

DIFFERENTIAL RESPONSES OF *BETULA COSTATA* AND *B. SCHMIDTII* SEEDLINGS TO SOIL SUBSTRATE AND FERTILIZATION REGIMES: IMPLICATIONS FOR EFFECTIVE SEEDLING PRODUCTION

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1. Abstract

We investigated the effects of substrate × fertilization regimes on the growth and nutrient uptake of *Betula costata* and *B. schmidtii* seedlings. They were subjected to two soil treatments, i.e., pure artificial substrate and a mixture of artificial substrate and sand-masato, and five fertilization treatments, i.e., liquid fertilizer (LF, Fert1), Controlled-Release Fertilizer (CRF) in summer (Fert2), CRF in summer and fall (Fert3), long-term CRF (Fert4), and CRF + LF (Fert5). We measured growth parameters (the Root Collar Diameter (RCD), height (HT), and biomass allocations) and foliar nutrient concentrations and analyzed changes in soil chemical properties. *B. costata* and *B. schmidtii* responded differently to soil and fertilization regimes and the growth pattern did not follow the quantity of total nutrient input in this study. Overall, *B. costata* preferred the mixed soil and responded sensitively to different fertilization regimes but *B. schmidtii* did not. The total biomass of *B. costata* seedlings was the largest in the combination of CRF and LF (Fert5). *B. schmidtii* seedlings yielded similar biomass to all treatments except Fert1. The highest foliar N concentration was found in Fert4 and the lowest in Fert1 and Fert2 for *B. schmidtii*; there was no significant effect of either soil or fertilization regimes on foliar N concentration in *B. costata*. The CRF + LF (Fert5) treatment was compatible for *B. costata* but not for *B. schmidtii*. Therefore, this study implies that seedlings can be effectively produced through appropriate soil and fertilization methods suitable for each species' traits rather than increasing nutrient supply.

2. Keywords: Biomass allocation; Controlled release fertilizer; Fertilization regimes; Liquid fertilizer; Nutrient release pattern; Sand-masato

3. Introduction

Fertilization is an essential factor supporting tree growth and productivity. However, excessive or unregulated use of fertilizer has become a common practice in many countries, leading to a

negative impact on the environment, including nutrient leaching, alteration of soil physicochemical characteristics, and accumulation of heavy metals (Agbede 2010). Efficient fertilizer application for increasing tree growth can play an important role in achieving several of the Sustainable Development Goals (SDGs) and green economy (Qu et al. 2020). However, there are challenges in managing nutrients to increase yield and ensure resource sustainability in forest ecosystems, particularly regarding the amount, type, timing, and form of fertilizer to be used depending on the tree species and substrate types. Addressing these questions may help synchronize fertilizer application with plant nutritional needs for more efficient and eco-friendly fertilization. Therefore, it is necessary to investigate practical strategies for improving fertilizer application to increase tree growth and productivity while creating less environmental pollution.

Choosing the right fertilizer and understanding the nutrient availability and release pattern of applied fertilizer is crucial for providing the plants with sufficient nutrients depending on the season and nutritional needs of the plants (Dobrowolski et al. 2017). Liquid Fertilizer (LF) and Controlled-Release Fertilizers (CRFs) require different methods of application due to their unique effectiveness rates, properties, and release patterns. Liquid fertilizers are easily absorbed by plant roots or leaves, making them highly suitable for plants suffering from severe nutrient deficiencies. While LFs are commonly used for seedling production and quick nutrient boosts, they are also easily leached from the soil and more susceptible to volatilization. This quick-release nature of LFs suggests regular application to remain effective because it does not sustain soil for long time, making fertilization an expensive process. In contrast, CRFs are mainly nitrogenous fertilizers coated with different types of materials, which can reduce leaching. The use of CRF is an effective measure for improving fertilizers utilization, increase yield, and reducing environmental pollution (Li et al. 2022). Different variants of CRFs vary in total nutrient input amounts and recommended timing of application and thus differ in effectiveness. For example, Osmocote 11-11-17 has a controlled release of nutrients for about six to eight weeks, made possible by a specially developed coating. This special coating minimizes leaching influenced primarily by temperature, making it more effective in summer season when plants are actively growing. Due to its short-term controlled release, it can also be applied to some plant species during the fall season to catalyze root growth in preparation for the cold months. Another type of CRF is Osmocote 15-11-13 which has a longer duration of controlled release (i.e., 3-4 months) than Osmocote 11-11-17. Such a longer duration can ensure the availability of necessary nutrients during the entire growing season. This feature of CRF ensures adequate nutrient supply for plant uptake during and post growing season, resulting in increased yield, nutrient use efficiency, root growth, delayed leaf senescence, and reduced greenhouse gas emissions (Wang et al. 2015). Moreover, the application of a two-phase fertilizer, which combines the advantages of liquid and controlled-released fertilizers, is a promising method to fill-in the limitations of each type simultaneously. For instance, CRFs can be applied in combination with LF to compensate for the high leaching potential of liquid fertilizers. However, how these two forms of fertilizers and their combination perform using forest tree species, such as

the fast-growing *Betula costata* and *B. schmidtii*, remain unclear as their effects may vary depending on species' nutritional requirements and substrate characteristics.

Plant responses to fertilization are known to be influenced by substrate characteristics, such as pH and texture (Pascual et al. 2018; Yang et al. 2018). Soil pH is an important factor affecting nutrient absorption and uptake, which in turn can impact tree growth for instance, acidic soil conditions can increase micronutrient availability to plants, but reduce phosphorus availability, whereas alkaline conditions can have the opposite effect. As a result, pH can influence plant traits such as height, girth, biomass, and reproduction (Jiang et al. 2017). Substrate texture can also affect plant growth, with rooting depth facilitated by some substrate types depending on the plant species (Li et al. 2012).

Peat-based potting medium has been widely used as a growth medium, but its high cost and environmental impact on peatland ecosystems have led to research for alternative, more sustainable substrates (Abad et al. 2001, Benito et al. 2005). Information on how to lessen the use of peat-based substrates by adding other materials, such as sand and masato stones, may also be considered an efficient option for providing optimal growth conditions for plants. Masato stones are a form of substrate amendment that is widely used in some countries to grow sensitive plants due to their ability to promote faster root growth, plant development, and proper drainage. Stony soils also have a significant impact on soil physicochemical properties (Poesen & Lavee 1994). Several studies have found that incorporating stones or rock fragments into soil can improve water retention, infiltration, gas exchange processes, soil organic carbon, nutrient dynamics, and erosion susceptibility (Zhou et al. 2011, Rabot et al. 2018, Ceacero et al. 2020). This suggests that combining pure peat-based substrate with masato stones could allow for increased plant development while decreasing reliance on peat-based supplies.

