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Effects of Drought, Phosphorus Fertilization and Provenance on the Growth of Common Beech and Sessile Oak

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Abstract: The negative impact of drought on plant growth may be modified by the different availability of mineral nutrients and by their adaptation to different local habitat conditions. In this study, we examine the impact of drought, fertilization with phosphorus and provenance, as well as their interactions, on the growth and allometric growth relationships between the belowground and aboveground organs of common beech (*Fagus sylvatica* L.) and sessile oak (*Quercus petraea* (Matt.) Liebl.). The research was conducted on saplings originating from two mature mixed stands (dry and wet provenances) dominated by these species. In the common garden experiment, saplings were exposed to regular watering and drought in interaction with moderate and high phosphorus concentrations in the growing substrate (achieved by phosphorus fertilization). The obtained results indicate the negative impact of drought and phosphorus fertilization on the growth of both species. In common beech, a negative impact of phosphorus fertilization on the adaptive capacity to drought was demonstrated by unfavorable ratios between fine root mass and the mass of other organs. The sessile oak provenances under the impact of drought showed a different root collar diameter/stem height increment ratio, which indicates their different phenotypic plasticity as a consequence of adaptation to different frequencies of dry periods in their natural habitats.

Keywords: *Fagus sylvatica*; *Quercus petraea*; allometric growth relationship; adaptation to drought; luxury nutrition with phosphorus

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1. Introduction

Common beech (*Fagus sylvatica* L.) and sessile oak (*Quercus petraea* (Matt.) Liebl.) represent two species of forest trees that form mixed forest stands throughout Europe, with very high biodiversity and economic, ecological and social value [1]. However, forest ecosystems across Europe have recently been increasingly exposed to negative impacts of climate change, i.e., long-lasting drought periods [2,3] and severe drought stress [4–6]. Such events have negative effects on vitality [7], carbon storage [8,9], biomass production [10,11] and the natural regeneration of forest trees [12].

For this reason, scientists and forestry experts invest a lot of effort in finding appropriate solutions to mitigate the negative impact of drought on the growth of forest trees and the survival of entire forest ecosystems. One way to mitigate the negative impact of drought on the growth and vitality of forest trees is the selection of more drought-tolerant genotypes and/or provenances [13]. Common beech and sessile oak provenances often show differentiation in physiological or morphological traits, which are conditioned by their adaptation to specific local habitat conditions [14–16]. Under the impact of experimentally induced drought, provenances originating from dry habitats have better survival and higher stem diameter and height growth increment compared to the ones from wet habitats. They also have bigger leaf areas and leaf thickness, take deeper roots, and invest more resources in the development of belowground (fine and coarse roots) organs at the expense of aboveground (leaves and stems) ones. [15,17–24]. This indicates their better adaptation to drought [25,26]. Therefore, the use of forest reproductive material (seeds and saplings) originating from dry provenances for the establishment of new forest stands and the regeneration of existing ones could mitigate the negative impact of drought on their growth and survival in the future [27,28].

Most saplings used for the establishment of new forest stands and the regeneration of existing ones are produced in forest nurseries. During nursery production, saplings are fertilized with mineral fertilizers, which positively affects their quality [29–32] and capacity for drought tolerance [33–36]. High-quality saplings have well-developed stems and roots, as well as the optimal concentration of mineral nutrients in the leaves, stems and roots [37,38]. Based on previous experience and knowledge, samplings of higher quality exhibit improved survival and growth when transplanted into natural habitats affected by drought compared to those of lower quality [39,40].

The positive effect of fertilization with NPK (complex) mineral fertilizers or individual nitrogen (N) fertilizers on the growth of forest trees in the initial stages of their development (seedlings and saplings) is quite well documented [9,41–43]. However, the effect of fertilizing with phosphorus (P) mineral fertilizers on the growth of forest trees has rarely been investigated so far [44–47]. Current knowledge about the effect of P fertilization on plant growth and its physiology is prevalently based on research conducted on annual plants, mainly on crops. These studies indicate that P fertilization has a positive effect on their antioxidant metabolism [48,49], cell membrane stability [50,51], leaf conductance and nitrate reductase activity [52–54], water balance [55], photosynthesis and leaf area [51,56], root growth [57] and the ratio of belowground and aboveground growth [58]. However, some studies report negative effects of P fertilization on the growth of annual plants. For example, the exposure of the model species *Oryza sativa* and *Arabidopsis thaliana* to high P concentrations in a growing substrate negatively affects their photosynthesis and root morphological traits [59,60]. Abrupt exposure to elevated phosphorus availability negatively impacts the growth of species adapted to relatively low phosphorus concentrations in the soils of their natural habitats [61]. Thus, the contradictory results of previous research indicate that the effect of P fertilization on plant growth and adaptation to drought is still relatively unknown.

Natural forest soils in Europe are generally poorly supplied with P [62–65]. Earlier reports about the negative impact of the sudden exposure of plants to high P availability on their growth [61], especially on the root system [59,60], lead to the assumption that P fertilization could have a negative impact on the growth of European forest trees and their adaptive capacity to drought, primarily because the adaptation of forest trees to drought largely depends on the morphological traits of their root system [66]. The effect of P fertilization or different concentrations of P in the natural soil on the growth of common beech and sessile oak is currently poorly investigated [47,67]. Previous research, mainly on common beech, has focused on inter- and intraprovenance differences in the uptake and internal P allocation mechanisms during the growing season and leaf phenology [47,62,68–73]. Research on sessile oak has focused on the effect of P fertilization on leaf P concentration and total biomass production [67] or leaf phenology [73]. The effect of drought in interaction with P fertilization on the growth of common beech and sessile oak, nor other European forest tree species, has not yet been investigated. However, the results of recent research conducted on two Chinese forest tree species (*Phoebe zhennan* and *Alnus cremastogyne*) indicate that P fertilization in interaction with drought has a positive effect on total root biomass (only for *Phoebe zhennan*), while it has no significant effect on the growth of other aboveground (leaves and stem) and belowground (fine and coarse root) organs [45,46].

To explore the effects of drought and P fertilization on common beech and sessile oak growth, we established an experiment with saplings originating from two mixed stands (provenances). One originating from a wet habitat and the other from a dry, with a low P concentration in the soil of both provenances. The aims of the research were to

1. examine the effects of drought, P fertilization and provenance on the growth of common beech and sessile oak;
2. examine how fertilization with P affects the growth and allometric growth relationships between belowground and aboveground organs of common beech and sessile oak, i.e., their adaptation capacity to drought;
3. examine the common beech and sessile oak provenance differentiation with regard to different local habitat conditions.

2. Materials and Methods

2.1. Plant Material and Provenance Habitat Conditions

Four-year-old saplings of common beech and sessile oak were collected in two mature mixed stands (provenances) dominated by these species in the continental part of the Republic of Croatia (RH). One is 100 years old, in the northwestern part of RH, near the city of Karlovac (KA provenance, 15.524041 N, 45.466135 E, 170 m a.s.l.), and the other is 105 years old, in the eastern part of RH, near the city of Slavonski Brod (SB provenance, 17.973173 N, 45.273451 E, 245 m a.s.l.) (Figure A1). In both provenances, during early March 2021, saplings were carefully excavated with minimal damage to their root system, under mature trees, at least 100 m apart. More details about the investigated provenances' habitat conditions (phytosociological, geomorphological, climatological and meteorological traits, as well as mechanical, physical and chemical soil traits) can be found in Sever et al. [16]. It is important to point out that the mean annual precipitation for the period from 1949 to 2019 in KA provenance (1111.8 mm) was higher than in SB provenance (770.3 mm). However, in the period from 2016 to 2020 (during the growth of four-year-old saplings in their natural habitats), 17 moderately to extremely dry months were recorded in KA provenance (9 during the growing seasons), compared to SB provenance where only 9 moderately to extremely dry months (4 during the growing seasons) were recorded in the given period. The mean maximum snow depths in the months with snow cover for the period from 1949 to 2019 were higher in the KA (32 cm) compared to the SB (18 cm) provenance. Most of the physical and/or chemical soil traits were similar in both provenances, including P concentration. In KA provenance, it was 0.50 ± 0.32 mg P_2O_5 100 g^{-1} of soil, and in SB provenance, it was 0.64 ± 0.21 mg P_2O_5 100 g^{-1} of soil, indicating a low P concentration in the soils (depth of 0–30 cm) of both provenances. The soil mechanical composition (depth of 0–30 cm) described by the relative proportion of sand, silt and clay in KA provenance was 21.3, 59.6 and 19.1%, respectively, and in SB provenance, it was 2.4, 73.8 and 23.8%, respectively.

2.2. Experimental Design and Growth Conditions

The excavated saplings with an average height of 36.6 ± 8.01 cm were transported to the garden of the Faculty of Forestry and Wood Technology, University of Zagreb, where the common garden experiment was established (45.82065 N, 16.02303 E, 120 m a.s.l.). Saplings were transplanted into four wooden boxes (dimensions $155 \times 275 \times 80$ cm, with a volume of 3.41 m^3) which were previously filled with Klasmann TS 3 substrate (3800 L in each box) with a P_2O_5 concentration of 160 mg L^{-1} of substrate (Figure A1). In two boxes, we added 1182 g of triple superphosphate (Triplex) fertilizer, containing 45% of P_2O_5, to increase the concentration of P_2O_5 up to 300 mg L^{-1} of substrate, which is considered a high concentration of easily accessible P. In the other two (non-fertilized) boxes, the concentration of P_2O_5 was 160 mg L^{-1} of substrate, which is considered a moderate concentration of easily accessible P.

