimes (Student's t-test)
Tablica 1. Usporedba širina godova borovih i bukovih mladica u 2010. i 2011. godini u različitim režimima (Student›s t-test)

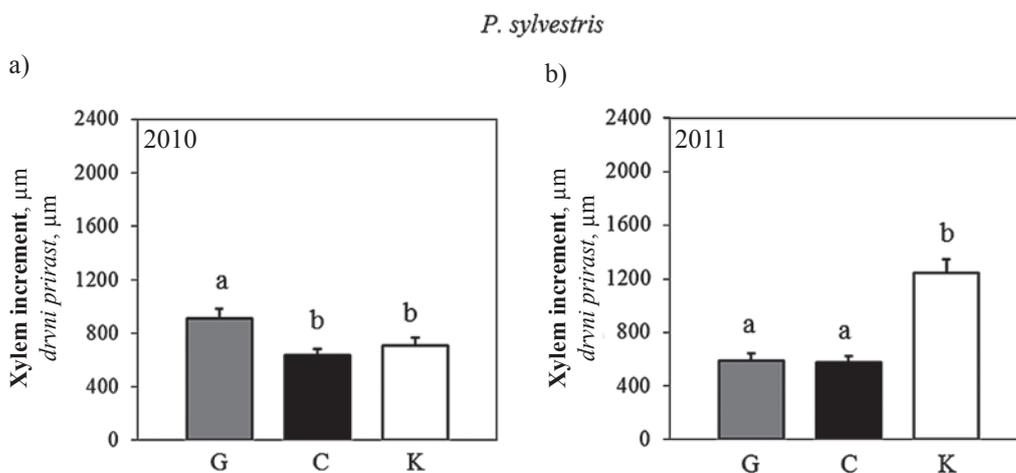|	*P. sylvestris*	*F. sylvatica*
Greenhouse /*Staklenik*	$t = 3.78817$ $p = 0.00147$	$t = -1.03099$ $p = 0.317877$
Cooling chamber *Rashladna komora*	$t = 0.992511$ $p = 0.334101$	$t = -5.02165$ $p = 0.000105$
Control / *Kontrola*	$t = -4.45788$ $p = 0.000304$	$t = -4.03033$ $p = 0.00109$

P. sylvestris

a)

b)