The present study aims to investigate the interactive effects of substrate types and fertilization regimes on the growth and foliar nutrient concentrations of *B. costata* and *B. schmidtii* seedlings. We hypothesize that the interaction of substrate and fertilizer will significantly affect the growth and foliar nutrient concentrations of the seedlings. Specifically, we expect that a mixture of substrate types could amplify the positive effects of either liquid or controlled-release fertilizer on the growth and nutrient uptake of the seedlings. Additionally, we anticipate that the two species may respond differently to substrate media and various fertilization regimes. The findings of this study could help guide appropriate substrate and fertilizer management practices for producing high-quality seedlings.

4. Materials and Methods

4.1. Study site description

The experiment was conducted in a greenhouse at Chungnam National University (36°22'12"N, 127°21'17"E) in Yuseong-gu, Daejeon, Republic of Korea from April to October 2020. The

environmental data was collected using the weatherproof HOBO Pro v2 temperature/relative humidity data logger with built-in sensors that are durable in humid environments. These sensors were installed at 1.5 m above the ground in the middle of the greenhouse. During the experiment, the recorded monthly average temperature and humidity were 24.2°C and 72.6%, respectively (Figure 1). A knitted shade cloth was installed on the roof of the greenhouse, and the lower half of the window was kept open when necessary. Weed proliferation and pests were controlled using weedicide and pesticide (Etofenprox and Imidacloprid). The plants were irrigated using a sufficient amount of water for plant growth applied by sprinklers.

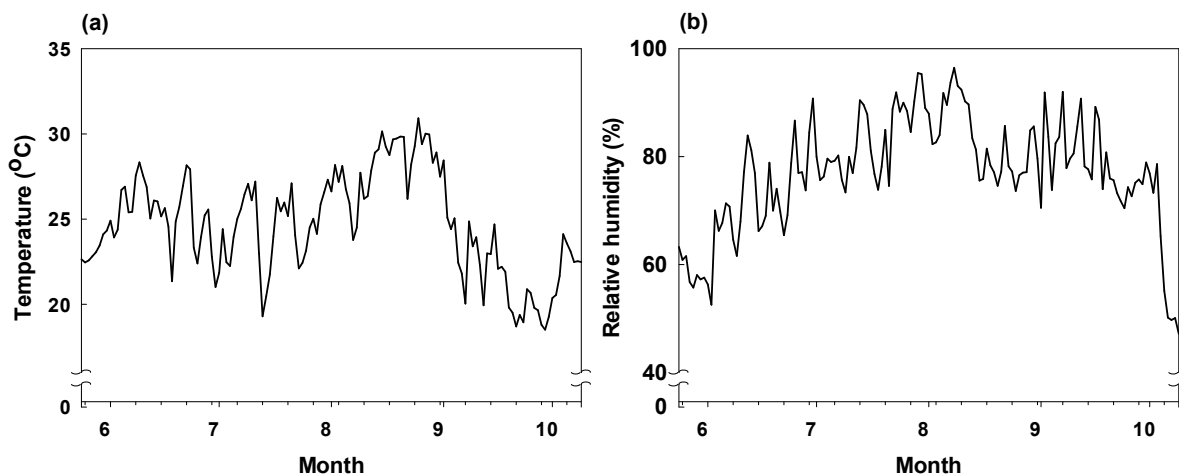


Figure 1: (a) Daily mean temperature and (b) relative humidity during the experiment.

4.2. Experimental materials and design

One-year-old bare root seedlings of *B. costata* and *B. schmidtii* were used in the study. Both species are deciduous broadleaved trees with contrasting shade and drought tolerances, growth rates, and soil preferences (Table 1). *B. costata* grows naturally in mixed coniferous and broadleaved forests, whereas *B. schmidtii* is usually present in temperate broad-leaved forests. Both species are widely used for the manufacture of pulp and other fiber-based products or for any tough and durable materials because of their dense wood characteristics.

	<i>Betula costata</i> Trautv.	<i>Betula schmidtii</i> Regel
Distribution	Northeast China, Subalpine regions of Korea	Russian Far East, China, Korea, Japan
Functional types	Deciduous broadleaved tree	Deciduous broadleaved tree
Habitat	Mixed forests of coniferous and broad-leaved trees at 600-2,500 m altitude; well-drained loamy soil	Temperate broad-leaved forests at 700-800 m altitude; rocky crests and stony slopes; well-drained loamy soil
Tolerance	High dry-tolerance	High cold-tolerance; low dry- and shade-tolerance

Growth rate	Fast growing	Moderate growth rate
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Table 1: Contrasting characteristics of *B. costata* and *B. schmidtii* seedlings used in the present study.

The chemical properties of the soil (artificial substrate and sand-masato) used in the study were analyzed before the treatment imposition (Table 2). The pure artificial substrate was acidic with a pH of 5.52, whereas the sand-masato was basic (i.e., 7.92). Organic Matter (OM), Total Nitrogen (TN), nitrate, ammonium, available phosphorus (AP), Cation Exchange Capacity (CEC), exchangeable cations were higher in pure artificial substrate than those in the sand-masato. Total nitrogen of the soil was 9.81 g pot⁻¹ in the pure artificial substrate and 7.31 g pot⁻¹ in the mixture of 70 % artificial substrate and 30 % sand-masato in volumetric ratio. Bulk densities (g cm⁻³) were 0.18, 0.5, and 1.15 for artificial substrate, mixture, and sand-masato, respectively.

	Artificial substrate			Sand-masato		
pH	5.52	(0.01)		7.92	(0.53)	
EC	0.58	(0.02)	dS m ⁻¹	0.46	(0.15)	dS m ⁻¹
OM	58.50	(1.14)	%	1.26	(0.03)	%
TN	283.38	(7.82)	mg L ⁻¹	36.41	(3.44)	mg kg ⁻¹
NO ₃ -N	230.83	(5.43)	mg L ⁻¹	21.72	(1.98)	mg kg ⁻¹
NH ₄ -N	16.83	(2.95)	mg L ⁻¹	9.42	(0.80)	mg kg ⁻¹
AP	394.27	(6.85)	mg L ⁻¹	3.54	(1.64)	mg kg ⁻¹
CEC	51.92	(1.15)	cmol ⁺ L ⁻¹	7.09	(0.30)	cmol ⁺ kg ⁻¹
Exchangeable cations						
K ⁺	13.76	(0.32)	cmol ⁺ L ⁻¹	0.23	(0.04)	cmol ⁺ kg ⁻¹
Ca ²⁺	19.72	(0.17)	cmol ⁺ L ⁻¹	5.92	(0.21)	cmol ⁺ kg ⁻¹
Mg ²⁺	13.53	(0.49)	cmol ⁺ L ⁻¹	0.71	(0.05)	cmol ⁺ kg ⁻¹
Na ⁺	4.91	(0.17)	cmol ⁺ L ⁻¹	0.22	(0.03)	cmol ⁺ kg ⁻¹
Soil texture of Sand-masato is loamy sand EC: Electrical Conductivity; OM: Organic Matter; TN: Total Nitrogen; AP: Available Phosphorus; CEC: Cation Exchange Capacity Standard errors are in parenthesis (n=3).						