After fertilization, we transplanted 25 common beech and 25 sessile oak saplings per provenance (KA and SB) in each box (100 saplings in each box), according to a random design, with 20×18 cm spacing, i.e., 400 plants were planted in the whole experiment. During the growing season of 2021, all transplanted saplings were exposed to natural meteorological conditions with regular watering during the summer to achieve better acclimatization and survival. During the growing season of 2022, all boxes were covered with a transparent

PVC roof to prevent natural precipitation. We established four different treatments: regular watering and fertilization with P (W/+P treatment), regular watering and non-fertilization with P (W/−P treatment), drought and fertilization with P (D/+P treatment) and drought and non-fertilization with P (D/−P treatment) (Figure A1). Two boxes (one fertilized with P and the other non-fertilized with P) were manually watered with 40 L of water per box every four days during the growing season. The other two boxes (one fertilized with P and the other non-fertilized with P) were exposed to drought (from 15 May to 1 September 2022 when the drought period was stopped by re-watering). During that period, they were watered with 20 L of water per box only at the moment of the appearance of wilting leaves, indicating drought stress, to prevent them from dying. This happened only three times: at the end of July, the beginning of August and the middle of August.

2.3. Soil Water Content and Chemical Traits

The seasonal water dynamics in the substrate of all treatments was controlled using a data logger and sensors for the measurement of the volumetric water content (VWC) in the soil (Spectrum Technologies, Inc., Aurora, CO, USA). In each treatment, there were four sensors installed at a depth of 5–20 cm. Sampling for the substrate chemical trait determination was carried out in mid-September 2021 (six months after the P fertilization). In each box (treatment), one composite sample was collected, formed with nine subsamples collected in a diagonal (X) arrangement. The samples of each treatment were subjected to soluble component extraction by mixing with deionized water at a 1:2 ratio. The material was mixed for 1 h using a rotating mixer. Then, the suspension was filtered through filter paper, and the clear filtrate was analyzed to determine the pH reaction, total nitrogen (N total), nitrate (NO_3^-), ammonium (NH_4^+), phosphorus (PO_4^{3-}), potassium (K^+), calcium (Ca^{2+}), magnesium (Mg^{2+}), chloride (Cl^-) and sodium (Na^+) ions and salt, as well as electrical conductivity (E.C.), in the substrate of each treatment separately. The chemical analysis methodology applied is described in more detail in Page et al. [74].

2.4. Leaf Water Potential, Growth and Dry Mass Production

The investigation was carried out on 192 saplings. After the establishment of the common garden experiment in the spring of 2021, in each treatment, 12 common beech and 12 sessile oak saplings per provenance (48 saplings per treatment) were randomly selected and labeled. On three of the selected common beech, i.e., sessile oak saplings per provenance in each treatment (12 saplings per treatment), we measured pre-down leaf water potential (Ψ), using a portable pressure chamber (PMS Instrument Company, Albany, OR, USA). The first measurements were performed on the 26 May (at the beginning of the drought period), and the second measurements were conducted on the 31 August 2022 (at the end of the drought period). The root collar diameter (D) in mm and the stem height (H) in cm were measured twice for all 48 labeled saplings. The first time was in March, before the drought treatment (D_{March} and H_{March}), and the second time was in mid-September after the drought treatment ($D_{September}$ and $H_{September}$). The root collar diameter increment ($D_{increment}$) and stem height increment ($H_{increment}$) were calculated as the differences between the D or H measured in September and March of 2022. At the beginning of September (shortly after the drought period was stopped by re-watering), the labeled saplings were carefully excavated from the substrate, and their tap root length (TR_{length}) in cm and total leaf area (L_{area}) in m^2 were measured. Leaf area was measured using the software package WinFOLIA 2005b (Regent Instruments, Quebec City, QC, Canada). After drying at 105 °C for 48 h (to constant mass), using an analytical balance with a precision of 0.01 g, the dry mass of leaves (L_{mass}), stem (ST_{mass}), coarse roots > 2 mm (CR_{mass}) and fine roots < 2 mm (FR_{mass}) was determined for each sapling. The total dry mass of aboveground ($AG_{mass} = L_{mass} + ST_{mass}$) and belowground ($BG_{mass} = CR_{mass} + FR_{mass}$) organs was also calculated. Based on previously measured growth parameters, the following allometric growth relationship parameters were calculated: D/H_{March}, $D_{increment}/H_{increment}$, $D/H_{September}$, $TR_{length}/H_{September}$, CR_{mass}/ST_{mass}, FR_{mass}/L_{mass}, FR_{mass}/ST_{mass}, FR_{mass}/CR_{mass}, $FR_{mass}/L + ST + CR_{mass}$ and BG_{mass}/AG_{mass}, which describes the growth of belowground (coarse and fine roots) compared to aboveground (leaves and stems) organs.

2.5. Leaf Chemical Traits

After determining the leaf dry mass and leaf area, dry leaves were grounded, homogenized and subjected to chemical analysis to determine the nutrition of the investigated plants with mineral nutrients. The concentration of N was determined using the Kjeldahl method. Digestion was performed with concentrated nitric acid (HNO_3) and perchloric acid ($HClO_4$). The concentration of P was determined spectrophotometrically. The concentration of K was determined by a flame photometer. The concentrations of Ca, Mg and Fe were determined by atomic absorption spectrophotometry with a previous digestion with concentrated HNO_3 and $HClO_4$. The aforementioned analyses were performed according to standardized international protocols [75].

2.6. Statistical Analysis

All statistical tests were performed using the SAS statistical 15.1 software package (SAS Institute Inc., Cary, NC, USA). Assumptions of residual normality and variance homogeneity were tested using the Shapiro–Wilk and Levine's tests with the GLM and UNIVARIATE procedures in SAS. Residuals were plotted as a function of fitted values to test for variance homogeneity, and the distribution of residuals was also tested. A factorial ANOVA was performed to evaluate the fixed effects of drought, P fertilization and provenance, as well as the interaction of these effects on leaf water potential, concentrations of mineral nutrition in leaves, growth parameters and allometric growth relationship parameters, for each species separately. In all cases, an LSD post hoc test was performed to determine the significance of differences ($p < 0.05$) between the studied effect levels.

3. Results

3.1. Soil Water Conditions and Sapling Water Balances

Under regular watering in the W/+P and W/−P treatments, the volumetric water content (VWC) in the substrate during the entire growing season was between 18.3 and 40.6%. The water deprivation in the D/+P and D/−P treatments resulted in a continuous decrease in VWC in the substrate, which was reduced to 8.0 and 10.1% until the end of August (at the end of the dry period), respectively (Figure 1). Regular watering had a significant and positive effect on the Ψ of both species (Table 1 and Figure 1). Accordingly, Ψ in regularly watered saplings of common beech and sessile oak was not lower than −0.4 MPa, neither in May nor at the end of August. However, Ψ in the drought-treated saplings of common beech and sessile oak until the end of August reached mean values of −2.5 and −3.0 MPa, respectively (Figure 1).

Table 1. Main effects of drought (regularly watered vs. drought-treated saplings), fertilization (saplings fertilized with phosphorus vs. non-fertilized with phosphorus), provenance (saplings originated from Karlovac vs. Slavonski Brod provenance) and their interactions on pre-down leaf water potential measured in May (Ψ_{May}) and August (Ψ_{August}), as well as on the leaf phosphorus concentration (P_{Leaves}), of common beech and sessile oak saplings, as calculated with a factorial ANOVA.

Species	Parameter	Drought (D)	Fertilization (P)	Provenance (Pr)	D × P	D × Pr	P × Pr	D × P × Pr
Common beech	Ψ_{May}	*	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
	Ψ_{August}	***	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
	P_{Leaves}	n.s.	***	n.s.	n.s.	n.s.	n.s.	n.s.
Sessile oak	Ψ_{May}	*	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
	Ψ_{August}	***	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
	P_{Leaves}	n.s.	***	n.s.	n.s.	n.s.	n.s.	n.s.

Levels of significance: * $p < 0.05$; *** $p < 0.001$; n.s., not significant.

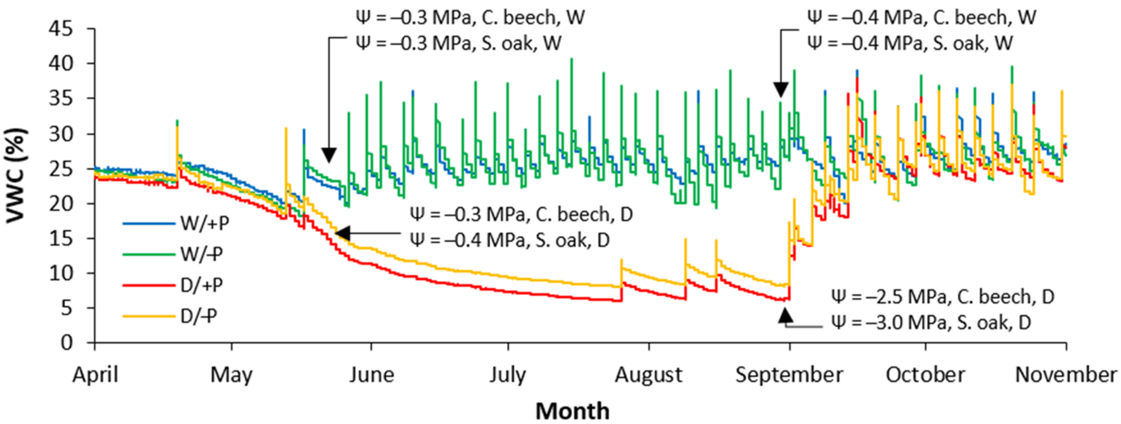

Figure 1. Patterns of substrate volumetric water content (VWC) in the regularly watered and phosphorus fertilization treatment (W/+P), regularly watered and non-phosphorus fertilization treatment (W/−P), drought and phosphorus fertilization treatment (D/+P) and drought and non-phosphorus fertilization treatment (D/−P) with the mean values of pre-down leaf water potential (Ψ) in regularly watered (W) and drought-treated (D) saplings of common beech (C. beech) and sessile oak (S. oak), measured on 26 May and 31 August.