Figure 6 Xylem increment of pine saplings under different regimes during the growing seasons 2010 ($F = 6.09$, $p = 0.0068$) (a) and 2011 ($F = 27.62$, $p = 0.0000$) (b) (mean ± SE, $n = 10$ independent saplings). Different letters indicate statistically significant differences between regimes (One-way ANOVA). C = cooling chamber, G = greenhouse, K = outdoors
Slika 6. Prirast drva borovih mladica u različitim režimima tijekom vegetacije u 2010. godini (a) ($F = 6,09$, $p = 0,0068$) i u 2011. godini (b) ($F = 27,62$, $p = 0,0000$) (srednja vrijednost ± SE, $n = 10$ neovisne mladice); različita slova označavaju statistički značajne razlike među režimima (One-way ANOVA); C – rashladna komora, G – staklenik, K – otvoreni prostor
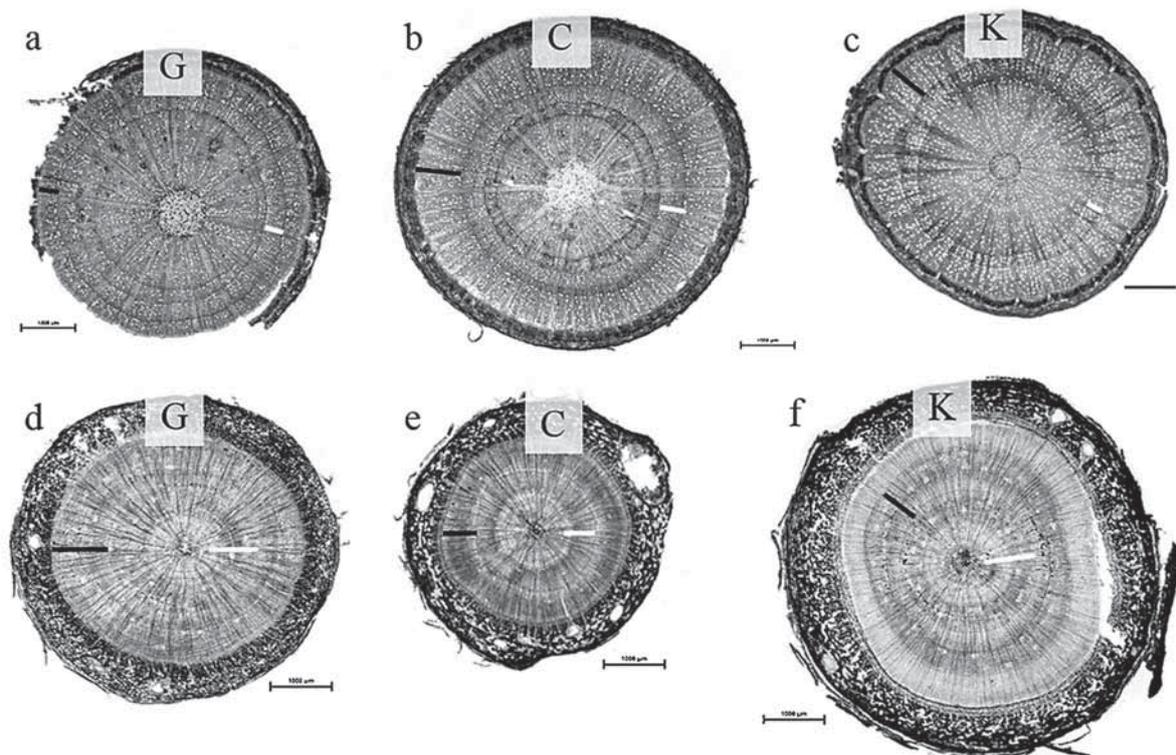
Figure 7 Transverse sections of typical beech (a-c) and pine (d-f) saplings in: greenhouse (a-beech, d-pine), cooling chamber (b-beech, e-pine) and outside (c-beech, f-pine). White line indicates xylem increment in 2010 and black line xylem increment in 2011. C = cooling chamber, G = greenhouse, K = outdoors. Bars – 1000 μm
Slika 7. Poprečni presjeci bukovih i borovih mladica u stakleniku (a – bukva, d – bor), rashladnoj komori (b – bukva, e – bor) i na otvorenom prostoru (c – bukva, f – bor); bijela crta pokazuje drvni prirast u 2010. godini, a crna u 2011. godini (C – rashladna komora, G – staklenik, K – otvoreni prostor); trake – 1000 μm
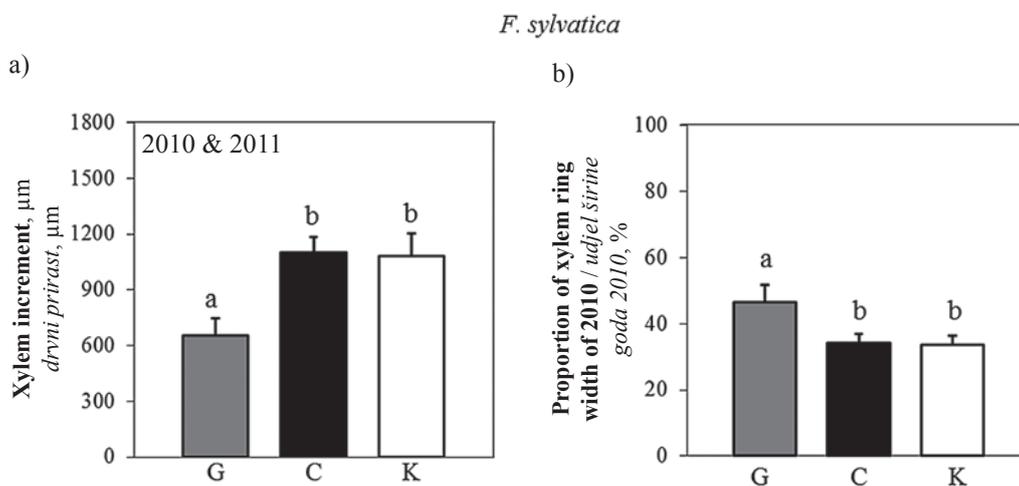

