

BIOMASS ALLOCATION SHIFTS OF *FAGUS SYLVATICA* L. AND *PINUS SYLVESTRIS* L. SEEDLINGS IN RESPONSE TO TEMPERATURE

PRERAZPOREDITEV BIOMASE PRI SADIKAH *FAGUS SYLVATICA* L. IN *PINUS SYLVESTRIS* L. KOT ODZIV NA TEMPERATURO

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ABSTRACT

Biomass allocation shifts of *Fagus sylvatica* L. and *Pinus sylvestris* L. seedlings in response to temperature

Since the impact of temperature on seedling growth and biomass allocation of different tree species remains relatively unknown, the influence of different temperature conditions on stem diameter (xylem and bark), stem and root extensions, as well as below- and aboveground woody biomass, in three-year old European beech (*Fagus sylvatica* L.) and Scots pine (*Pinus sylvestris* L.) seedlings in 2010–2011 were studied. One-year-old seedlings were grown outdoors (mean temperature during the growing season = 17–19°C), in the greenhouse (mean temperature during the growing season = 22–24°C) and climatized room (mean temperature during the growing season = 15–17°C) for two years. In terms of radial increment, xylem increments were narrowest in the case of increased temperature for beech and decreased temperature for pine. There was no difference in the thickness of the bark in beech seedlings exposed to different temperature conditions whereas in pine, the bark proportion was highest in control seedlings with the widest diameters. The periderm thickness was comparable in seedlings exposed to different temperatures and represented 10–14 % and 15 % of the bark tissue in pine and beech, respectively. Comparison of the total radial increments of seedlings of the two species under different TEMPERATURE conditions showed that they were wider in pine in all three regimes. Increment of the main root was considerably higher in both species and represented about 90 % of the total length increment in beech and 74–87 % in pine. In addition, woody biomass was substantially higher aboveground in both tree species (by about 70–80 %). With beech, above- and belowground biomass was reduced in the case of elevated temperature, with the smallest share of roots. In pine, lower temperature diminished amount of biomass and caused its greatest allocation to belowground, which represented almost half of the total biomass accumulation. The short-term

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Prerazporeditev biomase pri sadikah *Fagus sylvatica* L. in *Pinus sylvestris* L. kot odziv na temperaturo

Malo je znanega o vplivu temperature na rast sadik in alokacijo biomase pri različnih drevesnih vrstah, zato smo raziskali vpliv različnih temperaturnih razmer na debelinsko rast debla (tj. les in skorja), vršno rast debla in korenin ter na podzemno in nadzemno lesno biomaso pri triletnih sadikah navadne bukve (*Fagus sylvatica* L.) in rdečega bora (*Pinus sylvestris* L.) v obdobju 2010–2011. V ta namen so bile enoletne sadike dve leti izpostavljene trem različnim temperaturnim režimom: na prostem (povprečna temperatura v času rastle sezone = 17–19°C), v rastlinjaku (povprečna temperatura v času rastle sezone = 22–24°C) in v hladilni komori (povprečna temperatura v času rastle sezone = 15–17°C). Lesni prirastki so bili najmanjši v primeru povišane temperature pri bukvi, pri boru pa pri zmanjšani temperaturi. Pri sadikah bukve izpostavljenih različnim temperaturnim razmeram ni bilo razlik v širini skorje, medtem ko je bil delež skorje pri boru največji pri kontrolnih sadikah, ki so imele tudi najširše premere. Debelina periderma je bila primerljiva pri sadikah izpostavljenih različnim temperaturam in je predstavljala 10–14 % tkiva skorje pri bukvi in 15 % tkiva pri boru. Debelinski prirastki so bili v vseh režimih širši pri boru kot pri bukvi. Prirastek glavne korenine je bil znatno večji kot prirastek debla pri obeh vrstah in je predstavljal približno 90 % celotne vršne rasti pri bukvi in 74–87 % pri boru. Nadzemna lesna biomasa je bila pri obeh drevesnih vrstah bistveno večja (za približno 70–80 %) v primerjavi s podzemno biomaso. Pri bukvi je bila celotna biomasa zmanjšana pri povišani temperaturi z najmanjšim deležem korenin. Pri boru je bila najmanjša količina biomase pri znižani temperaturi, ko smo zabeležili največjo prerazporeditev biomase v podzemne dele, ki so predstavljali skoraj polovico celotne lesne biomase. Kratkoročni poskusi kažejo, da okoljske razmere za optimalno rast proučevanih drevesnih vrst niso primerljive, kar se odraža v različnih pr-

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treatments clearly show that biomass allocation shifts of pine and beech in response to temperature seem to be a species-specific. The observed differences could be viewed as a plastic adjustment to environmental heterogeneity.

Key words: European beech, Scots pine, radial increment, stem, root, bark, xylem

erazporeditvah biomase pri boru in bukvi pri različnih temperaturnih režimih.