3.2. Substrate P Concentration and Sapling Nutrition with P

Fertilization with P had a significant and positive effect on the substrate and leaf P concentrations of both species (Table 1 and Figure 2). Accordingly, substrate P concentration in the W/+P and D/+P treatments was high, while in the W/−P and D/−P, it was moderate (Figure 2A). The range of mean leaf P concentration in common beech saplings fertilized with P was between 1.79 and 1.97 mg P g^{-1} DW, indicating a nutrition with P between upper normal and surplus (Figure 2B), while in the sessile oak saplings fertilized with P, it was between 1.92 and 1.99 mg P g^{-1} DW, indicating an upper normal nutrition with P (Figure 2C). The range of mean leaf P concentration in common beech saplings non-fertilized with P was between 1.49 and 1.69 mg P g^{-1} DW, indicating a central normal nutrition with P (Figure 2B), while in the sessile oak saplings non-fertilized with P, it was between 1.41 and 1.55 mg P g^{-1} DW, indicating a lower normal nutrition with P (Figure 2C). Other chemical traits of the substrate and the concentration of other mineral nutrients in the leaves of common beech and sessile oak were similar in all treatments (Tables A1 and A2).

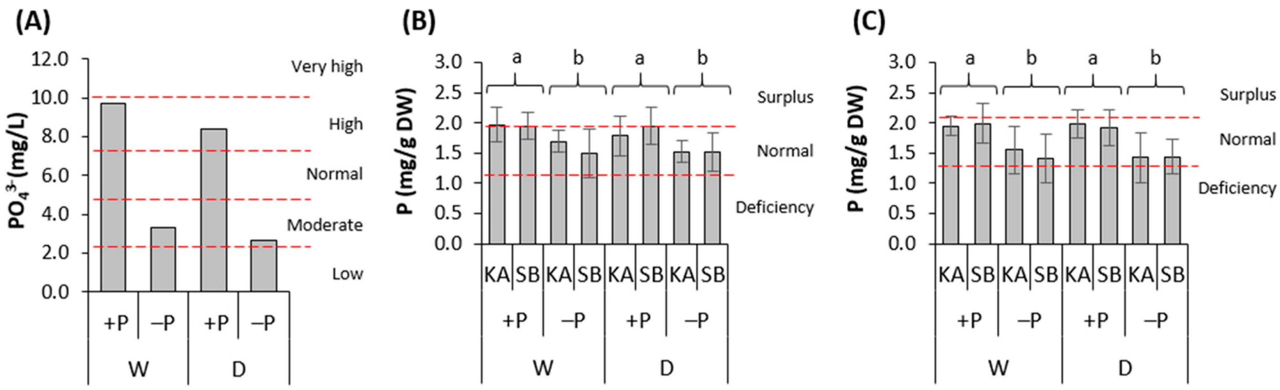

Figure 2. Total phosphorus concentration in the substrate (**A**) and leaves (means ± SD) of common beech (**B**) and sessile oak (**C**) saplings originated from Karlovac (KA) and Slavonski Brod (SB) provenances, fertilized with phosphorus (+P), non-fertilized with phosphorus (−P), regularly watered (W) and drought-treated (D). Different small letters indicate significant differences among saplings fertilized and non-fertilized with phosphorus at $p < 0.05$. Red horizontal dashed lines indicate critical phosphorus concentrations in the substrate [74] and in the leaves of common beech and sessile oak saplings [76].

3.3. Effect of Drought on Sapling Growth

The drought had a negative impact on the growth of both species, indicated by the lower mean values of all measured growth parameters in drought-treated saplings compared to regularly watered ones. The mean values of almost all allometric growth relationship parameters were higher in drought-treated saplings than in those regularly watered for both species. However, in common beech, drought significantly reduced only $H_{increment}$ by 33%, and in sessile oak, $D_{increment}$, $H_{increment}$, $D_{September}$, $H_{September}$, ST_{mass}, AG_{mass} and L_{area} by 26, 28, 13, 18, 31, 26 and 26%, respectively. However, in sessile oak, drought significantly increased the ratios of $TR_{length}/H_{September}$ and CR_{mass}/ST_{mass} (Table 2).

Table 2. Mean values ± SD of growth and allometric growth relationship parameters for regularly watered (W) and drought-treated (D) common beech and sessile oak saplings, with the main effect of drought (D effect) as calculated with a factorial ANOVA (W vs. D saplings). Relative values in parenthesis indicate negative (red) and positive (green) differences between the measured parameters of D saplings compared to W saplings.

Parameters		Common Beech			Sessile Oak		
		D Effect	W	D	D Effect	W	D
Growth	D_{March} (mm)	n.s.	7.78 ± 2.26	7.70 ± 1.91 (−1%)	n.s.	7.73 ± 2.37	7.34 ± 2.04 (−5%)
	$D_{increment}$ (mm)	n.s.	1.97 ± 1.31	1.78 ± 1.13 (−10%)	*	5.03 ± 2.35	3.72 ± 2.49 (−26%)
	$D_{September}$ (mm)	n.s.	9.74 ± 2.92	9.48 ± 2.51 (−3%)	*	12.75 ± 3.52	11.06 ± 3.12 (−13%)
	H_{March} (cm)	n.s.	46.04 ± 14.88	46.20 ± 15.54 (0%)	n.s.	48.83 ± 22.77	42.84 ± 17.71 (−12%)
	$H_{increment}$ (cm)	**	14.47 ± 8.24	9.74 ± 5.66 (−33%)	**	24.24 ± 10.42	17.42 ± 9.73 (−28%)
	$H_{September}$ (cm)	n.s.	60.60 ± 16.67	55.94 ± 15.12 (−8%)	**	73.07 ± 25.00	60.26 ± 19.78 (−18%)
	L_{area} (m^2)	n.s.	0.25 ± 0.19	0.21 ± 0.18 (−16%)	*	0.35 ± 0.23	0.26 ± 0.16 (−26%)
	TR_{length} (cm)	n.s.	41.14 ± 12.63	38.29 ± 12.34 (−7%)	n.s.	63.15 ± 17.52	61.59 ± 15.38 (−2%)
	L_{mass} (g)	n.s.	7.44 ± 5.55	6.49 ± 4.80 (−13%)	n.s.	14.91 ± 10.15	12.30 ± 7.12 (−18%)
	ST_{mass} (g)	n.s.	19.33 ± 17.64	14.92 ± 10.36 (−23%)	*	24.90 ± 19.24	17.16 ± 11.31 (−31%)
	AG_{mass} (g)	n.s.	26.77 ± 22.74	21.41 ± 14.83 (−20%)	*	39.82 ± 28.70	29.46 ± 18.01 (−26%)
	FR_{mass} (g)	n.s.	3.55 ± 2.11	3.08 ± 1.77 (−13%)	n.s.	3.04 ± 1.91	2.82 ± 1.85 (−7%)
	CR_{mass} (g)	n.s.	10.60 ± 6.86	8.42 ± 4.49 (−21%)	n.s.	40.28 ± 29.92	30.26 ± 19.77 (−25%)
	BG_{mass} (g)	n.s.	14.15 ± 8.74	11.50 ± 5.87 (−19%)	n.s.	43.32 ± 31.30	33.09 ± 21.02 (−24%)
Allometric growth relationship	D/H_{March}	n.s.	0.17 ± 0.04	0.18 ± 0.04 (+6%)	n.s.	0.18 ± 0.07	0.19 ± 0.07 (+6%)
	$D_{increment}/H_{increment}$	n.s.	0.20 ± 0.29	0.28 ± 0.33 (+40%)	n.s.	0.25 ± 0.19	0.37 ± 0.53 (+48%)
	$D/H_{September}$	n.s.	0.16 ± 0.04	0.17 ± 0.04 (+6%)	n.s.	0.19 ± 0.06	0.20 ± 0.08 (+5%)
	$TR_{lenght}/H_{September}$	n.s.	0.70 ± 0.20	0.70 ± 0.22 (0%)	**	0.90 ± 0.21	1.10 ± 0.34 (+22%)
	CR_{mass}/ST_{mass}	n.s.	0.65 ± 0.23	0.69 ± 0.36 (+6%)	*	1.64 ± 0.52	1.88 ± 0.60 (+15%)
	FR_{mass}/L_{mass}	n.s.	0.55 ± 0.25	0.54 ± 0.22 (−2%)	n.s.	0.26 ± 0.18	0.26 ± 0.19 (0%)
	FR_{mass}/ST_{mass}	n.s.	0.23 ± 0.11	0.24 ± 0.10 (+4%)	n.s.	0.16 ± 0.11	0.19 ± 0.12 (+19%)
	FR_{mass}/CR_{mass}	n.s.	0.36 ± 0.14	0.39 ± 0.21 (+8%)	n.s.	0.11 ± 0.08	0.11 ± 0.06 (0%)
	$FR_{mass}/L + ST + CR_{mass}$	n.s.	0.11 ± 0.04	0.11 ± 0.04 (0%)	n.s.	0.05 ± 0.03	0.05 ± 0.03 (0%)
	BG/AG	n.s.	0.61 ± 0.20	0.62 ± 0.20 (+2%)	n.s.	1.09 ± 0.34	1.17 ± 0.37 (+7%)

Levels of significance: * $p < 0.05$; ** $p < 0.01$; n.s., not significant. Abbreviations: D—root collar diameter, $D_{increment}$—root collar diameter increment, H—stem height, $H_{increment}$—stem height increment, L—leaf, TR—tap root, ST—stem, AG—aboveground, FR—fine root, CR—coarse root, BG—belowground, mass—dry biomass.

