Nodulation of Snowbrush Ceanothus in Three Soilless Substrates[1]

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Abstract

Snowbrush ceanothus (*Ceanothus velutinus* Dougl. Ex Hook.) is a broadleaf evergreen shrub. It fixes nitrogen in symbiosis with nitrogen-fixing actinobacteria and plays a crucial role in soil-building. However, the effective induction of nodules in snowbrush ceanothus using soil containing *Frankia sp.* remains unclear. Therefore, the growth and nodulation of snowbrush ceanothus were investigated in three soilless substrates: calcined clay, peat-based mix, and perlite. Snowbrush ceanothus seedlings were transplanted into containers with calcined clay, peat-based mix, or perlite, and inoculated with 30 mL of native soil. Seedlings were grown for establishment in the first month and then harvested every two weeks to check for nodules. The results showed that nodules formed on seedlings' roots approximately four months after the inoculation of native soil. Interestingly, nodulation was more pronounced in seedlings grown in calcined clay compared to those in a peat-based mix and perlite. Notably, the substrates exhibited impacts on shoot dry weight, root dry weight, and leaf area. Seedlings grown in a peat-based mix had significantly greater shoot dry weight, root dry weight, and leaf area than those grown in calcined clay or perlite. Further investigation is necessary to explore the role of substrate composition on the nodulation and growth of snowbrush ceanothus.

Species used in this study: *Ceanothus velutinus* Dougl. Ex Hook., *Frankia sp.*

Index words: *Ceanothus velutinus*, *Frankia*, native plant, nodule, substrate.

Significance to the Horticulture Industry

Snowbrush ceanothus (*Ceanothus velutinus* Dougl. Ex Hook.), commonly found in arid regions, has shiny evergreen leaves and clusters of white flowers. It plays an important role in soil-building through nitrogen fixation in symbiosis with nitrogen-fixing actinobacteria. Understanding its nodulation process using soil containing *Frankia sp.* is necessary for the horticulture industry to optimize snowbrush ceanothus growth and nutrient uptake. Additionally, the evaluation of different soilless substrates (calcined clay, peat-based mix, and perlite) on the growth and nodulation of snowbrush ceanothus provides insights for substrate selection and management practices in nurseries and landscapes.

Introduction

Native species, defined by their evolutionary adaptations to specific regional factors, including climate, soil composition, rainfall patterns, and interactions within the surrounding community, play a crucial role in ecological systems (Callaway 2007, Palmer et al. 2003). Desert and dry-land native plant species, equipped with the ability to thrive with infrequent watering because of their deep root systems or other adaptations, are naturally adapted to arid and semiarid conditions. These plants also possess resistance to insects and fungi prevalent in their native habitats. Requiring fewer harsh chemicals such as fertilizers and pesticides, which can be detrimental to natural environments, native plants from arid and semiarid regions present excellent options for water-efficient landscaping.

The utilization of native plants has gained popularity in ecological landscape design, green building construction, and urban habitat development. According to the Plant Select® program at Colorado State University and Denver Botanic Gardens, sales of native plants increased from \$1.46 million in 2007 to \$1.68 million in 2012 (National Information Management and Support System 2020). It represents only a small portion of the national market for native plants. However, with the growing recognition and appreciation of these native plants, it is highly likely that the sales have surged even further since 2012. Consumers are increasingly interested in natural landscapes and demonstrate a willingness to pay a premium for native plant products (McCoy 2011).

Promoting native plants for nursery production requires an efficient production system, encompassing appropriate growing substrate, water management, and fertilization specifications. Observing plant performance in landscape conditions over the years is crucial for advocating these plants in water-efficient landscaping. This information is essential due to challenges in producing native plants in nursery or landscape conditions. While some native plants thrive in the wild, they prove challenging in nurseries, or when grown under landscape conditions, possibly due to a lack of natural symbioses with soil microorganisms. For

Received for publication February 26, 2024; in revised form August 9, 2024.