Ključne besede: navadna bukev, rdeči bor, debelinski prirastek, deblo, korenina, skorja, les

1 INTRODUCTION

Anticipated climate change associated with more frequent/severe extreme events are expected to alter the composition, structure and distribution of forests in many regions (SCHAR et al. 2004, IPCC 2014). This could result in increased tree mortality due to climate-induced physiological stress and other climate-mediated processes, such as insect outbreaks (ALLEN et al. 2010). Trees' ability to withstand such environmental changes also depends on their phenotypic plasticity, genetic diversity within and between populations, and gene flow (KRAMER et al. 2010). Phenotypic plasticity of ecologically important traits in response to different environments is thus a fundamental property of organisms, enabling them to cope with adverse environmental conditions (SULTAN 2000, MARTINEZ-MEIER et al. 2008). How trees may respond to these changes is particularly relevant for ecologically and economically important European tree species, such as European beech (*Fagus sylvatica* L.) and Scots pine (*Pinus sylvestris* L.), since future climate conditions will clearly influence their growth and competitive performance and consequently silvicultural practices (PRETZSCH et al. 2015).

European beech is a widespread species of European temperate forests with high competitive ability: as a juvenile, it is shade-tolerant and grows fast, while as a mature tree it forms a dense canopy outshading most other trees (VON WUEHLISCH 2008). In the past, the areal extension of beech forests decreased considerably due to human activity (DIEKMANN et al. 1999). However, as nature-based forestry has become widely accepted, an expansion of beech has been reported for most Central European countries, including Slovenia, which will have an impact on forest management and on wood processing technology (POLJANEC et al. 2010). Beech is known to be a drought-susceptible species (e.g. LEUSCHNER et al. 2001, FISCHER & NEUWIRTH 2013), which responds plastically to environmental conditions (e.g. ROSE et al. 2009, COCOZZA et al. 2016, PRISLAN et al. 2018), indicating that climatic conditions are important for its growth, in addition to genetic predisposition (EILMANN et al. 2014).

Scots pine is one of the most widely distributed tree species, spanning a vast climatic gradient from

eastern Siberia to southern Spain (MÁTYÁS et al. 2004). Owing to the long adaptation time, the phenology of secondary growth of native origins is generally well synchronized with local weather conditions (REPO et al. 2000). Scots pine has therefore been the object of several studies on geographical variation of different functional traits, including radial growth and structural plasticity in response to drought (e.g. MARTÍNEZ-VILALTA et al. 2008, RICHTER et al. 2012).

Plants regulate their growth in response to environmental cues such as photoperiod, temperature and the availability of water and nutrients (KOZŁOWSKY & PALLARDY 1997). The capacity of photosynthetic processes and competition for resources are constraining factors for tree growth (WARING 1987). Tree growth is directed hierarchically to the different tree parts according to their priority and demands. Foliage and buds are assumed to have the highest priority, followed by roots and mobile reserves, whereas protective chemicals and stems have the lowest priority (VAN NINEN & MÄKELÄ 2000). Carbon can only be converted into biomass to the extent chemical elements other than carbon, temperature or cell turgor permit (KÖRNER 2015). Of all processes related to plant growth, cell division and formation (expansion and wall development) are particularly sensitive to decline in turgor pressure (KÖRNER 2015, STEPPE et al. 2015).

Under stress, carbon allocation is altered (BLESSING et al. 2015). Biomass partitioning, i.e., the root-to-shoot ratio or the allometric function relating to above- and belowground biomass, can be a critical indicator of plant physiological processes (e.g. WILSON 1988). It reflects the different investment of photosynthates in above- and belowground organs and its variation is a response to differential selection for adaptations to different environmental conditions (e.g. YANG & LUO 2011). For example, tree species adapted to dry climatic regimes generally have higher root-to-shoot ratios and deeper root systems than species that are more suited to mesic climatic conditions (KOZŁOWSKY & PALLARDY 1997, HARTMANN 2011), in order to increase access to the limiting resources for growth, such as water and nutrients (OVERDIECK et al. 2007).

Although the short-term effects of adverse environmental factors on plant physiology or growth are well documented (e.g. OVERDIECK et al. 2007, GRIČAR 2014, BLESSING et al. 2015), the impact of temperature on seedling growth and biomass allocation of different tree species after one or two growing seasons remains largely unexamined. Belowground carbon allocation is considered to be one of the least understood processes in tree physiology and its quantification is necessary for accurate modelling of forest net primary productivity and net ecosystem productivity (JOHNSON et al.

2007). The influence of different temperature conditions on lateral (xylem and bark) and apical increments, as well as below- and aboveground woody biomass in three-year old pine (*Pinus sylvestris*) and beech (*Fagus sylvatica*) seedlings in 2010–2011 were studied. The main novelty of this work is that it provides fundamental information on the comparison of variation in radial increment separately for bark and xylem parts. In addition, combined analyses, which include aboveground biomass (height and radial increment) and underground biomass, are presented.