3.4. Effect of P Fertilization on Sapling Growth

Fertilization with P did not have a positive effect on the growth of common beech and sessile oak saplings. The lower mean values of almost all measured growth parameters in the saplings fertilized with P compared to those non-fertilized for both species (Table 3) indicate a negative effect of P fertilization on common beech and sessile oak growth. Moreover, P fertilization significantly reduced TR_{length} in common beech by 14% and FR_{mass} in sessile oak by 25%. In addition, in common beech, fertilization with P significantly decreased the ratio $TR_{length}/H_{September}$ (Table 3).

Table 3. Mean values ± SD of growth and allometric growth relationship parameters for common beech and sessile oak saplings fertilized with phosphorus (+P) and non-fertilized with phosphorus (−P), with the main effect of phosphorus fertilization (P effect) as calculated with a factorial ANOVA (+P vs. −P saplings). Relative values in parenthesis indicate negative (red) and positive (green) differences between the measured parameters of +P compared to −P saplings.

Parameters		Common Beech			Sessile Oak		
		P Effect	**+P**	**−P**	**P Effect**	**+P**	**−P**
Growth	D_{March} (mm)	n.s.	7.59 ± 2.18 (−4%)	7.89 ± 1.99	n.s.	7.15 ± 2.16 (−10%)	7.92 ± 2.21
	$D_{increment}$ (mm)	n.s.	1.68 ± 1.20 (−18%)	2.06 ± 1.22	n.s.	4.23 ± 2.67 (−6%)	4.51 ± 2.33
	$D_{September}$ (mm)	n.s.	9.27 ± 2.87 (−7%)	9.96 ± 2.53	n.s.	11.38 ± 3.18 (−8%)	12.43 ± 3.59
	H_{March} (cm)	n.s.	45.65 ± 13.85 (−2%)	46.69 ± 16.45	n.s.	45.13 ± 21.28 (−3%)	46.54 ± 19.92
	$H_{increment}$ (cm)	n.s.	12.23 ± 6.65 (+2%)	11.97 ± 8.19	n.s.	20.51 ± 9.93 (−3%)	21.15 ± 11.32
	$H_{September}$ (cm)	n.s.	57.89 ± 15.55 (−1%)	58.66 ± 16.60	n.s.	65.64 ± 23.08 (−3%)	67.70 ± 23.78
	L_{area} (m^2)	n.s.	0.21 ± 0.19 (−16%)	0.25 ± 0.18	n.s.	0.27 ± 0.19 (−23%)	0.35 ± 0.21
	TR_{length} (cm)	*	36.72 ± 14.16 (−14%)	42.71 ± 9.85	n.s.	63.53 ± 16.43 (+4%)	61.21 ± 16.49
	L_{mass} (g)	n.s.	6.53 ± 5.96 (−12%)	7.40 ± 4.30	n.s.	11.92 ± 7.05 (−22%)	15.29 ± 10.08
	ST_{mass} (g)	n.s.	16.75 ± 16.14 (−4%)	17.49 ± 12.95	n.s.	18.52 ± 12.88 (−21%)	23.55 ± 18.71
	AG_{mass} (g)	n.s.	23.29 ± 21.63 (−6%)	24.89 ± 16.81	n.s.	30.43 ± 19.52 (−22%)	38.84 ± 28.02
	FR_{mass} (g)	n.s.	2.99 ± 2.08 (−18%)	3.64 ± 1.77	*	2.51 ± 1.47 (−25%)	3.35 ± 2.14
	CR_{mass} (g)	n.s.	9.10 ± 6.80 (−8%)	9.92 ± 4.80	n.s.	31.60 ± 21.51 (−19%)	38.95 ± 29.10
	BG_{mass} (g)	n.s.	12.09 ± 8.62 (−11%)	13.56 ± 6.24	n.s.	34.11 ± 22.28 (−19%)	42.29 ± 30.73
Allometric growth relationship	D/H_{March}	n.s.	0.17 ± 0.03 (−6%)	0.18 ± 0.05	n.s.	0.19 ± 0.08 (0%)	0.19 ± 0.05
	$D_{increment}/H_{increment}$	n.s.	0.20 ± 0.22 (−31%)	0.29 ± 0.38	n.s.	0.27 ± 0.28 (−23%)	0.35 ± 0.50
	$D/H_{September}$	n.s.	0.16 ± 0.04 (−6%)	0.17 ± 0.04	n.s.	0.19 ± 0.08 (−5%)	0.20 ± 0.07
	$TR_{lenght}/H_{September}$	**	0.64 ± 0.20 (−16%)	0.76 ± 0.20	n.s.	1.03 ± 0.32 (+6%)	0.97 ± 0.28
	CR_{mass}/ST_{mass}	n.s.	0.68 ± 0.35 (+3%)	0.66 ± 0.25	n.s.	1.79 ± 0.57 (+3%)	1.74 ± 0.57
	FR_{mass}/L_{mass}	n.s.	0.56 ± 0.27 (+4%)	0.54 ± 0.19	n.s.	0.27 ± 0.22 (+8%)	0.25 ± 0.15
	FR_{mass}/ST_{mass}	n.s.	0.23 ± 0.12 (−4%)	0.24 ± 0.09	n.s.	0.18 ± 0.13 (0%)	0.18 ± 0.09
	FR_{mass}/CR_{mass}	n.s.	0.35 ± 0.14 (−13%)	0.40 ± 0.21	n.s.	0.11 ± 0.08 (0%)	0.11 ± 0.06
	$FR_{mass}/L + ST + CR_{mass}$	n.s.	0.11 ± 0.04 (0%)	0.11 ± 0.04	n.s.	0.05 ± 0.04 (0%)	0.05 ± 0.03
	BG/AG	n.s.	0.61 ± 0.20 (−2%)	0.62 ± 0.20	n.s.	1.16 ± 0.36 (+5%)	1.10 ± 0.35

Levels of significance: * $p < 0.05$; ** $p < 0.01$; n.s., not significant. Abbreviations: D—root collar diameter, $D_{increment}$—root collar diameter increment, H—stem height, $H_{increment}$—stem height increment, L—leaf, TR—tap root, ST—stem, AG—aboveground, FR—fine root, CR—coarse root, BG—belowground, mass—dry biomass.

3.5. Effect of Provenance on Sapling Growth

Provenance significantly affected only $D_{increment}$ in common beech and FR_{mass} in sessile oak saplings. Common beech originating from KA provenance had a 25% higher $D_{increment}$ compared to SB provenance. Sessile oak from KA provenance had a 28% higher FR_{mass} compared to SB provenance. In addition, ratios D/H_{March} and $D/H_{September}$ in common beech, as well as ratios FR_{mass}/L_{mass}, FR_{mass}/ST_{mass}, FR_{mass}/CR_{mass} and $FR_{mass}/L + ST + CR_{mass}$ in sessile oak were significantly higher in KA compared to SB provenance (Table 4).

3.6. Effect of Drought, P Fertilization and Provenance Interactions on Sapling Growth

Interactions of P fertilization × provenance, as well as drought × P fertilization × provenance, did not significantly affect any of the measured growth and/or allometric growth relationship parameters for both species (Tables A3 and A4). However, the interaction of drought × P fertilization significantly affected FR_{mass} and the ratios FR_{mass}/ST_{mass}, FR_{mass}/CR_{mass} and $FR_{mass}/L + ST + CR_{mass}$ in common beech (Table A3). An LSD post hoc test revealed a significantly lower FR_{mass} in drought-treated saplings fertilized with P compared to other treatments (Figure 3A), as well as significantly lower ratios of FR_{mass}/ST_{mass}, FR_{mass}/CR_{mass} and $FR_{mass}/L + ST + CR_{mass}$ in drought-treated saplings fertilized with P compared to drought-treated saplings non-fertilized with P (Figure 3B). The interaction of drought × provenance significantly affected the ratio $D_{increment}/H_{increment}$ in sessile oak (Table A4). An LSD post hoc test revealed a significantly higher $D_{increment}/H_{increment}$ ratio in drought-treated sessile oak saplings originating from KA compared to SB provenance, as well as compared to regularly watered sessile oak saplings originating from KA and SB provenances (Figure 4).

Table 4. Mean values ± SD of growth and allometric growth relationship parameters for common beech and sessile oak saplings originated from Karlovac (KA) and Slavonski Brod (SB) provenances, with the main effect of provenance (Pr effect) as calculated with a factorial ANOVA (saplings from KA vs. SB provenance). Relative values in parenthesis indicate negative (red) and positive (green) differences between the measured parameters of saplings originating from SB compared to KA provenance.