[1]This research was supported in part by the United States Department of Agriculture (USDA) National Institute of Food and Agriculture (NIFA) Hatch project UTA01381 and UTA01666, Horticulture Research Institute, the Center for Water-Efficient Landscaping, and the Utah Agricultural Experiment Station (UAES) at Utah State University. It is approved as UAES journal paper number 9797. In addition, funding for this project was made possible by the USDA's Agricultural Marketing Service through the Utah Department of Agriculture and Food Specialty Crop Block Grant. We are grateful for the technical assistance from Paul Harris and Alyssa Fenstermaker, and valuable comments from anonymous reviewers. The content is solely the responsibility of the authors and does not necessarily represent the official views of the funding agencies. Mention of a trademark, proprietary product, or vendor does not constitute a guarantee or warranty of the product by the USDA and does not imply its approval to the exclusion of other products or vendors that also may be suitable.

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Table 1. **Nutrient components and their final concentrations used to prepare nitrogen limited nutrient solution.**[z]

Nutrient components	Final concentration in solution (mM)
Boric acid (H_3BO_3)	40.0
Calcium chloride ($CaCl_2$)	1.5
Chelated iron (Fe-DTPA)	5.0
Copper chloride ($CuCl_2$)	4.0
Ferric chloride ($FeCl_3$)	5.0
Magnesium sulfate ($MgSO_4$)	0.8
Manganese chloride ($MnCl_2$)	3.0
Nickel chloride ($NiCl_2$)	0.1
Nitric acid (HNO_3)	0.5
Potassium dihydrogen phosphate (KH_2PO_4)	0.4
Potassium silicate (K_2SiO_3)	0.3
Potassium sulfate (K_2SO_4)	2.0
Sodium molybdate (Na_2MoO_4)	0.1
Zinc chloride ($ZnCl_2$)	3.0

[z]The nutrient solution was prepared by mixing nutrient components in reverse osmosis water.

example, snowbrush ceanothus, recognized as an actinorhizal plant (Benson et al. 2003), is difficult to produce in a nursery setting. One potential explanation for this might be the absence of natural symbiotic relationships with soil microorganisms in the environment. Actinorhizal plants form a symbiosis with nitrogen-fixing actinobacteria (*Frankia spp.*), enhancing soil health (Conard et al. 1985), providing nitrogen, and serving as antifungals, biocontrol agents, and plant growth promoters (Barka et al. 2016). Actinorhizal plants with nodulation potential are considered suitable candidates for nursery production due to their nitrogen-fixing ability (Beddes and Kratsch 2010).

Snowbrush ceanothus, an evergreen shrub in the *Rhamnaceae* family, is native to western North America, spanning from British Columbia south to California and east to Colorado. This plant can grow up to 0.9-2.5 m (3-8 ft) tall and thrives in full sun with coarse-textured, well-drained soils. Known for its heat and drought tolerance, snowbrush ceanothus fixes nitrogen through actinorhizal root formation. With attractive features such as shiny leaves and clusters of white flowers, snowbrush ceanothus has potential for urban landscapes (Mee et al. 2003, Paudel et al. 2022). As an actinorhizal plant, snowbrush ceanothus not only benefits its growth and survival through nitrogen fixation but also contributes to ecosystem health and functioning. Its deep root system helps prevent soil erosion, improves soil structure, and increases water infiltration. Additionally, snowbrush ceanothus provides habitat and food for various wildlife species, supporting biodiversity in its native ecosystem.

Plant growth-promoting rhizobacteria within the plant microbiome play a significant role in plant growth and development (Lugtenberg and Kamilova 2009). These beneficial bacteria enhance plants' ability to withstand environmental stresses such as salinity, heavy metals, and drought (Selvakumar et al. 2012). Plant growth-promoting rhizobacteria function by either releasing hormones like auxins, cytokinins, gibberellins, and ethylene, or by improving nutrient accessibility (Bent et al. 2001, Habibi et al. 2014). A study on the rhizosphere and endosphere microbiome of snowbrush ceanothus revealed the presence of several plant growth-promoting rhizobacteria (Ganesh 2021). Further studies are needed to establish suitable production practices for promoting nursery production and the use of snowbrush ceanothus in urban landscapes. Optimizing the induction process for nodulation in snowbrush ceanothus at various substrates will enhance its growth and development.

This study aimed to assess the impact of native soil addition on the growth and development of snowbrush ceanothus in calcined clay, peat-based mix, and perlite substrates. The objective was to investigate the effects of growing substrates on the plant's growth and nodulation.