Table 2: Soil properties used in this study.

Seedlings were planted in 35 L pots and allowed to acclimatize for several weeks before treatment imposition. The seedlings were subjected two soil treatments (i.e., pure artificial substrate and 70% artificial substrate+30% sand-masato, in volumetric ratio) and five fertilization treatments (Fert1-Fert5, see Table 3 for the details). These fertilization treatments differed in fertilizer type (i.e., liquid fertilizer or LF and controlled release fertilizer or CRF), fertilization method (i.e., LF at two weeks interval, CRF for short-term in summer, CRF short-term in summer and fall, and combined

LF and CRF fertilizer in summer), effectivity duration (i.e., weeks to months), and total N input ranging from 1.40 g to 5.25 g. CRFs are granulated fertilizers that are generally not affected by soil physical properties, microorganisms, soil acidity, and moisture content but gradually supply or release nutrients into the soil in response to temperature within a given period. We used Peters® Professional water-soluble fertilizer (N20-P20-K20) for the LF treatments and two types of CRF which are Osmocote® Start (N11-P11-K17, longevity 6-8 weeks) and Osmocote® Plus (N15-P11-K13, longevity 3-4 months) manufactured by ICL Specialty Fertilizers. A total of 200 seedlings (i.e., 2 species × 2 soil types × 5 fertilizations × 10 replicates) were used in the study following a completely randomized design.

Treatment	Fertilization method	Total nutrient input by fertilizer (g)			Other details
		N	P	K	
Fert1	1,000 dilution liquid fertilizer 1 L at 2 weeks interval (1g L ⁻¹)	1.40	0.63	1.19	Liquid Fertilizer
Fert2	Osmocote N11-P11-K17 (effective for 6-8 weeks) 17.5g in summer	1.93	0.84	2.47	Controlled Release Fertilizer-Short Term1
Fert3	Osmocote N11-P11-K17 17.5g in summer and fall	3.85	1.68	4.94	Controlled Release Fertilizer-Short Term2
Fert4	Osmocote N15-P11-K13 (effective for 3-4 months) 35g	5.25	1.68	3.78	Controlled Release Fertilizer-Long Term
Fert5	Osmocote N15-P11-K13 17g with liquid fertilizer in summer	3.55	1.25	2.66	Controlled Release Fertilizer-Long Term +Liquid Fertilizer

Table 3: Description of fertilization treatments employed in the experiment.

4.3. Growth measurement and calculation

The Root Collar Diameter (RCD) and seedling height (HT) were measured weekly using a digital caliper and a 2 m foldable ruler, respectively. The HT was measured from the soil surface up to the highest terminal bud of an orthotropic branch. At the end of the experiment, seedlings were harvested to determine the belowground and aboveground biomass allocations. To determine the biomass allocations, we classified the seedling components into leaf, stem, branch, fine root (< 2 mm), and coarse root (≥ 2 mm). The samples were oven-dried at 65°C for 72 hours in the laboratory.

Growth rate of RCD and HT was calculated as follows:

$$\text{Growth rate of RCD or HT (\%)} = 100 \times \frac{RCD \text{ or } HT_{t_2} - RCD \text{ or } HT_{t_1}}{RCD \text{ or } HT_{t_1}}$$

where RCD or HT_{t1} is the initial measured value and RCD or HT_{t2} is the final measured value. The RS (root to shoot) ratio was calculated by dividing belowground root (fine and coarse roots) mass with aboveground organ (leaves, stems, and branches) mass.

4.4. Leaf tissue and soil analyses

In this study, 2-5 healthy and fully expanded leaves were collected from each seedling at the end of the experiment. These leaves were mixed according to treatment and species, oven-dried at 65 °C for 72 hours, weighed, and then ground using a Wiley mill to pass through a 1 mm screen mesh. The foliar N and P concentrations were determined using an automated ion analyzer (Quik Chem AE, Lachat Instruments, Milwaukee, WI, USA). An atomic absorption spectrometer (AA280FS, Varian Inc., CA, USA) was used to determine foliar K concentrations.

Soil sampling and analysis were conducted before (n=3) and after (n=2) the experiment. Soil texture analysis was carried out using the hydrometer method. The soil pH was determined using a pH-meter (1:5 soil-water) method, Organic Matter (OM) and Total Nitrogen (TN) by the dry oxidation (utilizing C-N analyzer equipment) method, and available phosphorus (P) with the Lancaster method. The other soil properties such as Cation Exchange Capacity (CEC), electrical conductivity, and exchangeable K⁺, Ca²⁺, and Mg²⁺ were analyzed using the 1N ammonium acetate replacement leaching method, EC meter (1:5 soil-water) method, and 1N ammonium acetate leaching with the atomic absorption spectrophotometry method, respectively.

4.5. Statistical analysis

Two-way analysis of covariance (ANCOVA) was applied to investigate the effect of treatment (soil and fertilization) on seedling growth (RCD growth rate, HT growth rate, biomass) by removing any effect of covariates (initial root collar diameter of seedlings). Growth parameters (RCD, HT, dry weight biomass) were presented as adjusted means by the covariate. Tukey's HSD (honestly significant difference) test was used for post-hoc analysis. All statistical analyses were done by SAS 9.4 (SAS Institute, Cary, NC, USA).

5. Results

5.1. Effects of soil and fertilization regimes on the RCD and height growth

B. costata and *B. schmidtii* responded differently to soil and fertilization regimes. Soil and fertilization regimes respectively affected the RCD and HT growth rate of *B. costata*, whereas only fertilization tended to influence the RCD and HT of *B. schmidtii* (Figure 2 and 3; Table S1). The growth rate of RCD and HT increased in the mixture soil for *B. costata*. A reverse pattern was observed in *B. schmidtii*, although the result was not statistically significant.