2 MATERIAL AND METHODS

2.1 Tree material and growth conditions

The tree material consisted of Scots pine (*Pinus sylvestris* L.) and European beech (*Fagus sylvatica* L.) seedlings. For the experiment, 120 one-year-old pine and 90 one-year-old beech seedlings were bought from Omorika tree nursery (Muta, Slovenia) in November 2009. At that time, the stem diameter 2 cm above the root collar with a vernier calliper providing a precision to 0.010 mm and the height of each seedling using a measuring tape were measured. In addition, the volumes and lengths of the stem and root system of each seedling using a scanner and WinRHIZO software (Regent Instruments Inc. Quebec, Canada) at the beginning and at the end of the experiment in order to quantify and compare relative increase in above- and belowground biomass were separately measured. The seedlings were then planted in PVC pots (3 L). The bottom quarter of the pots was filled with silica sand to allow water drainage and the upper three quarters was filled with dystric cambisol originating from sandstone and slate ground rock collected from the upper soil horizon (0–30 cm) in a mixed forest, Roznik. The forest is near the Slovenian Forestry Institute in Ljubljana (46°03'N, 14°28'E, 323 m a.s.l.) and belongs to the *Blechno fagetum* forest association. After excavation, the soil was sieved through a 5x5 cm sieve, autoclaved and mixed with one third of vermiculite. No fertilizer was used during the experiment. Substrate consisted of 2/3 soil from the garden of the institute and 1/3 vermiculite to provide better ventilation in the root regions and better retention of moisture in the soil.

For the experiments, 30 beech and 40 pine seedlings were randomly selected and placed in each of the three different temperature conditions (GRIČAR 2014). Control seedlings (K) were grown outdoors, sheltered

from direct wind, while experimental conditions consisted of growth in either a greenhouse or in a climatized room (IMP Klima, Godovic, Slovenia). They were exposed to natural temperature variations in Ljubljana in 2010 and 2011. A weather station, which recorded average, maximum and minimum daily air temperature, was installed in the immediate vicinity of the plants. Seedlings in the greenhouse (G) were generally exposed to higher temperatures and in the climatized room (C) to lower temperatures than K during the growing season. Mean air temperature during the growing season was 17–19°C, 22–24°C and 15–17°C in K, G and C, respectively (GRIČAR 2014).

Air temperature and humidity were logged by USB dataloggers Voltcraft® DL-120 TH (Conrad Electronic UK Ltd, Barking, UK) at hourly intervals. CO₂ concentrations were monitored daily between 11:00–14:00 during the growing seasons using an infrared gas analyser Li-840 (Li-Cor Inc., Lincoln, USA). The relative air humidity was constantly monitored and kept between 70 % and 90 %. Water supply was not a limiting factor under any regime. Seedlings were watered with filtered tap water without additional nutrients, either by hand or via an automatic watering system that kept the soil moisture at 10–15 % during the growing season.

2.2 Monitoring radial increment of seedlings and histometric analysis

At the end of the experiment, i.e., in winter 2011, three-year-old beech and pine seedlings 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 stem were extracted from each seedling and immediately placed in FAA 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 replaceable blades for universal knives, 20–25 mm thick cross-sections of stems were prepared, stained in an aqueous mixture of safranin (Merck, Darmstadt, Germany) (0.04 %) and astra blue (Sigma-Aldrich, Steinheim, Germany) (0.15 %) dyes (WERF VAN 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 image 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). The widths of: (a) xylem increments in 2010 and 2011; (b) bark, also separately for periderm were measured. 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 increment characteristics of pine and beech seedlings 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 variance in the samples. Student's t-test was used to compare the widths of xylem increments for 2010 and 2011 under an individual regime.

3 RESULTS

3.1 Stem and root increments

At the end of the experiment, seedling survival was 90–95 % and 85–90 % for beech and pine, respectively. Seedling increment in length was separated into stem and root extensions. Root extension was considerably higher in both species and represented about 90 % of the total length increment in beech and 74–87 % in pine (Figure 1). With beech, stem and root increments were largest in C (9.4 ± 0.76 cm and 98.9 ± 13.95 cm,

respectively). Stem increments were comparable in G and K (6.1 ± 0.57 cm and 6.9 ± 0.36 cm, respectively), whereas root increment was significantly lower in G (G: 49.5 ± 6.59 cm; K: 88.2 ± 12.91 cm) (Fig. 1a). The lowest stem and root increments of pine seedlings were detected in C (5.9 ± 0.59 cm and 39.8 ± 3.49 cm, respectively) (Figure 1b). The largest stem increment was detected in K pines (15.8 ± 0.85 cm) and of root in G pines (56.3 ± 4.15 cm). Comparison of the total seedling increment in the length of both species showed