Materials and Methods

Snowbrush ceanothus seeds, procured from the Native Seed Foundation (Polson, MO), were stored in a refrigerator at 2 C (36 F) until use. To enhance germination, seeds were wrapped in cheesecloth and dipped in a 90 C (194 F) hot-water bath (Isotemp 102, Fisher Scientific, Canada) for 10 s, followed by immediate immersion in a cold-water bath with ice at 6 C (43 F) for 1 h. Subsequently, the treated seeds were then wrapped in moist paper towels and kept in a resealable plastic bag with sufficient space for aeration. Stratification occurred in a 2 C (36 F) refrigerator for three months, with regular inspections to ensure the substrate remained moist. After stratification, seeds were planted in trays filled with a 1:1 mixture of perlite (Hess perlite, Malad City, ID) and peatmoss (SunGro Horticulture, Agawam, MA) and placed on the mist bench. Once germinated, seedlings were transferred to a research greenhouse with temperatures maintained at 25.2 ± 1.6 C (77.4 ± 2.9 F) (mean ± SD) during the day and 21.8 ± 2.7 C (71.2 ± 4.9 F) at night.

Native soil was collected from the root zone of a snowbrush ceanothus plant in Tony Grove, UT, and stored at 4 C (39 F) until use. This soil tends to retain a significant amount of water and does not drain easily. On 17 June 2021, seedlings without nodules were transplanted into 656-mL cone-shaped black containers (D40H, Stuewe and Sons, Tangent, OR). These containers were filled with MetroMix® 820 substrate (Canadian sphagnum peat moss, 35-45% composted pine bark, coir, coarse perlite, and dolomitic limestone; SunGro® Horticulture, Agawam, MA), perlite (Hess perlite; Malad City, ID), or calcined clay (Turface MVP™; Profile Products, Buffalo Grove, IL). The MetroMix® 820 substrate is henceforth referred to as peat-based mix for simplicity. To prevent the loss of substrate through the drain holes, a thin white cloth (A.M. Leonard, Piqua, OH) was placed at the bottom of the container before filling it with calcined clay or perlite. In each container, 30 mL of native soil was applied to the top of the substrate.

A nitrogen-limited nutrient solution (Bugbee 2004, Table 1), totaling 250 mL, was applied to each container after transplanting. The reverse osmosis water was used to prepare the nutrient solution to ensure the absence of additional nutrients that could affect the experiment's results. Subsequently, 50-100 mL of nitrogen-limited nutrient solution was applied to each container every other day. Distilled water was added when the top (~1 cm) substrate

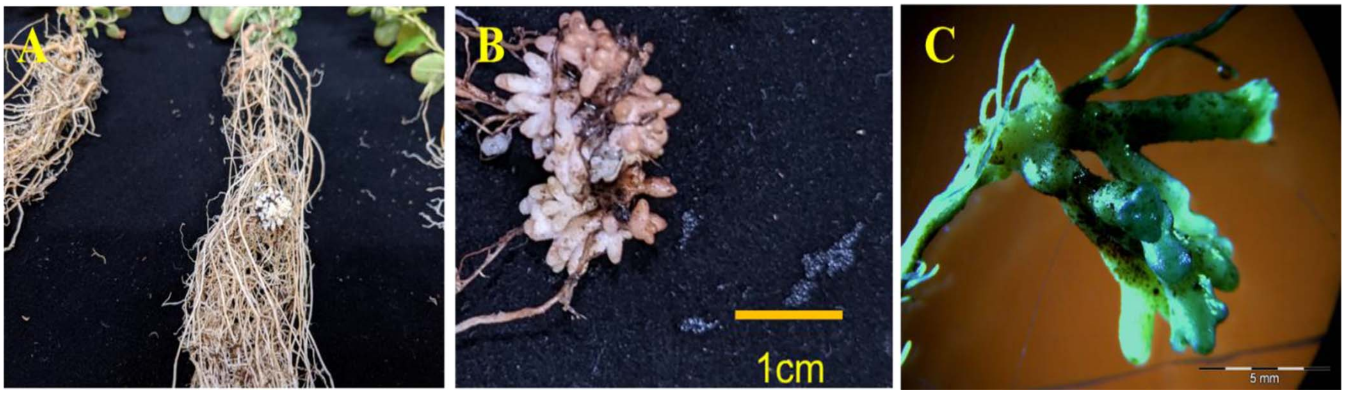

Fig. 1. **Photographs of representative root nodules observed on snowbrush ceanothus (*Ceanothus velutinus*) seedlings during the experiment. Root system with root nodule (A), closer view of nodules (B), and high magnification view of individual nodule (C).**

was dry. Regular monitoring of the seedlings was conducted, and any plants that did not survive were promptly replaced. Seedlings grown in calcined clay substrate had a comparatively higher mortality rate compared to those grown in a peat-based mix and perlite (data not shown). During the establishment phase, a 60% shade cloth was hung at the top of the seedlings to protect them from direct sunlight. The shade cloth was removed on 20 July 2021. After one month of establishment, healthy plants were selected for the experiment.