Parameters		Common Beech			Sessile Oak		
		Pr Effect	KA	SB	Pr Effect	KA	SB
Growth	D_{March} (mm)	n.s.	7.96 ± 2.11	7.52 ± 2.05 (−6%)	n.s.	7.65 ± 2.39	7.41 ± 2.03 (−3%)
	$D_{increment}$ (mm)	*	2.14 ± 1.21	1.60 ± 1.17 (−25%)	n.s.	4.26 ± 2.35	4.49 ± 2.66 (+5%)
	$D_{September}$ (mm)	n.s.	10.10 ± 2.57	9.12 ± 2.79 (−10%)	n.s.	11.91 ± 3.19	11.90 ± 3.66 (0%)
	H_{March} (cm)	n.s.	44.55 ± 16.70	47.79 ± 13.37 (+7%)	n.s.	45.84 ± 19.40	45.83 ± 21.78 (0%)
	$H_{increment}$ (cm)	n.s.	12.88 ± 7.71	11.33 ± 7.12 (−12%)	n.s.	19.21 ± 10.35	22.46 ± 10.70 (+17%)
	$H_{September}$ (cm)	n.s.	57.43 ± 15.49	59.11 ± 16.62 (+3%)	n.s.	65.05 ± 22.41	68.28 ± 24.34 (+5%)
	L_{area} (m^2)	n.s.	0.24 ± 0.17	0.22 ± 0.20 (−8%)	n.s.	0.29 ± 0.18	0.32 ± 0.22 (+10%)
	TR_{length} (cm)	n.s.	39.79 ± 12.24	39.64 ± 12.89 (0%)	n.s.	60.23 ± 18.07	64.51 ± 14.44 (+7%)
	L_{mass} (g)	n.s.	7.30 ± 4.72	6.64 ± 5.64 (−9%)	n.s.	13.29 ± 7.57	13.92 ± 9.98 (+5%)
	ST_{mass} (g)	n.s.	18.06 ± 14.82	16.18 ± 14.39 (−10%)	n.s.	19.99 ± 13.90	22.08 ± 18.26 (+10%)
	AG_{mass} (g)	n.s.	25.36 ± 19.12	22.81 ± 19.57 (−10%)	n.s.	33.28 ± 20.92	36.00 ± 27.59 (+8%)
	FR_{mass} (g)	n.s.	3.56 ± 1.79	3.06 ± 2.08 (−14%)	*	3.41 ± 2.04	2.45 ± 1.56 (−28%)
	CR_{mass} (g)	n.s.	10.21 ± 6.15	8.81 ± 5.56 (−14%)	n.s.	35.39 ± 25.51	35.16 ± 26.21 (−1%)
	BG_{mass} (g)	n.s.	13.77 ± 7.73	11.88 ± 7.26 (−14%)	n.s.	38.80 ± 26.98	37.60 ± 27.32 (−3%)
Allometric growth relationship	D/H_{March}	*	0.19 ± 0.04	0.16 ± 0.04 (−16%)	n.s.	0.19 ± 0.07	0.18 ± 0.07 (−5%)
	$D_{increment}/H_{increment}$	n.s.	0.29 ± 0.38	0.20 ± 0.21 (−31%)	n.s.	0.37 ± 0.53	0.25 ± 0.21 (−32%)
	$D/H_{September}$	*	0.18 ± 0.04	0.16 ± 0.04 (−11%)	n.s.	0.20 ± 0.07	0.19 ± 0.07 (−5%)
	$TR_{lenght}/H_{September}$	n.s.	0.71 ± 0.22	0.69 ± 0.19 (−3%)	n.s.	0.98 ± 0.33	1.01 ± 0.26 (+3%)
	CR_{mass}/ST_{mass}	n.s.	0.68 ± 0.34	0.66 ± 0.27 (−3%)	n.s.	1.82 ± 0.61	1.70 ± 0.52 (−7%)
	FR_{mass}/L_{mass}	n.s.	0.54 ± 0.19	0.56 ± 0.27 (+4%)	**	0.31 ± 0.21	0.21 ± 0.13 (−32%)
	FR_{mass}/ST_{mass}	n.s.	0.23 ± 0.09	0.23 ± 0.11 (0%)	***	0.22 ± 0.13	0.14 ± 0.08 (−36%)
	FR_{mass}/CR_{mass}	n.s.	0.37 ± 0.14	0.38 ± 0.21 (+3%)	**	0.13 ± 0.08	0.09 ± 0.05 (−31%)
	$FR_{mass}/L + ST + CR_{mass}$	n.s.	0.11 ± 0.04	0.11 ± 0.05 (0%)	**	0.06 ± 0.04	0.04 ± 0.02 (−33%)
	BG/AG	n.s.	0.61 ± 0.17	0.62 ± 0.22 (+2%)	n.s.	1.17 ± 0.38	1.09 ± 0.33 (−7%)

Levels of significance: * $p < 0.05$; ** $p < 0.01$, *** $p < 0.001$; n.s., not significant. Abbreviations: D—root collar diameter, $D_{increment}$—root collar diameter increment, H–stem height, $H_{increment}$—stem height increment, L—leaf, TR—tap root, ST—stem, AG—aboveground, FR—ine root, CR—coarse root, BG—belowground, mass–dry biomass.

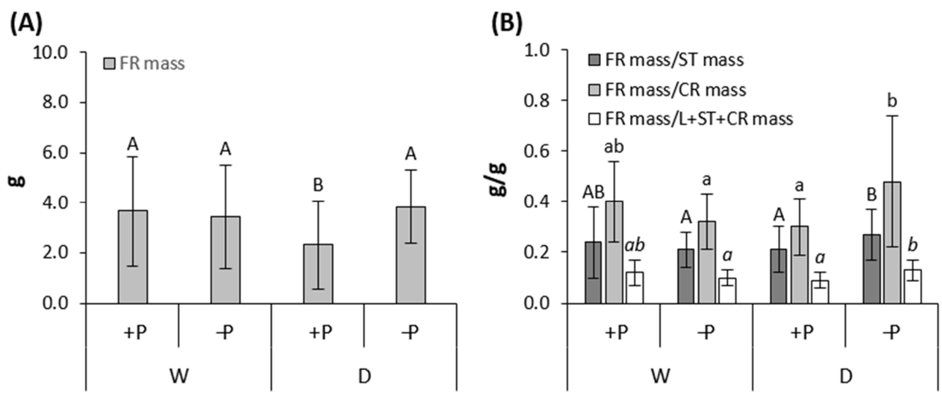

Figure 3. Mean values ± SD of fine root dry mass (FR_{mass}) in common beech saplings (**A**), as well as mean ratios ± SD of fine root/stem dry mass (FR_{mass}/ST_{mass}), fine root/coarse root dry mass (FR_{mass}/CR_{mass}) and fine root/total dry mass of leaves, stem and coarse root ($FR_{mass}/L + ST + CR_{mass}$) in common beech saplings (**B**), which were regularly watered (W), drought-treated (D), fertilized with phosphorus (+P) and non-fertilized with phosphorous (−P). Different capital (for FR_{mass} and FR_{mass}/ST_{mass}), small (for FR_{mass}/CR_{mass}) and italic small (for $FR_{mass}/L + ST + CR_{mass}$) letters indicate significant differences among W/+P, W/−P, D/+P and D/−P saplings at $p < 0.05$.

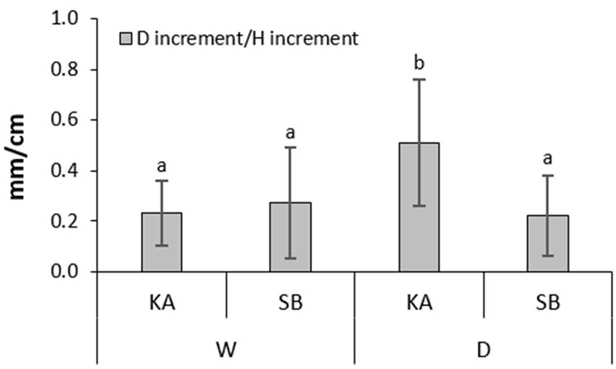

Figure 4. Mean ratio ± SD of root collar diameter increment/stem height increment ($D_{increment}/H_{increment}$) of regularly watered (W) and drought-treated (D) sessile oak saplings originated from Karlovac (KA) and Slavonski Brod (SB) provenances. Different small letters indicate significant differences among W/KA, W/SB, D/KA and D/SB saplings at $p < 0.05$.

4. Discussion

The investigated saplings of common beech and sessile oak grew with the same dynamics in the period between transplanting from natural habitats (March 2021) and the beginning of the research (March 2022). This is confirmed by a similar D_{March} and H_{March} at the beginning of the study (in March 2022) in regularly watered and drought-treated saplings (Table 2), in saplings fertilized and non-fertilized with P (Table 3) and in saplings originated from KA and SB provenances (Table 4). Such a result justifies the further interpretation of the obtained results during the growing season of 2022 when the investigation was conducted.

4.1. Effect of Drought on Sapling Growth

According to previous research carried out on common beech and sessile oak, a Ψ (measured before dawn) higher than −0.4 MPa indicates a regular water supply, while a value lower than −2.0 MPa suggests severe drought stress [77–82]. Thus, in our case, common beech and sessile oak saplings treated with drought experienced severe drought stress (Figure 1 and Table 1).

The negative effect of drought on the growth of aboveground and belowground organs, as well as its positive effect on ratios between the growth of belowground and aboveground organs in both species (Table 2), aligns with the findings of previous research conducted under experimental conditions [16,17,19,66,83–88]. According to Brunner et al. [89], such a response of plants to drought is related to optimizing water uptake and simultaneously minimizing water loss from transpiration.

However, our results indicate that the impact of drought on the growth of sessile oak was more negative than that on common beech (Table 2). Under favorable environmental conditions after spring growth, the saplings of forest trees (including common beech and sessile oak) usually have a subsequent secondary and/or tertiary growth that occurs during the summer [90–92]. Their subsequent summer growth is accompanied by the production of new leaves and xylem vessels, which increases their leaf area and stem diameter [90–100]. Accordingly, the regularly watered beech saplings had only secondary stem growth (which ended in mid-June), while sessile oak saplings had secondary and tertiary stem growth (which ended in mid-July). In drought-treated saplings, secondary and/or tertiary stem growth was almost completely absent for both species (unpublished data). This quite well explains why the negative impact of the drought was more pronounced in sessile oak than in common beech (Table 2).