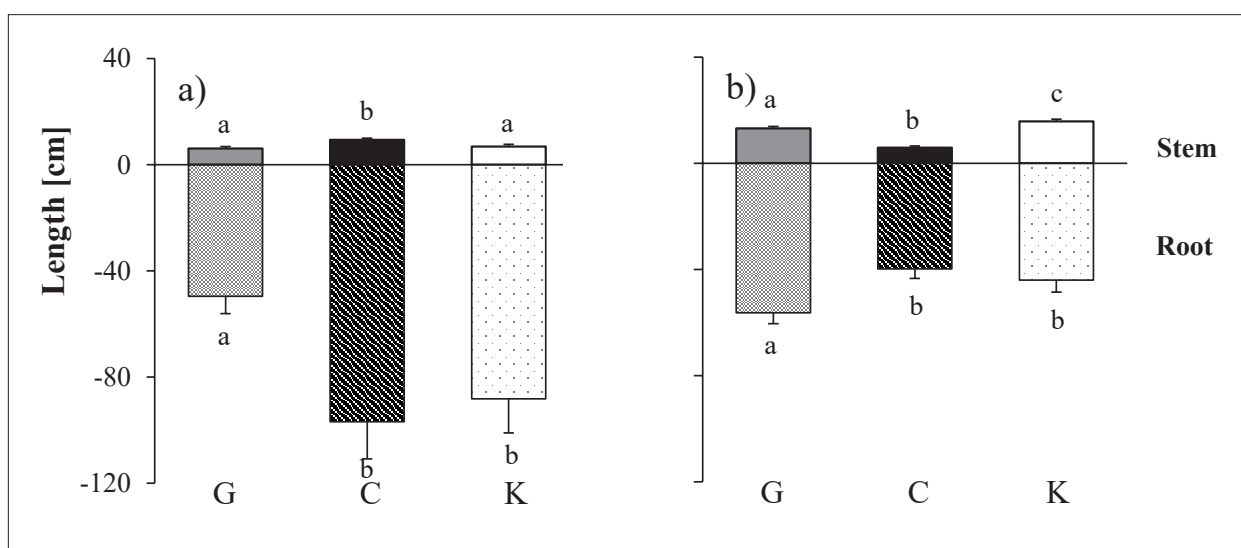


Figure 1: Stem and root increments in the length in seedlings of (a) *Fagus sylvatica* and (b) *Pinus sylvestris*.
Slika 1: Vršni prirastki debla in korenin pri sadikah (a) *Fagus sylvatica* in (b) *Pinus sylvestris*.

that only in G was it smaller in beech (for about 20 %), whereas in C and K it was about 132 % and 58 % greater, respectively.

3.2 Radial increment

Radial increment was divided into the widths of bark and xylem increments of 2010 and 2011 (Figure 2). With beech, all three measured parameters were widest in C (xylem in 2010: $380.9 \pm 45.0 \mu\text{m}$; xylem in 2011: $755.0 \pm 57.9 \mu\text{m}$; bark: $375.7 \pm 22.3 \mu\text{m}$) and narrowest in G (xylem in 2010: $282.0 \pm 94.5 \mu\text{m}$; xylem in 2011: $371.4 \pm 80.8 \mu\text{m}$; bark: $340.5 \pm 9.4 \mu\text{m}$) (Figure 2a). In the case of pine, radial increments, with the exception of xylem increments in 2010, were widest in K (xylem in 2010: $708.9 \pm 68.9 \mu\text{m}$; xylem in 2011: $1242.6 \pm 104.3 \mu\text{m}$; bark: $906.8 \pm 57.4 \mu\text{m}$) and narrowest in C (xylem in 2010: $636.1 \pm 43.1 \mu\text{m}$; xylem in 2011: 572.7 ± 47.1

μm ; bark: $614.7 \pm 25.1 \mu\text{m}$) (Figure 2b). Comparison of the total radial increments of seedlings of the two species under different temperature conditions showed that they were wider in pine in all three regimes; by about 54 % in G, 19 % in C and 50 % in K (GRIČAR 2014). Considering only the xylem part, total two-year xylem increment was wider in pine in all three cases; by about 57 % in G, 9 % in C and 45 % in K (GRIČAR 2014). However, distinguishing xylem increments formed in 2010 and 2011, only increments in 2011 of C beech were wider than those of pine.

Bark occupied only about 10 % of the total radial increment in beech in all cases and 23–30 % in pine. Only C pines with the widest stem diameters had statistically the widest bark ($906.8 \pm 181.6 \mu\text{m}$). Periderm thickness was comparable in pine seedlings under all conditions (78–88 μm) and represented 10–14 % of bark tissue, whereas in beech it was widest in C ($55.1 \pm 13.1 \mu\text{m}$) and occupied 15 % of bark tissue.

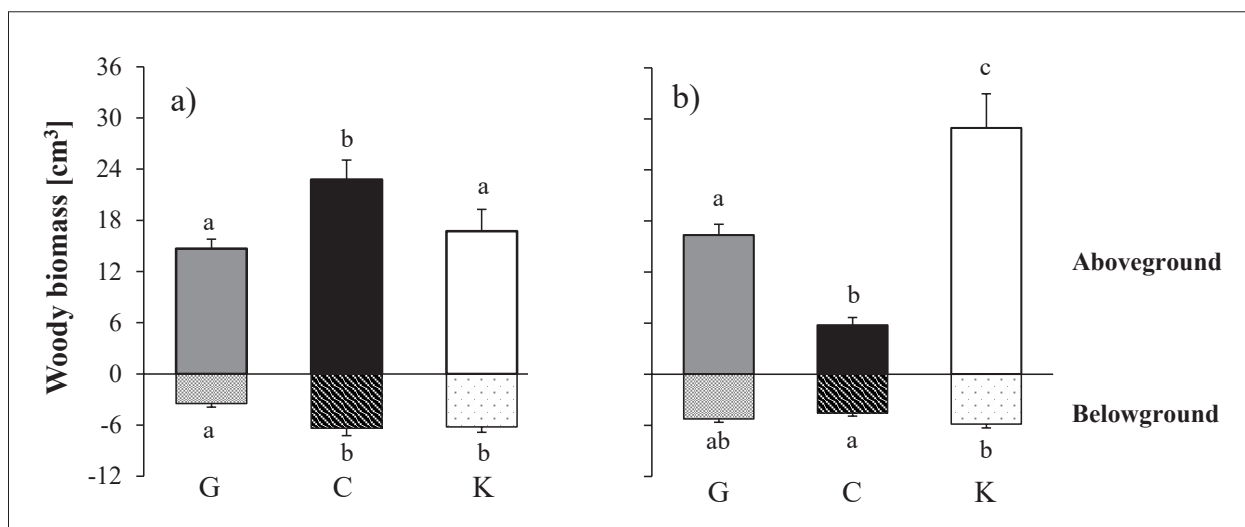


Figure 2: Radial increment, divided into widths of bark and xylem increments in 2010 and 2011, in seedlings of (a) *Fagus sylvatica* and (b) *Pinus sylvestris*.