After the establishment period, which lasted one month, five seedlings from each substrate treatment were harvested once every two weeks for 31 weeks, and nodules were checked while recording plant growth data. Following the harvest, leaf area (square cm) was measured using a leaf area meter (LI-3100; LI-COR® Biosciences, Lincoln, NE). Additionally, the shoot dry weight (stem dry weight + leaf dry weight) and the root dry weight of plants were determined by drying the plants for 1 week at 60 C. Furthermore, the total dry weight of the nodules and the diameter of the largest nodule were recorded.

Dried snowbrush ceanothus leaves from the 15th harvest on 12 February 2022 were ground using a grinder (Model 80393, Hamilton Beach, VA). The powdered samples were then analyzed at the Utah State University Analytical Laboratories for mineral contents. Concentrations of calcium (Ca), iron (Fe), magnesium (Mg), nitrogen (N), phosphorus (P), and potassium (K) were determined following the protocol described in Gavlak et al. (2005).

Experimental design and statistical analyses. The experiment was conducted using a completely randomized design

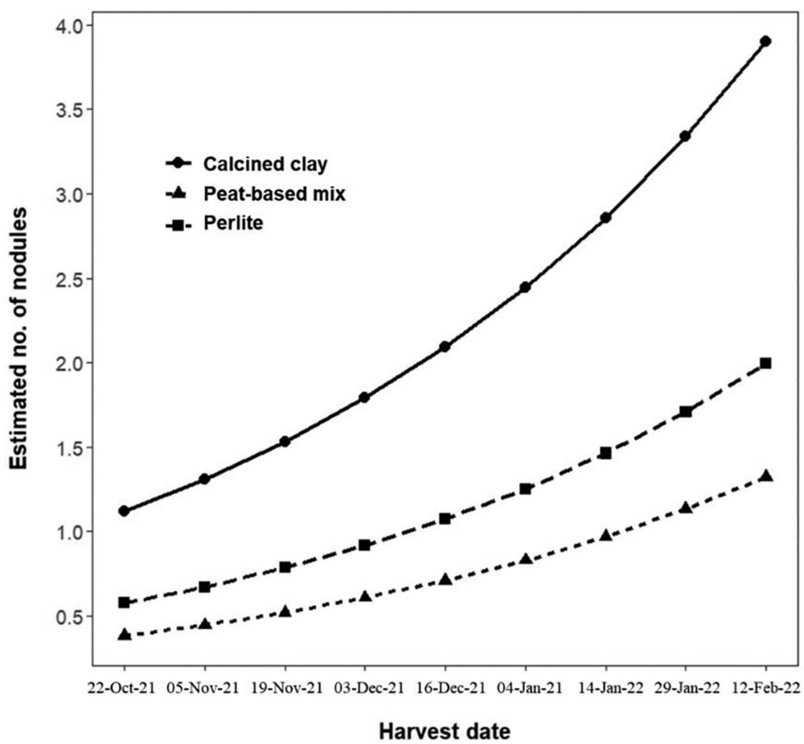

Fig. 2. **Estimated number of nodules on the roots of snowbrush ceanothus (*Ceanothus velutinus*) seedlings from the 7th harvest on 22 October 2021, after four months of inoculation, to the 15th harvest on 12 February 2022, after seven months and three weeks of inoculation. Seedlings were inoculated with native soil on 17 June 2021.**