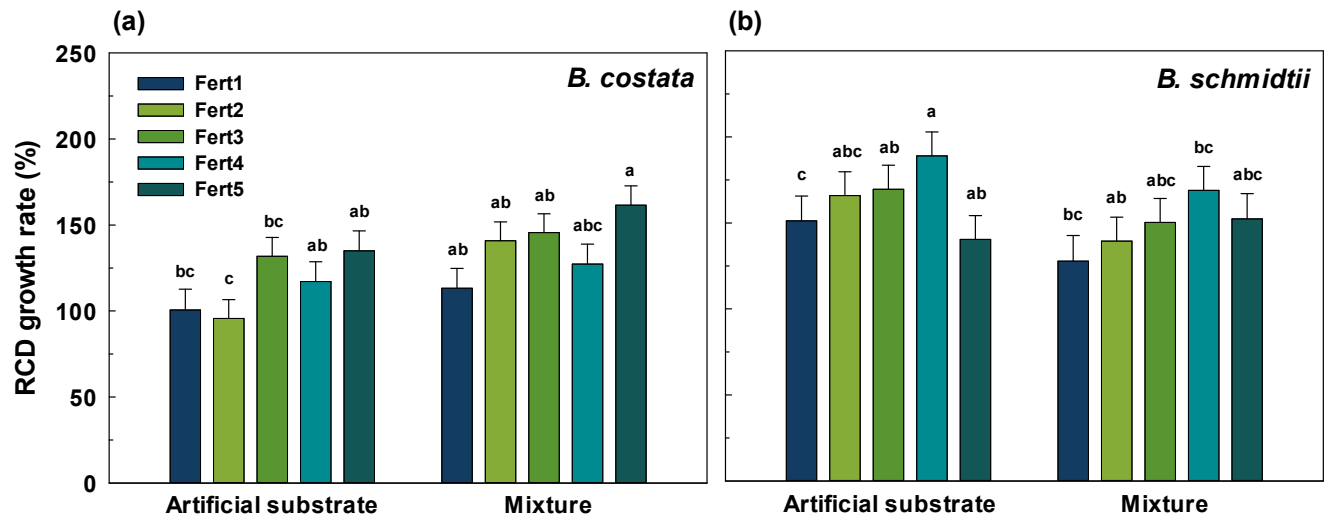


Figure 2: Growth rate of seedling Root Collar Diameter (RCD) of (a) *Betula costata* and (b) *B. schmidtii* after soil (Artificial substrate 100%; Mixture, artificial substrate 70%+sand-masato 30% in volumetric ratio) and fertilization treatments (Fert1, liquid fertilizer at 2 weeks interval; Fert2, Controlled-Release Fertilizer (CRF) in summer; Fert3, CRF in summer and fall; Fert4, CRF long-term; Fert5, CRF+LF) presented as the covariate adjusted means. Vertical bars represent standard errors (n=10). There is no significant interaction effect ($p < 0.05$). Different lower case letters indicate significant differences ($p < 0.05$, Tukey's HSD test) across soil and fertilization treatments.

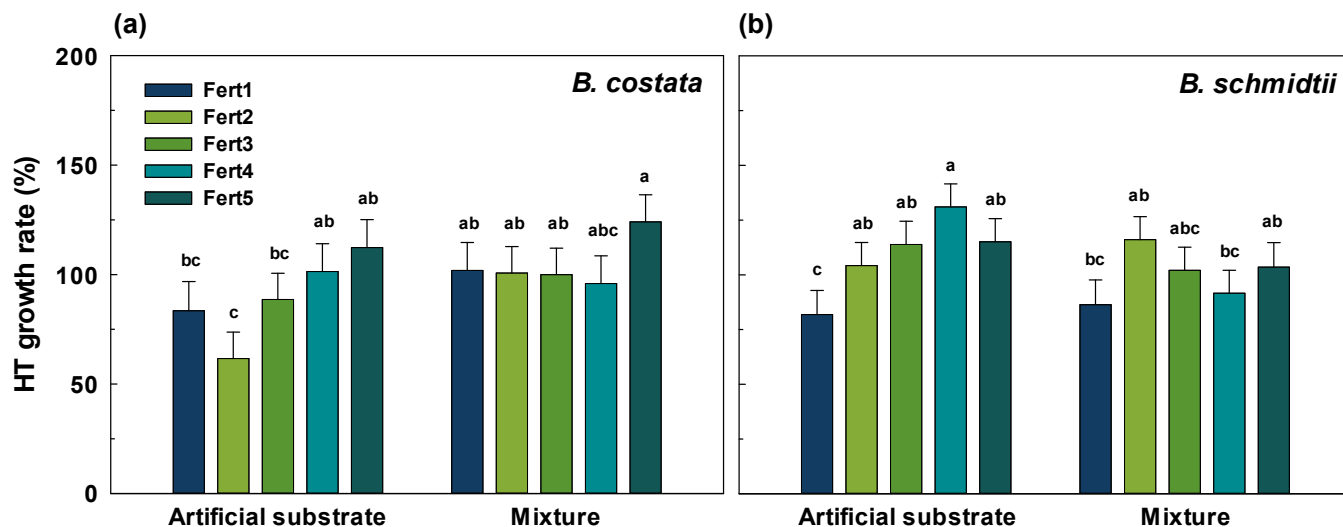


Figure 3: Growth rate of seedling height (HT) of (a) *Betula costata* and (b) *B. schmidtii* after soil (Artificial substrate 100%; Mixture, artificial substrate 70%+sand-masato 30% in volumetric ratio) and fertilization treatments (Fert1, liquid fertilizer at 2 weeks interval; Fert2, controlled-release fertilizer (CRF) in summer; Fert3, CRF in summer and fall; Fert4, CRF long-term; Fert5, CRF+LF) presented as the covariate adjusted means. Vertical bars represent standard errors (n=10). Different lower-case letters indicate significant differences ($p < 0.05$, Tukey's HSD test) across soil and fertilization treatments.

For *B. costata*, the highest RCD and HT growth rate was found in Fert5, which is CRF long-term fertilization with liquid fertilizer added during the growing season in summer, although the total N input by fertilization was less than Fert4 and Fert3 (Figure 2(a) and 3(a)). For *B. schmidtii*, the highest RCD and HT growth rate was found in Fert4, which supplied the biggest amount of N input by CRF long-term fertilization (Figure 2(b) and 3(b)). For both species, the lowest RCD and HT growth rate was observed in seedlings treated solely with liquid fertilizer (Fert1), except for the HT growth rate of *B. costata* in pure artificial substrate.

5.2. Effects of soil and fertilization regimes on biomass allocation

Biomass of *B. schmidtii* seedlings was about twice as much as that of *B. costata* on average (Figure 4). The interaction effect of soil and fertilization regimes was not statistically significant on the biomass production of each tissue, except for fine and coarse roots of *B. costata* (Table S1). Both species' biomass tended to be more affected by fertilization regimes than by soil treatment, and this tendency was more pronounced in *B. costata* seedlings, although the effects of soil were significant for stem and branch biomass of *B. Schmidtii*. *B. costata* tended to show higher biomass in mixture soil medium, whereas *B. schmidtii* grew well in the pure artificial substrate (Figure 4; Table S1).