Slika 2: Debelinski prirastek razdeljen v širino skorje in lesa v letih 2010 in 2011 pri sadikah (a) *Fagus sylvatica* in (b) *Pinus sylvestris*.

3.3 Woody biomass

Woody biomass was observed above- and belowground. It was in general substantially higher aboveground in both tree species (for about 70–80 %); only in C pine was it similar (Figure 3). With beech, the highest amount of total woody biomass (as well as above- and belowground) was detected in C (aboveground: $22.8 \pm 2.3 \text{ cm}^3$; belowground: $6.4 \pm 0.9 \text{ cm}^3$)

and lowest in G (aboveground: $14.7 \pm 1.1 \text{ cm}^3$; belowground: $3.5 \pm 0.4 \text{ cm}^3$) (Figure 3a). In the case of pine, the amount of woody biomass was highest in K (aboveground: $28.9 \pm 4.0 \text{ cm}^3$; belowground: $5.9 \pm 0.5 \text{ cm}^3$) and lowest in C (aboveground: $5.8 \pm 0.9 \text{ cm}^3$; belowground: $4.6 \pm 0.4 \text{ cm}^3$) (Figure 3b). Comparison of the total amount of woody biomass of seedlings of both species under different temperature conditions showed that it was highest in beech in C and in pine in K. It

was the same situation in the case of belowground biomass, whereas in G above- and belowground biomass

was higher in pine by about 10 % and 34 %, respectively.

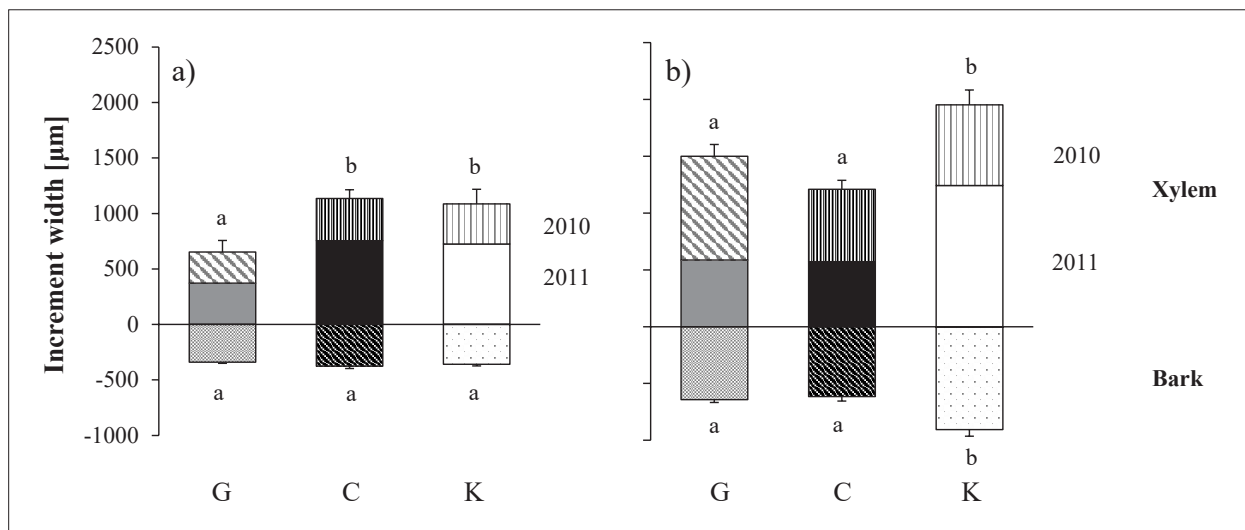


Figure 3: Above- and belowground woody biomass in seedlings of (a) *Fagus sylvatica* and (b) *Pinus sylvestris*.

Slika 3: Nadzemna in podzemna lesna biomasa pri sadikah (a) *Fagus sylvatica* in (b) *Pinus sylvestris*.

4 DISCUSSION

Phenotypic plasticity is the ability of an organism to change its phenotype in response to changes in the environment. In addition to allocational and morphological traits, anatomical traits may vary with the environment (SULTAN 2000). Although phenotypic plasticity may vary among different provenances, European beech and Scots pine are known as plastic tree species that generally adapt well to local environmental conditions (e.g. MEIER & LEUSCHNER 2008, RICHTER et al. 2012, EILMANN et al. 2014). The observations revealed a different response of beech and pine seedlings to temperature in terms of radial increment, stem and root extensions and biomass allocation.