Figure 8 Two-year xylem increment of beech saplings under different regimes ($F = 7.30$, $p = 0.0037$) (a) and proportion of xylem ring width from 2010 ($F = 3.52$, $p = 0.0472$) (b) (mean ± SE, $n = 10$ independent saplings). Different letters indicate statistically significant differences between regimes (One-way ANOVA). C = cooling chamber, G = greenhouse, K = outdoors
Slika 8. Dvogodišnji prirast drva borovih mladica u različitim režimima (a) ($F = 7,30$, $p = 0,0037$) i udjel širine goda 2010. godine (b) ($F = 3,52$, $p = 0,0472$) (srednja vrijednost ± SE, $n = 10$ neovisnih mladica); različita slova označavaju statistički značajne razlike među režimima (One-way ANOVA); C – rashladna komora, G – staklenik, K – otvoreni prostor

4 DISCUSSION AND CONCLUSIONS
4. RASPRAVA I ZAKLJUČAK

The pattern of radial growth of beech saplings exposed to different temperature conditions was similar, especially in 2010. An increase in radial diameter was generally observed one month later in 2010 than in 2011, probably due to transplant shock in 2010. In pines, on the other hand, such delays were not recorded. However, the growth ring patterns of beech exposed to different treatments differed in the studied growing seasons. The wood increment of beech was narrowest in G and widest in C in both years. In 2010, xylem growth rings of pines were widest in G and narrowest in C, whereas in 2011 they were widest in K. Two-year xylem increments of beech saplings were lowest in G, but similar in C and K.
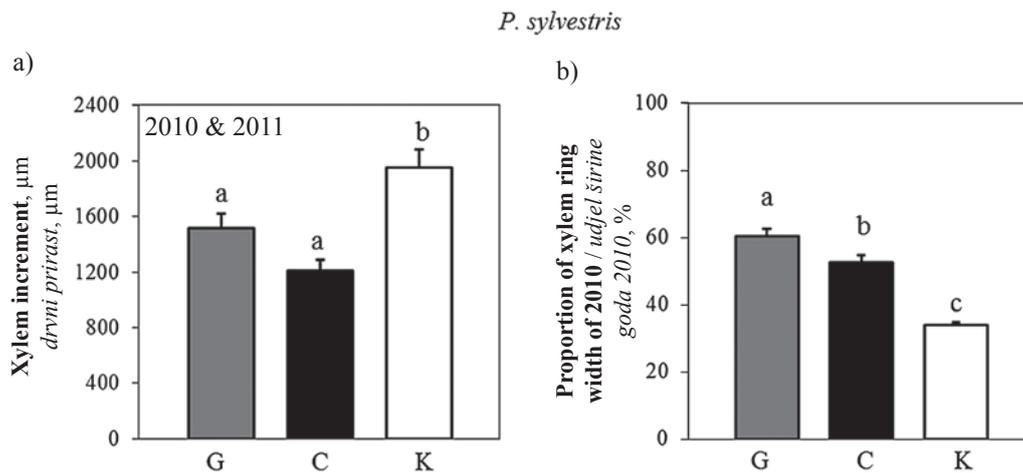
P. sylvestris

a)

b)

Figure 9 Two-year xylem increment of pine saplings under different regimes (*F* = 12.63, *p* = 0.0001) (a) and proportion of xylem ring width of 2010 (*F* = 55.58, *p* = 0.0000) (b) (mean ± SE, *n* = 10 independent saplings). Different letters indicate statistically significant differences between regimes (One-way ANOVA). C = cooling chamber, G = greenhouse, K = outdoors
Slika 9. Dvogodišnji prirast drva borovih mladica u različitim režimima (a) (*F* = 12,63, *p* = 0,0001) i udjel širine goda 2010. godini (b) (*F* = 55,58, *p* = 0,0000) (srednja vrijednost ± SE, *n* = 10 neovisnih mladica); različita slova označavaju statistički značajne razlike među režimima (One-way ANOVA); C – rashladna komora, G – staklenik, K – otvoreni prostor

In the case of pine, the two-year xylem increment was widest in K and narrowest in C. Comparison of xylem growth ring widths of pine and beech saplings in 2010 and 2011 under different regimes showed that widths in 2010 were wider in pines under all three regimes, whereas in 2011 increments of pines were narrower than those of beech only in C.