The significantly higher ratios between the growth of tap root and stem in the sessile oak treated with drought compared to regular watering (Table 2) confirm its very pronounced adaptation capacity to drought [101,102]. This adaptation is manifested by deeper rooting at the expense of stem height growth and/or the investment of more dry mass in the coarse root than in the stem [16,17,19,88].

4.2. Effect of P Fertilization and Interaction Drought × P Fertilization on Sapling Growth

In both species, the mean values of almost all measured growth parameters in saplings fertilized with P were lower compared to saplings non-fertilized with P, indicating a negative effect of P fertilization on the growth of common beech and sessile oak saplings (Table 3). Such results are contrary to earlier reports about the positive effect of P fertilization on the growth of some forest trees [39,44,46,103].

According to our results, the leaf P concentrations of both species fertilized with P were quite high (Figure 2), indicating their almost excessive (luxury) nutrition with P [76]. According to earlier reports, the luxury nutrition of plants with P in natural conditions is a very rare phenomenon. This mostly happens in species adapted to habitats with a low soil P concentration when they are suddenly exposed to a higher soil P concentration, which negatively affects their growth [59–61,104–108]. The soils of both provenances are poorly supplied with P [16]. That might explain the worse growth of common beech and sessile oak saplings fertilized with P compared to those non-fertilized with P (Table 3). In addition, the significantly lower tap root length and tap root length/stem height ratio in common beech, as well as fine root mass in sessile oak fertilized with P compared to non-fertilized with P (Table 3), aligns very well with the results of an earlier study. This study was conducted on the model species *Arabidopsis thaliana*, which responds to a high P concentration in the growth substrate by producing a shallow root system architecture and reducing primary root growth, root apical meristem size and meristematic activity [59].

However, a few studies carried out on common beech and/or sessile oak determined quite high leaf P concentrations which did not have a negative impact on their growth [62,67,109] and physiology [69,70,110]. Moreover, Newnham and Carlisle [67] point out that sessile oak achieves the best growth at a leaf P concentration of 2.2 mg/g DW, which roughly corresponds to our leaf P concentration of sessile oak fertilized with P (Figure 2). This suggests that in addition to excessive P nutrition, some other factor could negatively affect the growth of our common beech and sessile oak saplings. According to Güsewell [111], a N/P ratio <10 and >20 in plant biomass often corresponds to limited biomass production due to an unfavorable balance in plant nutrition with N or P. In our case, the N/P ratio in the leaves of both species fertilized with P was 11, whereas in the non-fertilized, it was 15 (Table A2). This indicates that an unfavorable N/P ratio in the leaves could also be one of the reasons for the worse growth of the common beech and the sessile oak saplings fertilized with P compared to those non-fertilized with P.

The drought in combination with P fertilization significantly reduced fine root mass in common beech, unlike the other combinations of water and P fertilization treatments (Figure 3A). Such a result is in accordance with earlier reports on the negative effect of drought on fine root growth in common beech [66,112–117]. Additionally, similar negative effects have been reported in common beech for elevated P concentrations in the substrate and/or excessive plant nutrition with P [59–61]. It is also consistent with earlier findings that indicate common beech, when in its natural habitats, tends to exhibit reduced fine root mass under conditions of high soil mineral nutrient concentrations compared to lower concentrations [71,118–120]. In addition, the ratios of fine root growth and growth of other aboveground organs in common beech under the impact of drought and fertilization with P were also significantly lower compared to the impact of drought and non-fertilization with P (Figure 3B). Such results indicate that P fertilization could have a negative effect on the ability of common beech to adapt to drought because of an unfavorable allometric growth relationship between the fine root (responsible for the uptake of water and mineral nutrients) and other organs (especially leaves and stems responsible for transpiration and/or assimilation).

4.3. Effect of Provenance and Interaction Drought × Provenance on Sapling Growth

Previous research indicates that saplings of forest trees with a higher root collar diameter/stem height ratio have greater mechanical stability, making them more resistant to storms and heavy snow drifts [17,121]. Higher maximum snow depths in months with snow cover in KA compared to SB provenance [16] could explain the significantly higher stem diameter increment, as well as stem diameter/stem height ratios in common beech saplings from KA provenance (Table 4). Furthermore, forest trees have better fine root growth in soils with a lower proportion of silt and clay, as opposed to a higher composition of these soil components [119,122]. A lower proportion of silt and clay, as well as a higher proportion of sand in the soil of KA provenance compared to SB provenance [16], could explain the significantly higher fine root mass and ratios between fine root mass and mass of the other organs in sessile oak saplings from KA provenance (Table 4). Such results indicate a genetic differentiation between common beech and/or sessile oak provenances as a consequence of adaptation to specific local habitat conditions.

European oaks from provenances with lower annual precipitation respond to experimentally induced drought with a higher root collar diameter/stem height ratio compared to provenances with higher annual precipitation. It suggests a more significant reinforcement of the root system, prioritizing efficient water uptake from arid soil conditions, at the cost of stem height growth in dry provenances compared to wet ones [17,19]. However, our result was contrary. Despite a lower annual precipitation in the period from 1949 to 2019 in SB than in KA provenance [16], drought-treated sessile oak saplings from SB provenance had a significantly lower stem diameter/stem height increment ratio compared to KA provenance (Figure 4). However, a similar stem diameter/stem height increment ratio in regularly watered saplings of both provenances compared to a significantly higher stem diameter/stem height increment ratio in drought-treated saplings from KA than from SB provenance indicates a higher phenotypic plasticity of saplings from KA provenance (Figure 4). According to earlier reports, changes in plant phenotypic plasticity can be triggered by epigenetic imprinting, which helps them adapt to drought [123]. In the period from 2016 to 2020 during the saplings' growth in their natural habitats, more dry months were recorded in KA than in SB provenance [16]. This could have triggered epigenetic changes in the sessile oak from KA provenance and resulted in a higher stem diameter/stem height increment ratio under the impact of experimentally induced drought (Figure 4).

5. Conclusions

The drought had a negative impact on the growth of both species but stimulated the growth of their belowground organs compared to those aboveground. Such an effect of drought on the growth and the allometric growth relationship between belowground and aboveground organs was more pronounced in sessile oak than in common beech. P fertilization did not have a positive effect on the growth of common beech and sessile oak. Moreover, in common beech, P fertilization had a negative effect on the tap root length and tap root length/stem height ratio, as well as on the fine root mass in sessile oak. Therefore, P fertilization during the nursery production of common beech and sessile oak saplings would probably not improve their quality. In the case of common beech, in contrast to sessile oak, P fertilization in interaction with drought had a negative effect on fine root mass and the ratios of fine root mass/mass of other aboveground organs, which could reduce its adaptive capacity to drought. This indicates that P fertilization could have a more negative impact on the survival of common beech saplings, compared to sessile oak, after transplanting into drought-affected natural habitats. It could reduce the biodiversity of common beech and sessile oak mixed stands established and/or regenerated with nursery-produced saplings that were fertilized with P.

Significantly different root collar diameter increments and root collar diameter/stem height ratios between common beech provenances could indicate its genetic differentiation as a consequence of adaptation to different snow depths during the winter months in its natural habitats. A significantly different fine root mass and the ratios of fine root mass/mass of other organs between sessile oak provenances could indicate its genetic differentiation as a consequence of adaptation to different soil mechanical compositions in its natural habitats. Significantly different root collar diameter/height growth increment ratios between sessile oak saplings treated with drought from KA and SB provenances could indicate its different phenotypic plasticity, as a consequence of its adaptation to the different frequency of dry periods in its natural habitats.

Author Contributions: Conceptualization, A.V. and K.S.; methodology, A.V., K.S., S.B. and Ž.Š.; validation, K.S.; formal analysis, A.V and K.S.; investigation A.V., K.S., S.B., Ž.Š., D.K., I.K.B., T.K., M.B. (Marko Bačurin) and M.B. (Magdalena Brener); resources, K.S.; data curation, A.V., K.S. and S.B.; writing—original draft preparation, A.V.; writing—review and editing, K.S., S.B., Ž.Š., D.K., I.K.B., T.K., M.B. (Marko Bačurin) and M.B. (Magdalena Brener); visualization, A.V., K.S. and Ž.Š.; supervision, K.S.; project administration, K.S. and A.V.; funding acquisition, K.S. All authors have read and agreed to the published version of the manuscript.

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Data Availability Statement: The data in this study are available from the corresponding author upon request.

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Conflicts of Interest: The authors declare no conflict of interest.