4.1 Alteration in radial increment in response to temperature

In terms of radial increment, xylem increments were narrowest in the case of increased temperature for beech and decreased temperature for pines. With the exception of C in the first year of the experiment, radial increments were wider in all cases in pine than in beech (GRIČAR 2014). This could be ascribed to transplant shock and demonstrates a different temporal ef-

fect of abruptly changed conditions on the radial increment of pine and beech seedlings. In addition to the xylem part, radial increment also includes bark part. There was no difference in the thickness of bark in beech seedlings exposed to different conditions, whereas in control pines, which had the widest xylem increments, the bark was also widest. It can be expected that width of the bark would increase with the stem diameter. However, variations in bark width are difficult to compare among tree species due to their specific and diverse structure and contemporary secondary changes occurring in old secondary and primary bark tissues (HOLDHEIDE 1951, ROSELL et al. 2014). In the study, young pine seedlings with no dead bark were included, so the exposure of the inner, living phloem and cambial regions to environmental conditions was comparable between the two species. Narrow bark accompanied by no or a thin layer of dead bark can also partly explain the greater sensitivity of young trees to exacerbated climatic conditions compared with adult trees (GRIČAR 2013). Nevertheless, bark was generally thicker in pine, which is in line with “spacing save strategy” of beech bark—that permanently retain only one periderm (HOLDHEIDE 1951).

4.2 Alteration in stem and root extensions in response to temperature

It was found in the study that variations in stem and root extensions to temperature were comparable; either greater or smaller than in controlled seedlings. Similarly as with radial increment, low temperature negatively affected stem and root extensions of pine but positively of beech. According to EKBERG et al. (1979), alternating temperature with a 10°C difference between night and day is optimal for shoot growth in *P. sylvestris* and *Pinus contorta*. In contrast, JUNTILA (1986) found no significant effect of alternating temperature on shoot extension in *P. sylvestris*. In addition, he observed that temperature during bud formation had a significant effect on stem length in the following year and that final shoot length was significantly affected by temperature during shoot elongation, with the optimum reached at 18–21°C of constant temperature (JUNTILA 1986).

Root extension was generally greater than that of stems in both species (on average 8–14 times in beech and 3–7 times in pines). In the case of pine, the ratio root:stem extension varied similarly as increments in length and radial diameter under different temperature treatments. It was lowest in K and highest in C, indicating that unfavourable temperature diminished stem and root extensions, although to a different degree, since it diminished stem length increment more. With beech, variations in the ratio root:stem extension in response to temperature did not follow the same pattern as radial diameter or stem and root extensions. It was precisely the reverse, lowest in G and highest in K. These differences could be attributed to leaf phenology, since pine is an evergreen tree and beech a deciduous one, which further influences the rate of photosynthesis and area of photosynthetic tissue. In addition to temperature control of photosynthetic capacity, temperature probably directly affects meristematic activity and the partitioning of photosynthetic products among plant parts.

4.3 Biomass allocation shifts in response to temperature

Quantitative assessments of biomass partitioning are essential for evaluating the responses of vegetation growth to ambient environmental conditions and for understanding root biomass distributions in terrestrial ecosystems (YANG & LUO 2011). Biomass allocation shifts of pine and beech in response to favourable or adverse temperature for increment in length and

diameter thus differ and are assumed to be a species-specific strategy for adaptation and survival in given environmental conditions. With beech, above- and belowground biomass was reduced in the case of elevated temperature, with the smallest share being in roots. Furthermore, it was found that a cool environment limited the growth of pines, which is in line with its pioneer character (MÁTYÁS et al. 2004). It resulted in the lowest amount of biomass and its highest allocation to belowground, which represented almost half of the total biomass accumulation. In particular, fine root biomass has been reported to increase in response to low temperature at the treeline (HERTEL & SCHÖLING 2011). DOMISCH et al. (2001) found that, after nine weeks of experiment, a low soil temperature of 5°C had a negative effect on shoot and root extension, resulting in the lowest biomass of Scots pine seedlings. In response to increasing soil temperature, belowground biomass increased markedly, resulting in a slightly higher allocation of biomass to belowground parts. The authors also observed that soil temperature of 13°C and 17°C affected shoot and root growth of Scots pine differently; the root elongation rate increased with soil temperature, whereas the shoot elongation rate was unaffected by an increase in soil temperature (DOMISCH et al. 2001). Roots are known to be essential for carbohydrate storage and the amount changes seasonally, with the lowest reserves in spring and highest late in the season or during dormancy (REGIER et al. 2010). These carbohydrates are the major substrates for respiring during winter and for respiration, growth and development early in the subsequent year (BRUNNER et al. 2015). The metabolic activity of the root system and its sink strength decrease at low soil temperatures, resulting in reduced belowground translocation of photosynthates (HUREWITZ & JANES 1983) and a corresponding aboveground accumulation of biomass, whereas at higher soil temperatures, the root system becomes a strong sink for photosynthates (LIPPU 1998). It is expected that soil warming will generally result in greater root production and mortality, and greater root carbon flux to the soil (PREGITZER et al. 2000). The age of a plant can also influence responses of roots to changing soil temperature. Young perennial plants invest relatively more carbon in tissue construction, while older plants allocate a higher proportion of their annual carbon budget to maintenance of the root system and the replacement of short-lived feeder roots (PREGITZER et al. 2000).