The influence of different environmental conditions on the radial growth of saplings was more distinct in pine than in beech. A cool environment thus limited the radial growth of pine, which is in line with its pioneer character. Lower temperatures limit the radial growth of pines, giving a shorter growing season, reflected in narrower xylem ring widths. Many pines respond to temperatures mainly by an alteration in radial growth dynamics, which emphasizes the importance of phenotypic plasticity. The functional phenological plasticity of wood formation has been commonly described as an important adaptation of trees to new, changed climatic conditions (De Luis *et al*, 2011). Tree species growing in different habitats are able to adapt to environmental conditions in terms of the beginning, end and dynamics of cambial activity, which reflect their flexibility and plasticity in terms of radial growth (De Luis *et al*, 2013). However, tree populations and species differ greatly in their phenotypic plasticity (Alpert and Simms, 2002).

Bioclimatic envelopes (i.e., conditions, under which species grow well) are expected to shift northwards and higher up in elevation. The range of Norway spruce and Scots pine might retreat from the south and west, while beech and other temperate broadleaved species might spread to the north. Conifer forests subjected to continuing disturbance show a more rapid shift to dominance of beech and other temperate broadleaves. Although beech adapts well to drought, the future dynamics of beech forest remains uncertain due to global warming. Beech is projected to face severe problems in regions in which temperatures are expected to rise and could be replaced by oaks due to the latter's lower sensitivity to water stress (European Forest Institute *et al*, 2008). Several dendroecological studies have emphasized the sensitivity of beech to increased temperature and drought, with growth declining with increasing temperature, but also indicating that this decline is not a direct response to temperature but to drought because of less rainfall (Cescatti and Piutti, 1998; Dittmar *et al*, 2003; Lebourgois *et al*, 2005). The relationship of phenological events and tree productivity to climate is complex and not a simple matter of threshold values and monotonic responses. Although phenology is related to some extent to temperature, phenological phases have been associated with different temperatures at different sites favourable for the growth of adult beech. The onset of cambial cell division has been associated not just with threshold temperature but with an extended period of preconditioning, which varied with site conditions (Prislan *et al*, 2013). Moreover, the difference in phenological patterns may be due to high intra-specific plasticity (Camarero *et al*, 2010). It is therefore impossible to assess the relative contribution of genetic determination, epigenetic regulation and somatic adaptation to growth and developmental processes.

However, it has been demonstrated that radial growth is an age-dependent process and that it differs in juvenile and adult trees in terms of dynamics and timing of wood production (Rossi *et al*, 2008; Rossi *et al*, 2011; Li *et al*, 2013). Cambial activity during spring and early summer may be critically important to the survival of saplings, especially in the first part of the growing season after planting, when the root system has not yet developed and newly formed wood is crucial for providing enough conductive tissue for water transport and storage of photosynthates (De Luis *et al*, 2011). The response of an individual tree species will thus also depend on tree age, among other things, and it will not therefore be the same for juvenile and mature trees, indicating that ex-

perimental results obtained on saplings cannot be simply transferred to adult trees and *vice versa*.

In terms of wood formation, any change in morphological characteristics of cells probably modifies the hydraulic and mechanical properties of wood and thus affects the survival and efficiency of the living tree (e.g., Rao *et al*, 1997). In this respect, saplings may be especially vulnerable to predicted climate changes, since their ability to survive may be restricted. This could affect both natural regeneration and the success of reforestation, leading to a change in the distribution of the species in the future (De Luis *et al*, 2011).

Studies of the seasonal dynamics of radial growth of trees and structure of xylem and phloem can be helpful in understanding the mechanism of these processes and their dependence on environmental conditions. Our findings imply different phenotypic plasticity of pine than of beech saplings in terms of radial growth. Nevertheless, the two-year experiment clearly demonstrates that a continuation of such observations over several growing seasons is necessary to capture the short- and long-term response of tree growth under changing environmental conditions.

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