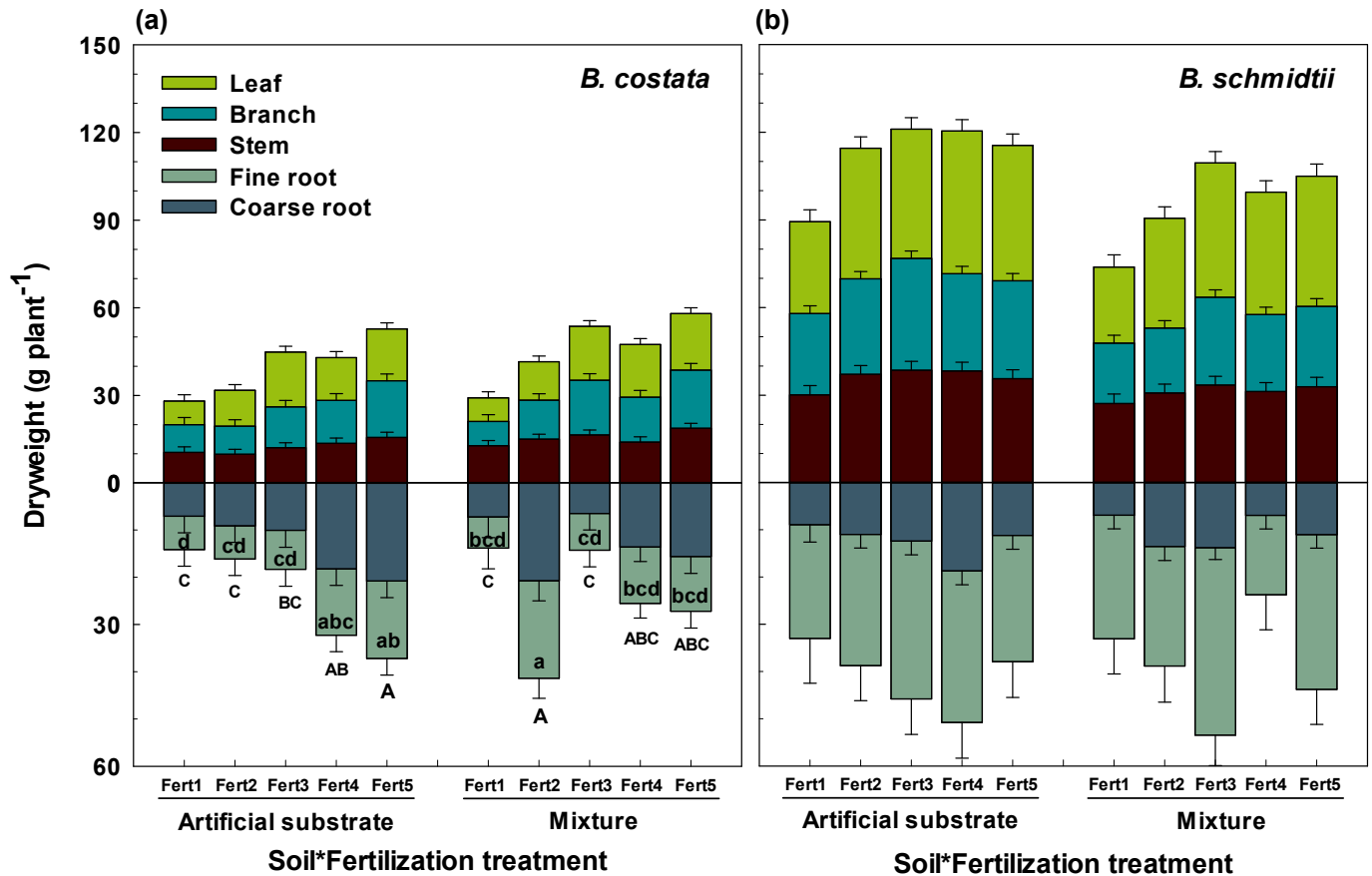


Figure 4: Dry weight of aboveground (leaf, stem, and branch) and belowground (coarse root and fine root) of (a) *Betula costata* and (b) *B. schmidtii* after soil (Artificial substrate 100%; Mixture, artificial substrate 70%+sand-masato 30% in volumetric ratio) and fertilization treatments (Fert1, liquid fertilizer at 2 weeks interval; Fert2, Controlled-Release Fertilizer (CRF) in summer; Fert3, CRF in summer and fall; Fert4, CRF long-term; Fert5, CRF+LF) presented as the covariate adjusted means. Vertical bars represent standard errors (n=10). Different lower- and upper-case letters indicate significant differences of fine root (lower-case) and belowground biomass (upper-case) ($p < 0.05$, Tukey's HSD test) across soil and fertilization treatments if there is a significant interaction effect.

Each tissue and total biomass of *B. costata* was the highest in the Fert5 treatment and the total biomass was not significantly different from Fert4, which had the largest nitrogen input by fertilizer. It seemed that the highest biomass was observed in seedlings with the Fert5 treatment but above- and belowground of *B. costata* responded differently to fertilization regimes. Belowground biomass of *B. costata* seedlings in Fert2 (with N content half of that in Fert5) in mixture medium showed similarly high production to that in Fert4 and Fert5 in both substrate types. Seedlings treated by Fert3, Fert4, and Fert5 showed similarly high biomass for the aboveground part (leaf, stem, and branch).

B. schmidtii and *B. costata* responded differently to various fertilization regimes in terms of biomass. *B. schmidtii* seedlings treated with Fert1 (only liquid fertilizer) and Fert3 yielded the smallest and largest biomass, respectively. Fert3, Fert4, and Fert5 treatments tended to have similar effects on biomass allocations although the total nitrogen input by fertilization regimes was the highest in Fert4, followed by Fert3 (3.85 g) and Fert5 (3.55 g).

5.3. Effects of soil and fertilization regimes on foliar N, P, and K concentrations and contents

The foliar N, P, and K concentrations of *B. costata* seedlings did not differ significantly between treatments of either soil or fertilization regimes. However, the foliar N and K concentrations of *B. schmidtii* showed significant differences depending on soil and/or fertilization regimes (Table 4). The leaf N, P, and K contents of *B. schmidtii* were significantly different by fertilization regimes.

Species	Soil	Fertilization	Concentration (%)						Content (g)						
			N		P		K		N		P		K		
<i>B. costata</i>	Artificial	Fert1	2.90	(0.57)	3.32	(1.06)	1.22	(0.05)	4.65	(0.65)	5.49	(2.03)	1.98	(0.19)	
		substrate	Fert2	2.76	(0.85)	1.84	(0.03)	1.32	(0.04)	6.11	(1.59)	4.12	(0.16)	2.96	(0.24)
		Fert3	2.88	(0.50)	1.51	(0.10)	1.23	(0.04)	6.42	(0.96)	3.36	(0.12)	2.75	(0.16)	
		Fert4	3.74	(0.49)	2.50	(0.09)	1.14	(0.02)	8.99	(0.62)	6.06	(0.17)	2.77	(0.13)	
		Fert5	2.40	(0.20)	2.79	(0.65)	1.32	(0.23)	5.61	(0.53)	6.53	(1.59)	3.09	(0.57)	
<i>B. schmidtii</i>	Mixture	Fert1	2.65	(0.61)	3.23	(1.59)	1.14	(0.13)	3.05	(0.55)	3.85	(2.04)	1.33	(0.22)	
		Fert2	2.72	(0.33)	2.88	(0.12)	1.18	(0.11)	5.13	(1.02)	5.36	(0.21)	2.18	(0.02)	
		Fert3	3.58	(0.10)	1.83	(0.22)	1.08	(0.04)	8.18	(0.33)	4.17	(0.54)	2.46	(0.11)	
		Fert4	3.26	(0.04)	1.85	(0.20)	1.11	(0.31)	6.78	(0.31)	3.87	(0.63)	2.35	(0.78)	
		Fert5	2.75	(0.19)	2.64	(0.17)	1.00	(0.09)	5.71	(0.62)	5.48	(0.58)	2.07	(0.26)	
			p value												