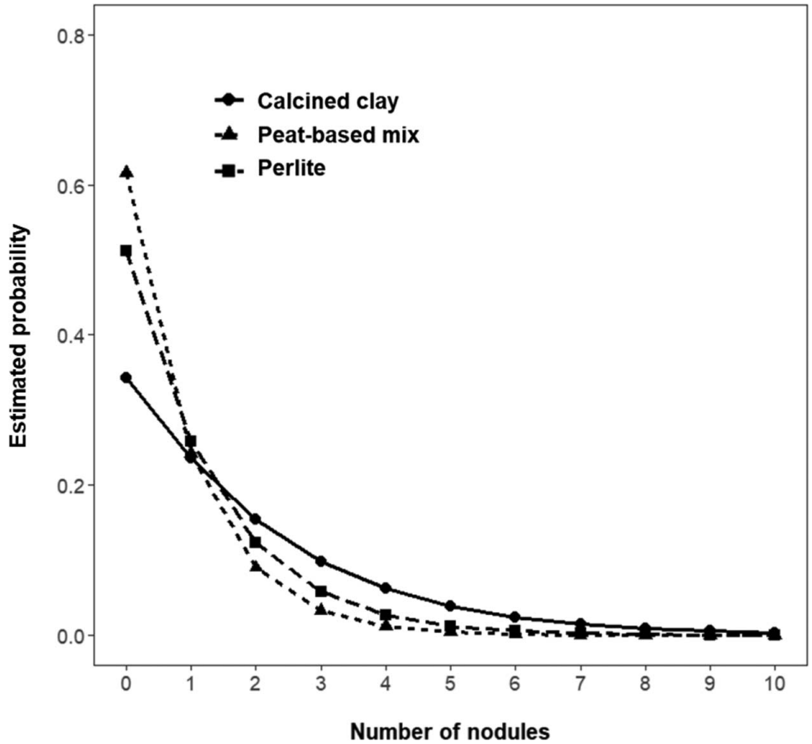

Fig. 3. Estimated probability of root nodulation on snowbrush ceanothus (*Ceanothus velutinus*) seedlings at the 10th harvest on 02 December 2021, after five months and two weeks of inoculation. Seedlings were inoculated with native soil on 17 June 2021.

(CRD). Five plants were harvested for each substrate type per harvest. Data analyses were performed only using the data from the 7th harvest on 22 October 2021 to the 15th harvest on 12 February 2022, since nodules were first observed at the 7th harvest, and plant growth was suboptimal after the 15th harvest. Log transformation was performed for data including the dry weight (DW) of nodules, diameter of the largest nodule, shoot DW, root DW, and leaf area. To evaluate the impact of harvest timing and substrate on nodule formation and nodule number, a negative binomial model was employed using PROC COUNTREG procedures. To analyze the plant growth and mineral content data, an analysis of variance and PROC GLIMMIX procedures were conducted using SAS University Edition (SAS Institute Inc., Cary, NC). Means separation among treatments was adjusted for multiplicity using Tukey-Kramer method with significant level specified at $\alpha \leq 0.05$.

Results and Discussion

Nodules. Nodules (irregularly shaped lobed masses) started to emerge on the roots of snowbrush ceanothus seedlings at the seventh week of harvest, four months after inoculation with native soil (Fig. 1 and 2). Time of harvest significantly influenced nodule formation ($P = 0.001$). As time prolonged, the chance to form nodules increased. Furthermore, a greater proportion of seedlings exhibited nodulation when grown in the calcined clay substrate ($P < 0.01$). Nodules were consistently present on all five seedlings grown in calcined clay substrate harvested on the last five dates, corresponding to 5-Nov-21, 19-Nov-21, 3-Dec-21, 4-Jan-22, and 12-Feb-22. The number of nodules formed increased as well with time (Fig. 2). In addition, significantly more nodules were formed in the calcined clay substrate compared to peat-based mix and perlite ($P < 0.01$) for all harvests.

During the 10th harvest on 3 December 2021, after five and a half months of inoculation with native soil, the probability of forming no nodules was greater in the peat-based mix and in perlite when compared to calcined clay (Fig. 3). Similarly, the probability of forming two or more nodules was greater in calcined clay. The chance for a seedling to form eight or more nodules was slim regardless of substrate.

There was no significant difference in the total dry weight of nodules, or the diameter of the largest nodule formed on seedlings grown in different substrates (Table 2). Seedlings grown in calcined clay, peat-based mix, and perlite substrate exhibited an average nodule dry weight of 0.012, 0.007, and 0.011 g, respectively. Similarly, the diameter of the largest nodule was 0.6, 0.5, and 0.5 cm, respectively, in seedlings grown in calcined clay, peat-based mix, and perlite substrate.