Appendix A

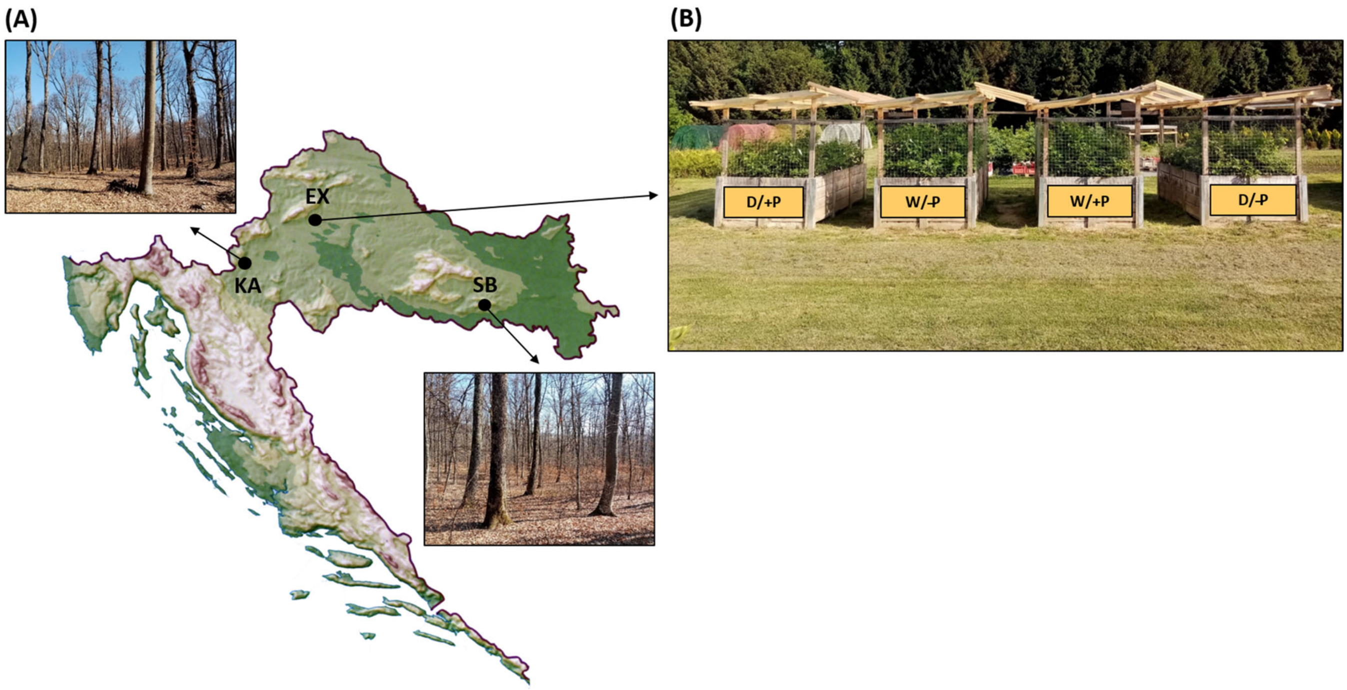

Figure A1. The geographical location of provenances Karlovac (KA) and Slavonski Brod (SB) and the common garden experiment (EX) on a map of the Republic of Croatia (**A**), as well as the appearance of the common garden experiment during the growing season of 2022 when the investigation was conducted (**B**).

Table A1. pH reaction and the concentration of water-extractable mineral nutrition in substrate sampled from the regularly watered and phosphorus fertilization treatment (W/+P), regularly watered and non-phosphorus fertilization treatment (W/−P), drought and phosphorus fertilization treatment (D/+P) and drought and non-phosphorus fertilization treatment (D/−P). A description of water-extractable mineral nutrition concentration was taken from Page et al. [74].

Parameter	W/+P		W/−P		D/+P		D/−P	
	Values	Description	Values	Description	Values	Description	Values	Description
pH (H_2O)	6.33	Slightly acidic	6.88	Neutral	6.81	Neutral	7.07	Neutral
PO_4^{3-} (mg/L)	9.7	High	3.31	Moderate	8.4	High	2.66	Moderate
NH_4^+ (mg/L)	12.13	Optimal	12.56	Optimal	13.24	Optimal	13.76	Optimal
NO_3^- (mg/L.)	69.8	Optimal	50.3	Optimal	59.5	Optimal	60	Optimal
N total (mg/L)	47.4	Medium–normal	46.57	Medium–normal	46.92	Medium–normal	49.69	Medium–normal
K^+ (mg/L)	59.9	Medium–normal	60.4	Medium–normal	63.0	Medium–normal	60.9	Medium–normal
Mg^{2+} (mg/L)	51.68	Moderate	53.52	Moderate	61.38	Moderate	54.53	Moderate
Ca^{2+} (mg/L)	196	Low	244	Low	204	Low	234	Low
Cl^- (mg/L)	57.3	Medium–normal	58.4	Medium–normal	54.8	Medium–normal	52.4	Low
Na^+ (mg/L)	35.49	Moderate	36.5	Moderate	34.79	Moderate	36.6	Moderate
E.C. (mS/cm)	1.198	Medium–normal	1.171	Medium–normal	1.185	Medium–normal	1.156	Medium–normal
Salt (%)	0.153	Medium–normal	0.149	Medium–normal	0.151	Medium–normal	0.147	Medium–normal

Table A2. Mean values ± SD of phosphorus (P), nitrogen (N), calcium (Ca), magnesium (Mg), potassium (K) and iron (Fe) concentration, as well as N/P ratio in leaves of common beech and sessile oak saplings treated by regular watering (W), drought (D), fertilization with phosphorus (+P) and non-fertilization with phosphorus (−P), originated from Karlovac (KA) and Slavonski Brod (SB) provenances. Bolded values indicate significant differences between W and D as well as +P and −P saplings, or between saplings originating from KA and SB provenances, as calculated with a factorial ANOVA at $p < 0.05$. Critical foliar concentration was taken from Mellert and Göttlein [76].

Species	Nutrients	Water Treatments		Fertilization Treatments		Provenances		Critical Foliar Concentration		
		W	D	+P	−P	KA	SB	Deficiency	Normal Range	Surplus
Common beech	P (mg g^{-1})	1.77 ± 0.34	1.70 ± 0.33	**1.91 ± 0.29**	**1.56 ± 0.29**	1.74 ± 0.29	1.73 ± 0.38	<1.2	1.2–1.9	>1.9
	N (mg g^{-1})	22.68 ± 4.55	21.53 ± 3.85	21.25 ± 4.44	22.96 ± 3.87	22.48 ± 4.13	21.73 ± 4.35	<18.7	18.7–23.2	>23.2
	Ca (mg g^{-1})	6.27 ± 2.00	5.99 ± 1.99	6.51 ± 2.32	5.75 ± 1.53	6.03 ± 2.12	6.23 ± 1.88	<6.7	6.7–14.0	>14.0
	Mg (mg g^{-1})	2.14 ± 0.42	2.16 ± 0.38	2.21 ± 0.41	2.09 ± 0.37	2.12 ± 0.37	2.18 ± 0.42	<1.1	1.1–2.3	>2.3
	K (mg g^{-1})	7.33 ± 1.58	7.31 ± 1.78	7.13 ± 1.86	7.51 ± 1.46	7.49 ± 1.79	7.15 ± 1.55	<6.1	6.1–9.7	>9.7
	Fe (mg g^{-1})	0.11 ± 0.03	0.12 ± 0.05	0.11 ± 0.03	0.12 ± 0.06	0.11 ± 0.05	0.12 ± 0.04	-	-	-
	N/P	13.27 ± 3.62	13.35 ± 3.92	**11.42 ± 3.07**	**15.20 ± 3.43**	13.24 ± 3.12	13.38 ± 4.33	-	-	-

Table A2. *Cont.*

Species	Nutrients	Water Treatments		Fertilization Treatments		Provenances		Critical Foliar Concentration		
		W	D	+P	−P	KA	SB	Deficiency	Normal Range	Surplus
Sessile oak	P (mg g^{-1})	1.72 ± 0.41	1.69 ± 0.40	**1.96 ± 0.26**	**1.46 ± 0.37**	1.73 ± 0.39	1.69 ± 0.42	<1.4	1.4–2.1	>2.1
	N (mg g^{-1})	20.94 ± 3.04	20.21 ± 2.93	20.77 ± 3.22	20.38 ± 2.77	20.47 ± 2.88	20.68 ± 3.14	<19.8	19.8–26.8	>26.8
	Ca (mg g^{-1})	9.78 ± 3.17	10.00 ± 3.46	10.27 ± 3.85	9.5 ± 2.64	9.70 ± 3.25	10.08 ± 3.39	<5.3	5.3–10.2	>10.2
	Mg (mg g^{-1})	2.47 ± 0.43	2.39 ± 0.40	2.44 ± 0.47	2.42 ± 0.37	2.40 ± 0.44	2.45 ± 0.40	<1.2	1.2–2.4	-
	K (mg g^{-1})	9.71 ± 1.98	9.43 ± 1.60	10.36 ± 1.91	8.78 ± 1.25	9.63 ± 1.96	9.51 ± 1.63	<7.2	7.2–11.4	>11.4
	Fe (mg g^{-1})	0.11 ± 0.05	0.12 ± 0.05	0.12 ± 0.06	0.11 ± 0.04	0.11 ± 0.04	0.12 ± 0.05	-	-	-
	N/P	13.13 ± 4.90	12.69 ± 3.84	**10.82 ± 2.41**	**15.00 ± 4.91**	12.68 ± 4.46	13.13 ± 4.34	-	-	-

Table A3. The main effects of drought (regularly watered vs. drought-treated saplings), phosphorus fertilization (saplings fertilized with phosphorus vs. non-fertilized with phosphorus), provenance (saplings originated from Karlovac vs. Slavonski Brod provenance) and their interactions on growth and allometric growth relationship parameters in common beech saplings, as calculated with a factorial ANOVA (F and *p* values). Bolded values indicate significant effects at *p* < 0.05.