In addition to temperature variations, it is known that biomass allocation can also be greatly modified by water availability (BLESSING et al. 2015). In order to

adapt to dry climatic regimes, tree species generally have higher root-to-shoot ratios and deeper root systems than species that are more suited to mesic climatic conditions (KOZŁOWSKY & PALLARDY 1997, HARTMANN 2011), in order to increase access to limiting resources for growth, such as water and nutrients (OVERDIECK et al. 2007, RICHTER et al. 2012). Furthermore, RICHTER et al. (2012) stressed that southern provenances and species were found to be less plastic than continental ones because limited phenotypic plasticity is beneficial in stressful environments (TOGNETTI et al. 1995, ROSE et al. 2009).

With the exception of pine in C, the stem increment in diameter in all cases exceeded the increment in length, whereas in the case of roots, it was just the opposite; increment in length was 13–16 and 7–11 times greater for beech and pine, respectively. Since a large supply of assimilates is required for both stem and radial increments, they internally compete for car-

bohydrates, although shoot apices and leaves have a higher-ranking priority than cambium as a sink for carbon (MINCHIN & LACOINTE 2005). Only after shoots have completed growth are resources allocated to the process of secondary wall formation of thick-walled latewood cells (ROSSI et al. 2009).

Plasticity in cambial and leaf phenologies is an important adaptation of trees to changed climatic conditions since species can avoid stress conditions by timing their growth (e.g. PRISLAN et al. 2013). It has been shown that the early emergence of Scots pine seedlings at its southern distribution limit increased the time period available for seedling development before the onset of summer drought, which increased seedling survival irrespective of the severity of the drought (CASTRO et al. 2006). Extended growing seasons as a result of rising temperature might thus buffer the negative impacts of summer drought on tree seedling establishment (RICHTER et al. 2012).

5 CONCLUSIONS

The short-term treatments clearly show that biomass allocation shifts of pine and beech in response to temperature seem to be a species-specific plastic adjustment to environmental heterogeneity. With a rapid global warming scenario (IPCC 2014), this individual plastic response may play an important role in acclimation to new environmental conditions (RENNENBERG et al. 2006). In addition, information on the extent to which provenance performance is related to environmental conditions and genetic predisposition in order to guarantee the vitality and productivity of future beech stands should be considered (ROSE et al. 2009, EILMANN et al. 2014). Finally, only differences at the bulk tissue level were compared in this study, although differences in the anatomical traits of xylem and bark (GRIČAR 2017), as well as tissues, is also crucial to better understanding the plasticity of the studied tree species (e.g. LACHENBRUCH & MCCULLOH 2014).

Seedlings may be especially vulnerable to predicted climate changes, since their ability to survive may be restricted. In future studies, it would be desirable to extend research to the underlying physiological processes. The short-term experiment shows 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 (GRIČAR 2014). Moreover, the results from this short-term experiment conducted with small seedlings may not be directly applicable to older trees, since the effects may be different if the responses are studied over longer periods of time (DOMISCH et al. 2001). Thus, in the context of future climate change, long-term adaptive responses and highly flexible resource allocation patterns of trees and forests must be taken into account.

6 POVZETEK

Podnebne spremembe in s tem povezani pogostejši in intenzivnejši ekstremni vremenski dogodki, kot so suše, vročinski valovi, pozebe in poplave, bodo nedvomno vplivali na drevesno sestavo in porazdelitev gozdnih sestojev v številnih regijah. Občutnejši stres na drevesa in gozdne ekosisteme lahko poveča dovzetnost

dreves za patogene organizme in sčasoma vodi do propadanja posamezne drevesne vrste in degradacije gozdov. V stresnih razmerah se porazdelitev ogljika vezanega v lesni biomasni spremeni. Porazdelitev biomase, tj. razmerje med koreninskim in debelnim prirastkom oziroma delež nadzemne in podzemne biomase, je

lahko pokazatelj fizioloških procesov v rastlini, saj odraža različno porazdelitev fotosintatov v nadzemne in podzemne organe. Spremembe v tej porazdelitvi pa lahko razumemo kot odziv na prilagoditev posamezne drevesne vrste različnim okoljskim razmeram. Načini odziva dreves na spremenjene okoljske razmere so zlasti ključni za ekološko in gospodarsko pomembne evropske drevesne vrste, kot sta na primer navadna bukev in rdeči bor, saj bo to vplivalo na njihovo rast in konkurenčno sposobnost ter posledično na gospodarjenje z gozdovi.