In nursery production, various soilless substrates are utilized to cultivate ornamental plants. Soilless substrates have benefits such as water retention, improved root aeration, and

Table 2. Dry weight (DW) of nodules and diameter of the largest nodule in snowbrush ceanothus (*Ceanothus velutinus*) seedlings grown in different substrates under greenhouse conditions.[z]

Substrate	DW of nodules (g)	Diameter of the largest nodule (cm)
Calcined clay	0.012 a	0.6 a
Peat-based mix	0.007 a	0.5 a
Perlite	0.011 a	0.5 a

[z]Same letters within the column are not significantly different among substrates by Tukey-Kramer method for multiplicity at $\alpha \leq 0.05$.

Table 3. **Shoot and root dry weight (DW) and leaf area of snowbrush ceanothus (*Ceanothus velutinus*) seedlings grown in different substrates under greenhouse conditions, recorded biweekly from 22 October 2021 to 12 February 2022.[z]**

Substrate	Shoot DW (g)	Root DW (g)	Leaf area (cm^2)
Calcined clay	0.4 b	0.5 b	17.2 b
Peat-based mix	0.9 a	1.2 a	34.8 a
Perlite	0.4 b	0.5 b	19.1 b
Substrate	NS	*	NS
Time	NS	**	NS
Substrate × Time	NS	NS	NS

[z]Same letters within the column are not significantly different among substrates by Tukey-Kramer method for multiplicity at $\alpha \leq 0.05$. NS, *, **: not significant or significant at $P < 0.05$ or $P < 0.01$, respectively.

enhanced nutrient uptake. However, a shallow soilless substrate possesses limitations compared to field soils, mainly because of the limited root zone volume (Narvaez-Ortiz et al. 2018). It is important to explore strategies to support the proper growth and development of plants. For actinorhizal plants, the preferred approach involves substrate inoculation to encourage the formation of symbiotic nodules. Previous research supports our current approach of using soil samples from the roots of wild actinorhizal plants to induce nodulation (Beddes and Kratsch 2010, Laws and Graves 2005). The presence of nodules observed in snowbrush ceanothus seedlings was possibly due to native soil inoculation, as nodules were not observed in seedlings that were not inoculated (data not shown). Similarly, Ganesh (2021) reported that inoculation with native soil induced nodules in the roots of snowbrush ceanothus. However, prior research on the time required for nodules formation in snowbrush ceanothus was lacking.

The nodulation process in actinorhizal plants is influenced by various factors, including substrate composition. The higher estimated number of nodules observed in calcined clay indicates that this substrate likely provides a more favorable environment for the formation and growth of nodules in snowbrush ceanothus. Calcined clay, an inorganic growing substrate, can have a porous structure that allows for better aeration, drainage, and root respiration (Ingram et al. 1993). Mee et al. (2003) reported that regular watering and effective drainage are necessary throughout the growth stages of snowbrush ceanothus, which usually grows in arid regions characterized by soil that is often impoverished and rocky in nature. Cultivating snowbrush ceanothus in calcined clay may mimic its native habitats and enhance nodulation. Additionally, Sriladda et al. (2016) utilized a well-drained inorganic substrate for cultivating hybrid buffaloberry (*Shepherdia* × *utahensis* 'Torrey') seedlings. Similarly, Chen et al. (2020) cultivated another actinorhizal plant, hybrid buffaloberry, in a calcined clay substrate and suggested that a substrate with low organic matter may enhance nodule formation. While perlite also has low organic matter and good drainage, other factors such as the specific physical and chemical properties of the substrates may influence nodulation success. Calcined clay may offer more stable moisture retention than perlite. In addition, perlite, being lightweight and porous, may not provide a stable structure for the anchorage of nodules compared to calcined clay. Furthermore, peat-based mix, rich in organic matter, may have lower oxygen levels due to its dense composition, in contrast to the soil composition typically found in arid regions (Heaton and Koenig 2010).