		Soil	0.8 5		0.8 3		0.1 3		0.2 8		0.4 3		0.0 2	
		Fertiliza tion	0.3 0		0.2 2		0.9 2		0.0 04		0.4 2		0.0 8	
		Soil*Fe rtilizati on	0.7 5		0.7 5		0.8 5		0.1 9		0.4 7		0.8 4	
<i>B.</i>	Artifi cial	Fert1	2.2 1	(0. 32)	2.8 4	(0. 48)	1.4 3	(0. 32)	0.7 9	(0. 15)	1.0 0	(0. 12)	0.5 1	(0. 14)
	subst rate	Fert2	1.8 2	(0. 16)	2.5 4	(0. 54)	1.1 7	(0. 28)	1.1 3	(0. 22)	1.5 9	(0. 51)	0.7 4	(0. 25)
		Fert3	2.6 6	(0. 03)	3.3 7	(0. 20)	1.3 0	(0. 07)	2.5 0	(0. 25)	3.1 5	(0. 10)	1.2 1	(0. 05)
		Fert4	2.6 9	(0. 45)	2.6 6	(0. 46)	1.2 3	(0. 21)	1.7 7	(0. 27)	1.7 5	(0. 28)	0.8 1	(0. 13)
		Fert5	2.7 7	(0. 15)	3.5 6	(0. 13)	1.1 2	(0. 15)	2.2 2	(0. 31)	2.8 4	(0. 35)	0.8 8	(0. 04)
	Mixt ure	Fert1	1.5 2	(0. 23)	3.5 5	(0. 65)	0.9 3	(0. 05)	0.5 5	(0. 01)	1.2 7	(0. 07)	0.3 4	(0. 03)
		Fert2	1.7 2	(0. 29)	1.8 3	(0. 51)	0.9 1	(0. 09)	1.1 2	(0. 12)	1.2 3	(0. 41)	0.6 0	(0. 09)
		Fert3	2.4 8	(0. 04)	2.6 1	(0. 35)	0.9 6	(0. 09)	2.3 0	(0. 57)	2.3 3	(0. 24)	0.8 6	(0. 13)
		Fert4	2.7 9	(0. 04)	2.7 4	(0. 27)	1.0 5	(0. 01)	2.2 7	(0. 15)	2.2 3	(0. 33)	0.8 5	(0. 05)
		Fert5	2.0 9	(0. 03)	2.4 3	(0. 22)	0.9 9	(0. 09)	2.0 3	(0. 13)	2.3 5	(0. 09)	0.9 6	(0. 13)
			p val ue											
		Soil	0.0 5		0.1 9		0.0 2		0.8 6		0.3 3		0.1 9	
		Fertiliza tion	0.0 04		0.2 0		0.9 0		0.0 00 3		0.0 01		0.0 04	
		Soil*Fe rtilizati on	0.3 3		0.2 4		0.8 2		0.6 1		0.2 1		0.4 5	

Mixture, 70% artificial substrate + 30% sand-masato in volumetric ratio
 Fert1, liquid fertilizer at 2 weeks interval; Fert2, Controlled-Release Fertilizer (CRF) in summer;
 Fert3, CRF in summer and fall; Fert4, CRF long-term; Fert5, CRF+LF
 Standard errors are shown in parentheses (n=2). P values are from the result of two-way ANOVA to detect the effect of soil and fertilization regimes on leaf nutrient concentration and content within each species. Bold p values denote statistical significance at $\alpha=0.05$.

Table 4: Leaf nutrient concentration (%) and content (g) of seedlings after the experiment.

Although statistically insignificant, the foliar N concentration of *B. costata* was the highest in Fert4 which had the highest nitrogen input by fertilizer. However, the seedlings in Fert1, which had the lowest phosphorus input (0.63 g, Table 2) by liquid fertilizer, showed the highest foliar P concentrations.

The foliar N, P, and K concentrations of *B. schmidtii* were higher on average in the pure artificial substrate than in the mixture. Only the N concentrations of *B. schmidtii* foliage showed a significant difference according to the fertilization regimes, with the highest concentration found in the Fert4 and the lowest in the Fert1 and Fert2 treatments. However, leaf N, P, and K contents were the highest in Fert3 and the lowest in Fert1 regardless of soil types, which was statistically significant.

5.4. Soil chemical properties after the experiment

Soil chemical properties such as EC, TN (total nitrogen), AP (available phosphorus), and exchangeable K^+ varied significantly between the two types of soil media for all species (Table 5). Specifically, fertilizer treatment was significant for pH in both species, but it was significant for nitrogen in *B. costata* and for P in *B. Schmidtii*. The remaining soil total nitrogen of *B. costata* in Fert1 was not statistically different from that in Fert4, although the total nitrogen input by Fert4 was approximately four times higher than Fert1. Lastly, soil in Fert1 was the least acidic compared with other fertilization regimes in both soil media, regardless of species, although all treatments had acidic soil pH after the experiment.

Spec ies	Soil	Fertilizati on	pH		EC		TN	AP	Exchangea ble K^+			
					dS m ⁻¹	%	mg kg ⁻¹	mg kg ⁻¹				
<i>B. costa ta</i>	Artifi cial subst rate	Fert1	5.6 9	(0. 03)	0.1 1	(0.0 0)b	0.58	(0. 01)	1964 .48	(169. 12)	123. 50	(15. 45)
		Fert2	5.3 0	(0. 03)	0.2 3	(0.0 4)a	0.50	(0. 03)	2284 .28	(267. 71)	132. 77	(8.0 5)