	Parameter	Drought (D)		Fertilization (P)		Provenance (Pr)		D × P		D × Pr		P × Pr		D × P × Pr	
		F	*p*	F	*p*	F	*p*	F	*p*	F	*p*	F	*p*	F	*p*
Growth	D_{March} (mm)	0.029	0.866	0.502	0.480	1.019	0.315	1.370	0.245	0.248	0.620	0.323	0.571	0.384	0.537
	$D_{increment}$ (mm)	0.602	0.440	2.463	0.120	**4.957**	**0.029**	0.003	0.955	0.095	0.759	0.470	0.495	1.610	0.208
	$D_{September}$ (mm)	0.223	0.638	1.540	0.218	3.112	0.081	0.784	0.378	0.274	0.602	0.553	0.459	0.006	0.940
	H_{March} (cm)	0.000	0.983	0.107	0.744	1.050	0.308	0.065	0.799	0.170	0.681	0.090	0.765	1.117	0.293
	$H_{increment}$ (cm)	**10.433**	**0.002**	0.033	0.857	1.125	0.292	1.284	0.260	0.001	0.973	0.032	0.859	0.692	0.408
	$H_{September}$ (cm)	1.956	0.166	0.053	0.818	0.256	0.614	0.066	0.799	0.165	0.686	0.131	0.718	0.405	0.526
	L_{area} (m^2)	0.757	0.387	1.566	0.214	0.321	0.573	2.766	0.100	0.189	0.665	0.182	0.671	0.103	0.749
	TR_{length} (cm)	1.259	0.265	**5.585**	**0.020**	0.004	0.951	0.603	0.439	0.449	0.505	0.336	0.564	0.047	0.828
	L_{mass} (g)	0.781	0.379	0.642	0.425	0.377	0.541	1.153	0.286	0.081	0.776	0.169	0.682	0.000	0.988
	ST_{mass} (g)	2.118	0.149	0.059	0.809	0.386	0.536	0.549	0.461	0.005	0.945	0.004	0.952	0.163	0.687
	AG_{mass} (g)	1.783	0.185	0.158	0.692	0.402	0.528	0.718	0.399	0.001	0.981	0.024	0.877	0.091	0.764
	FR_{mass} (g)	1.470	0.229	2.778	0.099	1.652	0.202	**5.042**	**0.027**	0.004	0.948	0.052	0.821	0.132	0.718
	CR_{mass} (g)	3.261	0.074	0.459	0.500	1.341	0.250	0.089	0.766	0.232	0.631	0.367	0.546	0.016	0.901
	BG_{mass} (g)	2.959	0.089	0.906	0.344	1.516	0.222	0.642	0.425	0.130	0.719	0.174	0.678	0.000	0.995

Table A3. *Cont.*

	Parameter	Drought (D)		Fertilization (P)		Provenance (Pr)		D × P		D × Pr		P × Pr		D × P × Pr	
		F	*p*	F	*p*	F	*p*	F	*p*	F	*p*	F	*p*	F	*p*
Allometric growth relationship	D/H_{March}	0.119	0.731	0.996	0.321	**11.745**	**0.001**	0.619	0.434	0.094	0.760	1.153	0.286	0.009	0.923
	$D_{increment}/H_{increment}$	1.633	0.205	2.053	0.155	1.762	0.188	1.060	0.306	0.173	0.678	2.322	0.131	0.029	0.865
	$D/H_{September}$	1.946	0.167	2.553	0.114	**9.133**	**0.003**	2.352	0.129	0.011	0.915	1.010	0.318	0.167	0.683
	$TR_{lenght}/H_{September}$	0.015	0.903	**8.513**	**0.004**	0.316	0.575	1.837	0.179	0.101	0.752	0.438	0.510	0.449	0.505
	CR_{mass}/ST_{mass}	0.376	0.541	0.064	0.801	0.075	0.785	3.816	0.054	0.510	0.477	0.347	0.558	0.184	0.669
	FR_{mass}/L_{mass}	0.011	0.917	0.154	0.696	0.164	0.687	3.231	0.076	0.047	0.829	0.048	0.827	0.251	0.617
	FR_{mass}/ST_{mass}	0.139	0.710	0.533	0.467	0.018	0.894	**4.278**	**0.042**	0.215	0.644	0.123	0.727	0.518	0.474
	FR_{mass}/CR_{mass}	0.694	0.407	1.936	0.168	0.030	0.862	**13.164**	**0.000**	0.000	1.000	0.790	0.377	0.836	0.363
	$FR_{mass}/L + ST + CR_{mass}$	0.163	0.687	0.869	0.354	0.002	0.962	**8.957**	**0.004**	0.094	0.760	0.094	0.760	0.876	0.352
	BG/AG	0.017	0.896	0.025	0.876	0.056	0.814	0.861	0.356	0.175	0.677	0.048	0.827	0.025	0.874

Abbreviations: D—root collar diameter, $D_{increment}$—root collar diameter increment, H—stem height, $H_{increment}$—stem height increment, L—leaf, TR—tap root, ST—stem, AG—aboveground, FR—fine root, CR—coarse root, BG—belowground, mass—dry biomass.

Table A4. The main effects of drought (regularly watered vs. drought-treated saplings), phosphorus fertilization (saplings fertilized with phosphorus vs. non-fertilized with phosphorus), provenance (saplings originated from Karlovac vs. Slavonski Brod provenance) and their interactions on growth and allometric growth relationship parameters in sessile oak saplings, as calculated with a factorial ANOVA (F and p values). Bolded values indicate significant effects at $p < 0.05$.

	Parameter	Drought (D)		Fertilization (P)		Provenance (Pr)		D × P		D × Pr		P × Pr		D × P × Pr	
		F	*p*	F	*p*	F	*p*	F	*p*	F	*p*	F	*p*	F	*p*
Growth	D_{March} (mm)	0.707	0.403	2.874	0.094	0.282	0.597	0.673	0.414	0.946	0.333	0.039	0.844	0.013	0.910
	$D_{increment}$ (mm)	**6.663**	**0.011**	0.295	0.589	0.211	0.647	0.518	0.474	0.221	0.639	0.560	0.456	0.000	0.990
	$D_{September}$ (mm)	**6.096**	**0.015**	2.336	0.130	0.000	0.990	1.162	0.284	0.989	0.323	0.179	0.674	0.004	0.948
	H_{March} (cm)	1.974	0.164	0.111	0.740	0.000	0.997	0.003	0.957	1.373	0.245	0.082	0.775	0.110	0.741
	$H_{increment}$ (cm)	**10.623**	**0.002**	0.094	0.759	2.407	0.124	0.109	0.742	0.000	0.982	0.003	0.959	0.198	0.657
	$H_{September}$ (cm)	**7.416**	**0.008**	0.192	0.662	0.471	0.494	0.009	0.923	1.148	0.287	0.080	0.778	0.010	0.919
	L_{area} (m^2)	**4.404**	**0.039**	3.847	0.053	0.565	0.454	0.193	0.661	0.603	0.439	0.010	0.919	0.771	0.382
	TR_{length} (cm)	0.209	0.649	0.468	0.496	1.591	0.210	0.133	0.716	0.147	0.702	1.950	0.166	0.096	0.757
	L_{mass} (g)	2.124	0.149	3.539	0.063	0.121	0.729	0.113	0.737	1.355	0.248	0.131	0.719	0.138	0.711
	ST_{mass} (g)	**5.686**	**0.019**	2.405	0.125	0.416	0.521	0.060	0.807	1.480	0.227	0.098	0.755	0.189	0.665
	AG_{mass} (g)	**4.442**	**0.038**	2.930	0.090	0.306	0.582	0.081	0.776	1.510	0.222	0.115	0.735	0.179	0.673
	FR_{mass} (g)	0.329	0.567	**5.006**	**0.028**	**6.733**	**0.011**	0.026	0.872	0.373	0.543	0.008	0.928	0.000	0.994
	CR_{mass} (g)	3.618	0.060	1.949	0.166	0.002	0.965	0.010	0.919	0.023	0.879	0.798	0.374	0.038	0.846
	BG_{mass} (g)	3.422	0.068	2.190	0.143	0.047	0.830	0.008	0.931	0.035	0.852	0.734	0.394	0.034	0.854

Table A4. *Cont.*

Parameter		Drought (D)		Fertilization (P)		Provenance (Pr)		D × P		D × Pr		P × Pr		D × P × Pr	
		F	*p*	F	*p*	F	*p*	F	*p*	F	*p*	F	*p*	F	*p*
Allometric growth relationship	D/H_{March}	0.610	0.437	0.007	0.934	0.058	0.811	0.209	0.648	1.334	0.251	0.020	0.888	0.016	0.901
	$D_{increment}/H_{increment}$	1.998	0.161	1.187	0.279	2.425	0.123	0.159	0.691	**4.069**	**0.047**	0.074	0.787	1.175	0.281
	$D/H_{September}$	0.498	0.482	0.275	0.602	0.375	0.542	0.000	0.994	0.184	0.669	0.338	0.562	0.002	0.969
	$TR_{lenght}/H_{September}$	**11.186**	**0.001**	1.252	0.266	0.344	0.559	0.006	0.939	0.147	0.702	2.032	0.158	0.556	0.458
	CR_{mass}/ST_{mass}	**4.108**	**0.046**	0.187	0.666	1.098	0.298	0.011	0.915	0.611	0.436	0.008	0.929	1.168	0.283
	FR_{mass}/L_{mass}	0.026	0.873	0.269	0.605	**7.636**	**0.007**	0.704	0.404	0.025	0.875	0.506	0.479	0.068	0.795
	FR_{mass}/ST_{mass}	2.046	0.156	0.110	0.741	**13.779**	**0.000**	0.108	0.743	0.138	0.711	1.560	0.215	0.704	0.404
	FR_{mass}/CR_{mass}	0.001	0.970	0.021	0.885	**9.347**	**0.003**	0.319	0.573	0.000	0.993	0.761	0.385	0.091	0.764
	$FR_{mass}/L + ST + CR_{mass}$	0.163	0.688	0.051	0.821	**11.147**	**0.001**	0.348	0.557	0.014	0.906	1.175	0.281	0.134	0.715
	BG/AG	0.980	0.325	0.494	0.484	1.231	0.270	0.336	0.564	0.791	0.376	0.005	0.943	0.487	0.487

Abbreviations: D—root collar diameter, $D_{increment}$—root collar diameter increment, H—stem height, $H_{increment}$—stem height increment, L—leaf, TR—tap root, ST—stem, AG—aboveground, FR—fine root, CR—coarse root, BG—belowground, mass—dry biomass.

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