Plant growth and mineral nutrients. Snowbrush ceanothus seedlings grown in a calcined clay or perlite substrate had lower shoot dry weight, root dry weight, and leaf area compared to seedlings cultivated in the peat-based mix ($P < 0.0001$, Table 3). More vigorous growth was observed in seedlings in the peat-based mix compared to those grown in calcined clay and perlite (Fig. 4). Seedlings in the peat-based mix had an average of 0.9 g, 1.2 g, and 34.8 cm^2 for shoot dry weight, root dry weight, and leaf area, respectively. Furthermore, the effect of time ($P = 0.006$) on the root dry weight of seedlings was found to be significant, with root dry weight increasing as the duration of growth increased.

The higher shoot dry weight, root dry weight, and leaf area of snowbrush ceanothus seedlings grown in the peat-based mix suggest a more favorable growth environment. Peatmoss is considered the most popular substrate component used to produce greenhouse-grown ornamentals (Gruda 2019). Known for its high-water holding capacity, peatmoss provides a consistent moisture level in the root zone, mitigating the risk of drought stress and ensuring adequate hydration for optimal plant growth. Similarly, Rose and Haase (2000) reported that Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*] exhibited significantly larger size when grown in a peatmoss substrate compared to those grown in a coir-based substrate.

In the leaves of snowbrush ceanothus, N, P, K, Ca, and Mg contents were consistent for seedlings grown across all three substrates (Table 4), ranging from 20-22 $mg \cdot g^{-1}$ for N, 5-7 $mg \cdot g^{-1}$ for P, 8-11 $mg \cdot g^{-1}$ for K, 17-20 $mg \cdot g^{-1}$ for Ca, and 4-5 $mg \cdot g^{-1}$ for Mg. However, the Fe

Fig. 4. **Photographs of representative snowbrush ceanothus (*Ceanothus velutinus*) seedlings grown in calcined clay (A), peat-based mix (B), and perlite (C) substrates harvested on 22 October 2021, after four months of inoculation with native soil.**

Table 4. **Content of nitrogen (N), phosphorus (P), potassium (K), iron (Fe), calcium (Ca), and magnesium (Mg) in leaves of snowbrush ceanothus (*Ceanothus velutinus*) seedlings grown in different substrates under greenhouse conditions.**[z]

Substrate	Ion content ($mg \cdot g^{-1}$)					
	N	P	K	Fe	Ca	Mg
Calcined clay	21.48 a	6.69 a	7.58 a	0.12 a	16.72 a	4.83 a
Peat-based mix	20.10 a	5.45 a	10.66 a	0.07 b	19.85 a	3.91 a
Perlite	21.38 a	6.66 a	10.31 a	0.06 b	19.18 a	4.38 a

[z]Same letters within the column are not significantly different among substrates by Tukey-Kramer method for multiplicity at $\alpha \leq 0.05$.

content was greater in seedlings grown in the calcined clay substrate ($0.12\ mg \cdot g^{-1}$) compared to the peat-based mix ($0.07\ mg \cdot g^{-1}$, $P = 0.01$) or perlite ($0.06\ mg \cdot g^{-1}$, $P = 0.004$).

Substrate type is known to play a crucial role in nutrient availability for plants (Atzori et al. 2021), but our results suggest that other factors such as uniformity in growing conditions or inherent characteristics of snowbrush ceanothus may have contributed to maintaining consistent nutrient levels. However, the choice of substrate impacted the Fe content, with the calcined clay substrate leading to higher Fe content in the leaves of snowbrush ceanothus seedlings. This observation may be attributed to the presence of iron oxide, which serves as the primary colorant in clay materials, with more than 5% ferric oxide (Fe_2O_3) present in it (Martirena et al. 2020). The elevated Fe content in the leaves grown in calcined clay may have implications for plant health and growth. Further investigation is needed to understand the mechanisms underlying the substrate-induced variation in Fe content.

In conclusion, the results of this study suggest that inoculation of plants with native soil containing *Frankia sp.* bacteria helps root nodulation in snowbrush ceanothus. The peat-based mix promoted more vigorous plant growth, while the calcined clay substrate showed potential for enhancing nodulation. These findings enhance our understanding of the factors influencing the growth and nodulation of snowbrush ceanothus and can inform future cultivation practices for this plant species. Further research into the specific mechanisms underlying these observations can provide valuable insights for optimizing substrate selection to enhance nodulation and overall plant performance of snowbrush ceanothus. Furthermore, it is necessary to understand the influence of varying nitrogen levels on the nodulation and growth of snowbrush ceanothus.

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