		Fert3	5.4 0	(0. 07)	0.2 3	(0.0 1)a	0.34	(0. 16)	2982 .38	(449. 64)	139. 78	(6.6 2)
		Fert4	5.3 2	(0. 20)	0.1 7	(0.0 1)ab	0.59	(0. 01)	3458 .48	(585. 90)	120. 83	(7.5 2)
		Fert5	5.5 5	(0. 04)	0.1 2	(0.0 1)ab	0.49	(0. 00)	2158 .44	(34.4 6)	134. 22	(20. 08)
	Mixt ure	Fert1	5.7 4	(0. 10)	0.0 6	(0.0 0)b	0.12	(0. 02)	643. 61	(133. 86)	56.2 6	(2.2 5)
		Fert2	5.5 0	(0. 03)	0.1 2	(0.0 1)ab	0.14	(0. 05)	623. 57	(91.3 7)	65.3 9	(0.0 1)
		Fert3	5.3 8	(0. 15)	0.0 7	(0.0 1)b	0.07	(0. 07)	846. 39	(78.5 4)	86.1 3	(11. 72)
		Fert4	5.4 3	(0. 07)	0.1 6	(0.0 5)ab	0.20	(0. 03)	975. 43	(194. 77)	63.9 4	(7.5 8)
		Fert5	5.5 7	(0. 01)	0.0 9	(0.0 1)b	0.13	(0. 02)	826. 35	(98.5 9)	76.2 6	(2.4 5)
			P val ue									
		Soil	0.2 3		0.0 003		<0.0 001		<0.0 001		<0.0 001	
		Fertilizati on	0.0 1		0.0 055		0.04		0.08		0.21	
		Soil*Ferti lization	0.7 8		0.0 3		0.21		0.60		0.93	
<i>B. schm idtii</i>	Artifi cial subst rate	Fert1	5.8 8	(0. 14)	0.1 1	(0.0 2)b	0.48	(0. 03)	1332 .09	(123. 43)	120. 26	(10. 77)
		Fert2	5.7 6	(0. 01)	0.1 0	(0.0 3)b	0.50	(0. 01)	1174 .20	(4.01)	117. 91	(28. 45)
		Fert3	5.2 7	(0. 02)	0.2 2	(0.0 1)a	0.61	(0. 01)	2700 .26	(624. 37)	127. 69	(21. 93)
		Fert4	5.3 5	(0. 02)	0.1 3	(0.0 2)ab	0.57	(0. 03)	1971 .69	(1102 .86)	136. 31	(35. 17)
		Fert5	5.4 3	(0. 05)	0.0 9	(0.0 1)b	0.51	(0. 06)	1741 .66	(302. 17)	120. 65	(7.0 0)
	Mixt ure	Fert1	5.9 0	(0. 02)	0.0 7	(0.0 1)b	0.12	(0. 00)	670. 86	(56.9 0)	66.5 9	(5.4 0)

	Fert2	5.5 5	(0. 20)	0.0 8	(0.0 0)b	0.11	(0. 02)	464. 07	(29.6 6)	71.1 9	(4.0 2)
	Fert3	5.4 1	(0. 01)	0.0 7	(0.0 3)b	0.15	(0. 01)	586. 70	(105. 80)	84.3 1	(11. 26)
	Fert4	5.4 9	(0. 09)	0.0 9	(0.0 1)b	0.17	(0. 01)	644. 41	(99.3 9)	70.1 8	(4.1 6)
	Fert5	5.5 5	(0. 01)	0.1 0	(0.0 1)b	0.15	(0. 02)	578. 69	(72.1 4)	65.1 5	(1.6 0)
		p val ue									
	Soil	0.4 2		0.0 01		0.00 1		<0.0 001		0.00 06	
	Fertilizati on	0.0 005		0.0 2		0.40		0.02		0.90	
	Soil*Ferti lization	0.2 5		0.0 07		0.46		0.25		0.97	
<p>EC, electrical conductivity; TN, total nitrogen; AP, available phosphorus Mixture, 70% artificial substrate + 30% sand-masato in volumetric ratio Fert1, liquid fertilizer at 2 weeks interval; Fert2, Controlled-Release Fertilizer (CRF) in summer; Fert3, CRF in summer and fall; Fert4, CRF long-term; Fert5, CRF+LF Standard errors are shown in parentheses (n=2). P values are from the result of two-way ANOVA to detect the effect of soil and fertilization on each soil property within each species. Bold p values denote statistical significant at $\alpha=0.05$. Different lower-case letters indicate significant differences ($p < 0.05$, Tukey's HSD test) across soil and fertilization treatments if there is a significant interaction effect.</p>											

Table 5: Soil chemical properties after the experiment.

6. Discussion

The interaction of soil \times fertilization had no significant effect on most parameters, except for the fine root and total belowground biomass of *B. costata* seedlings. This partially supported our hypothesis that their interaction would have a significant effect on seedling growth, but only belowground. Fert2 in the mixture soil medium showed the highest fine root dry weight among the treatments. This suggests that the type and mode of fertilizer application affect the soil nutrient supply, thereby affecting the root system (Beare et al. 1994). Zhang et al. (2021) found a similar result with *Prunus* species, where Controlled-Release Fertilizer (CRF) promoted the production of new roots and fine roots, and improved fertilizer utilization efficiency. Similarly, Ha et al. (2018) observed a significant increase in the root weight of *Phalaenopsis* with the application of 1.5 g pot⁻¹ of CRF. However, Rowe & Cregg (2002) reported that incorporating CRF (0.77 g L⁻¹) in substrate had no effect on the root growth of herbaceous perennials, but increased shoot dry

weights. The results may be attributed to the controlled release property of the fertilizer, which was applied at a short-term duration, and improved soil drainage resulting from the addition of sand-masato to the mixture. This is because the release rate of CRF is directly proportional to the nutrient concentration in the soil (Zhang et al. 2021). The application of Fert2 in summer with a smaller amount of N and controlled release of nutrients for only 6-8 weeks may have not fully provided the optimal nutritional needs of the seedlings throughout the growing season when the seedlings were actively growing. Hence, *B. costata* seedlings at Fert2 + mixture substrate may have invested more biomass to roots to enhance soil exploration and nutrient absorption from the bottom of the pots. Wang et al. (2016) found similar findings, stating that early root growth and dense fine roots improved macro- and micronutrient absorption in several plants. According to a review, increasing fine root growth increased the root radius and surface area of soil accessed for foraging and absorption (Goss et al. 1993). This is supported by the highest root/shoot ratio of seedlings planted at Fert2 + mixture substrate (i.e., 1.0) compared to the other treatments (i.e., < 0.66). Song et al. (2019) reported that seedlings of *Pistacia chinensis* Bunge treated with lower amounts of nitrogen (i.e., 100 – 200 mg) had a higher root/shoot ratio compared with high-N treated seedlings, indicating that a lower amount of nutrients in the soil promoted root growth. Moreover, the addition of sand-masato in the medium may have facilitated such soil exploration caused by high nutritional demands as the seedlings were actively growing. The mixture substrate may have enabled the better establishment of root systems, resulting in more efficient nutrient use and soil exploration throughout the growing season. Our findings are consistent with prior research that found positive relationships between fine rock fragments/sand content and belowground biomass, which improved the root system's environment (van Wesemael et al. 2000; Zheng et al. 2021).

In this study, the artificial substrate combined with Fert5 showed the highest belowground growth, particularly in fine roots. This result can be attributed to the interaction between the liquid fertilizer and CRF with the artificial substrate. The liquid fertilizer applied in summer may have penetrated the substrate immediately, providing faster access to nutrients. Our findings are consistent with those of Ji et al. (2017), who observed a significant increase in root growth by up to 78% in *Chrysanthemum* using liquid fertilizer. This is because liquid fertilizers, especially organic ones, can quickly deliver soluble organic ions and bio-stimulants, according to earlier studies (Nelson et al. 2010; Zhu et al. 2013).