Malo je znanega o vplivu temperature na rast sadik in alokacijo biomase pri različnih drevesnih vrstah, zato smo raziskali vpliv različnih temperaturnih razmer na debelinsko rast debla (les in skorja), vršno rast debla in korenin ter na podzemno in nadzemno lesno biomaso pri triletnih sadikah navadne bukve (*Fagus sylvatica* L.) in rdečega bora (*Pinus sylvestris* L.) v obdobju 2010–2011. Pozimi 2009/2010 smo 120 sadikam rdečega bora in 90 sadikam navadne bukve, ki smo jih kupili v drevesnici Omorika (Muta), s pomočjo sistema za analizo slike WinRHIZO in 3D skenerja izmerili volumen korenin in stebila, in sicer na začetku in koncu poskusa. Na ta način smo določili relativni prirastek nadzemne in podzemne lesne biomase za vsako sadiko posebej. Sadikam smo s kljunastim merilom izmerili še premer stebila, približno 2 cm nad koreninskim vratom (bor = 0,2–0,3 cm; bukev = 0,3–0,4 cm) ter višino (bor = 15–20 cm; bukev = 30–40 cm) z merilnim trakom, jih označili in posadili v plastične lonce. Eksperiment smo zastavili v treh različnih temperaturnih razmerah. V vsakem režimu je bilo tako 40 sadik bora in 30 sadik bukve, ki so bile naključno razvrščene v posamezne skupine. Kontrolne sadike so rasle na prostem, približno 10 m od rastlinjaka, in zaščitene pred dežjem in neposrednim vetrom. Izpostavljene so bile naravnim temperaturnim razmeram v Ljubljani v letih 2010 in 2011. Vremenska postaja, ki je beležila povprečne, maksimalne in minimalne dnevne temperature zraka in količino padavin, je bila nameščena v neposredni bližini sadik. Povprečna temperatura zraka med rastnima sezonama je bila = 17–19°C. Druga skupina sadik v rastlinjaku je bila podvržena višjim temperaturam (T tekom rastne sezone = 22–24°C), tretja skupina sadik v hladilni komori pa nižjim (T tekom rastne sezone = 15–17°C). Ob koncu poskusa, tj. pozimi 2011, smo sadike vzeli iz loncev in jih pripravili za nadaljnje analize. Za lesno-anatomske analize smo z drsnim mikrotomom pripravili 20–25 µm debele prečne prereze lesa in skorje in jih obarvali v vodni mešanici barvil safranin in astra modro. Vse potrebne histometrične analize smo opravili s svetlobnim mikroskopom Olympus BX51 in programom za

analizo slike Elements Basic Research v.2.3. Za statistične analize smo uporabili program Statgraphics, za izdelavo grafov pa Microsoft Excel.

Lesni prirastki so bili najmanjši v primeru povišane temperature pri bukvi, pri boru pa pri zmanjšani temperaturi. Pri sadikah bukve izpostavljenih različnim temperaturnim razmeram ni bilo razlik v širini skorje, medtem ko je bil delež skorje pri boru največji pri kontrolnih sadikah, ki so imele tudi najširše premere. Debelina periderma je bila primerljiva pri sadikah izpostavljenih različnim temperaturam in je predstavljala 10–14 % tkiva skorje pri bukvi in 15 % tkiva pri boru. Debelinski prirastki so bili v vseh režimih širši pri boru kot pri bukvi. Prirastek glavne korenine je bil znatno večji kot prirastek debla pri obeh vrstah in je predstavljal približno 90 % celotne vršne rasti pri bukvi in 74–87 % pri boru. Nadzemna lesna biomasa je bila pri obeh drevesnih vrstah bistveno večja (za približno 70–80 %) v primerjavi s podzemno biomaso. Pri bukvi je bila celotna biomasa zmanjšana pri povišani temperaturi z najmanjšim deležem korenin. Pri boru je bila najmanjša količina biomase pri nižani temperaturi, ko smo zabeležili največjo prerazporeditev biomase v podzemne dele, ki so predstavljali skoraj polovico celotne lesne biomase. V študiji so prikazane spremembe v širini dvoletnega debelinskega prirastka ločeno za les in skorjo, ki je dostikrat v tovrstnih analizah prezrta, vendar lahko pri sadikah ali mladih drevesnih predstavlja znaten delež lesnega tkiva. Vključena je bila tudi podzemna lesna biomasa, ki je ravno tako dostikrat prezrta, četudi je njena kvantifikacija nujna za natančno oceno in modeliranje neto primarne produktivnosti gozdov oziroma kopenskih ekosistemov.

Kratkoročni poskusi kažejo, da okoljske razmere za optimalno rast proučevanih drevesnih vrst niso primerljive, kar se odraža v različnih prerazporeditvah biomase pri boru in bukvi pri različnih temperaturnih režimih. Način in hitrost odziva posamezne vrste bo lahko v prihodnje njena pomembna konkurenčna prednost ali ovira pri prilagajanju na nove razmere. V raziskavi smo sicer primerjali le razlike na ravni tkiv, medtem ko denimo anatomskih značilnosti lesa in skorje nismo vključili. Vendar pa ravno značilnosti prevodnih elementov v lesu (traheje/ traheide) in skorji (sitasti elementi) ključni za razumevanje plastičnosti proučevanih drevesnih vrst na različna okolja. Sadike in mlada drevesa so še posebej občutljivi na podnebne spremembe in zmožnost preživetja, zato bi bilo smiselno v prihodnje združiti lesno-morfološke analize z eko-fiziološkimi meritvami. Dvoletni poskus kaže, da je smiselno nadaljevanje tovrstnih opazovanj v daljšem časovnem obdobju, s čimer bi zajeli kratkoročne

in dolgoročne odzive rasti dreves na spremenjene okoljske razmere. Rezultatov pridobljenih na sadikah ravno tako ni mogoče aplicirati na odrasla drevesa,

kjer so odzivi lahko povsem drugačni. Nenazadnje pa je potrebno upoštevati še dolgoročne prilagoditve dreves na spremenjene lokalne razmere.

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