The artificial substrate, which typically contains peat, vermiculite, perlite, and macro- and micronutrients, may have made it easier for nutrients from both liquid and CRF fertilizers to reach the soil. The properties of the artificial substrate, including aeration, cation exchange capacity, microbial communities, and enzyme activities, may have been enhanced by peat, vermiculite, and perlite, which may have increased the mineralization of the CRF over time, increased nutrient use efficiency, and decreased nutrient loss. Furthermore, the Fert4 treatment had the next greatest effect on belowground growth of *B. costata*, followed by Fert3, Fert2, and Fert 1 in artificial

substrate, indicating that the combination of liquid fertilizer and CRF is more effective than CRF- or liquid-alone treatments.

The mixture substrate, as a main factor, was effective in improving relative RCD and HT growth of *B. costata*, but neither factor was effective for *B. schmidtii* in terms of relative RCD and HT. Due to their contrasting life-history traits, the growth potential of these two *Betula* species may vary depending on soil medium factors, despite being from the same genus. Although both species are deciduous broadleaf trees, *B. costata* has a higher dry tolerance than *B. schmidtii*. Therefore, *B. costata* is more likely to respond favorably to a soil medium with sand-masato, which is characterized by loamy sand soil texture. Thus, *B. costata* may not grow well under waterlogged conditions due to a lack of aeration affecting the root system (Morales-Olmedo et al. 2015), although a field assessment indicated that the species may potentially grow and develop in disturbed secondary forests (Shitara & Suzuki 2021).

Our results can also be explained by growth economics of the two species, i.e., *B. schmidtii* has a moderate growth rate, whereas *B. costata* has a fast growth rate. Fast-growing species are highly adaptable in a wide range of environments. They are highly efficient in foraging for soil nutrients and fixing carbon even in low-resource environments (Colesie et al. 2020), which explains why *B. costata* was more responsive to soil and fertilization treatments than *B. schmidtii*.

In terms of the main effects of fertilization, higher Root Collar Diameter (RCD) and aboveground biomass of *B. costata* seedlings were generally observed in Fert5-treated seedlings compared to the other fertilization treatments in both substrate types. Results suggest that the combination of Controlled-Release Fertilizer (CRF) and liquid fertilizer was compatible and beneficial for improving the aboveground biomass of *B. costata* seedlings but not for *B. schmidtii*. The nutritional requirements of fast-growing species vary depending on several factors, including plant species, climate, irrigation method, and soil type. The controlled release of fertilizer may have synchronized with the nutritional requirements of *B. costata* seedlings, and the liquid fertilizer may have provided the CRF an initial nutrient charge that facilitated the mineralization process in soil or improved the digestibility and utilization of nutrients. Since the release of CRF depends on the type and thickness of coating, temperature, and moisture, the liquid fertilizer, which most plants utilize quickly, may have played a key role in correcting mid-season deficiencies and optimizing nutrition throughout the growth cycle of *B. costata* seedlings.

However, the fertilization treatments had no effect on foliar nutrient concentration in *B. costata*. This result can be attributed to the efficacy duration and amount of added N and/or other nutrients, as well as the nutrient-acquisition strategy of the species. A different pattern was observed in *B. schmidtii* seedlings where Fert4 resulted in a significantly higher foliar N concentration than the other treatments. Although the Fert4 is also a CRF, it had the highest initial amount of N (i.e., 5.25 g) with a longer duration of effectivity compared to other fertilization regimes.

The contrasting pattern observed in the foliar N concentration of *B. costata* can be explained by a conservative nutrient allocation strategy that minimizes energy for transport organs and maximizes the surface area of resource-acquiring and metabolically active organs belowground. The latter organs tend to exhibit a certain degree of conservatism, where they maintain a constant nutrient concentration when exposed to significant variations in nutrient availability (Yu et al. 2015). *B. costata* has a faster growth rate compared with *B. schmidtii*; hence, much of the energy investment may have been put into resource acquisition organs (e.g., roots) rather than transport or uptake of nutrients to minimize energy consumption as the seedling grew. This further explains the higher N leaf content of *B. costata* than that of *B. schmidtii* after the experiment. This could be one of the important responses of *B. costata* to resource heterogeneity.

7. Conclusions

In summary, this study examined for the first time the combined effects of substrate types and fertilization regimes on the growth and foliar nutrient responses of *B. costata* and *B. schmidtii* seedlings. We revealed that the interaction of soil \times fertilization had no significant impact on most of the measured parameters, except for fine root biomass and total belowground growth of *B. costata* seedlings. Additionally, the mixture substrate amplified the positive effects of either liquid or CRF on the root growth of *B. costata* seedlings. The two species responded differently to soil media and various fertilization regimes with *B. costata* seedlings being generally more suitable at a mixture substrate (70% artificial soil + 30% masato), while the *B. schmidtii* seedlings at pure artificial substrate. Furthermore, the combination of CRF and LF (Fert5) was generally compatible and beneficial for *B. costata* seedlings but not for *B. schmidtii*. These findings suggest that the type and release pattern of applied fertilizer and substrate characteristics are crucial for providing the seedlings with sufficient nutrients depending on the nutritional needs of the plants. Lastly, the results of this study have implications for promoting sustainable development in forestry by reducing the use or dependence on peat-based substrates for tree growth and productivity.

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Statements and Declarations

Conflict of Interest

The authors declare no competing interests.

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Supplementary Information

<i>Betula costata</i>											
	P value										
	RCD %	HT %	Leaf	Branch	Stem	AG	CR	FR	BG	Total	RS ratio
Soil	0.0038	0.0647	0.3986	0.2511	0.008	0.0954	0.8957	0.214	0.8169	0.9112	0.1788
Fert	0.0039	0.0567	<0.0001	0.0001	0.0275	<0.0001	0.0245	0.0282	0.0101	0.0101	0.0167
Soil*Fert	0.4851	0.4953	0.9013	0.6792	0.6936	0.9344	0.1981	0.0206	0.0457	0.2339	0.0468
<i>B. schmidtii</i>											
	P-value										
	RCD %	HT %	Leaf	Branch	Stem	AG	CR	FR	BG	Total	R/S ratio
Soil	0.1031	0.1958	0.142	<0.0001	0.0204	0.0034	0.307	0.8921	0.6897	0.1448	0.3306
Fert	0.0613	0.0667	0.0001	0.0003	0.1585	0.0009	0.4741	0.4616	0.553	0.0435	0.2181
Soil*Fert	0.6586	0.1559	0.753	0.9265	0.943	0.9074	0.1605	0.6207	0.4723	0.4493	0.4407
Fert, Fertilization regimes RCD: Root Collar Diameter; HT: height; AG: sum of leaf, branch, and stem; CR: Coarse Root; FR: Fine Root; BG: sum of coarse root and fine root; Total: sum of AG and BG; RS ratio, root to shoot ratio Significant p values in bold.											

Table S1: Result of two-way ANCOVA for the effect of soil and fertilization regimes on RCD growth rate, HT growth rate, leaf, branch, stem, coarse root, fine root biomass, and RS ratio by species.

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