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RESEARCH ARTICLE

No short-term benefits of inoculation with ericoid mycorrhizal fungi for highbush blueberry (*Vaccinium corymbosum*: *Ericaceae*) cultivated under controlled conditions in rhizotrons

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Abstract. Ericoid mycorrhizal fungi (ErMF) enhance nutrient uptake in highbush blueberry (*Vaccinium* sp.); however, it is unclear whether inoculating plants with ErMF is actually beneficial. A 40-day rhizotron trial evaluated the effects of two ErMF isolates (*Hyaloscypha hepaticicola* and *Oidiodendron maius*), individually and combined, on growth and root development of the 'Duke' and 'Legacy' varieties of highbush blueberry, *Vaccinium corymbosum* s. l. Fungal inoculation increased leaf nitrogen concentration in the 'Duke' cultivar plants; a decrease in root biomass was also recorded for the 'Legacy' cultivar plants compared to the uninoculated plants. The total root length in the 'Duke' cultivar was lower with *O. maius* or combined inoculum, and leaf potassium concentration in the 'Legacy' cultivar decreased with *H. hepaticicola* or combined inoculum. These findings suggest no short-term benefits of ErMF inoculation for highbush blueberry under the tested conditions. Further research is needed to evaluate potential long-term effects and optimize inoculation strategies.

Keywords: mycorrhizal colonization, nutrient uptake, plant biomass, root architecture, *Vaccinium corymbosum*

Introduction

Cultivation of highbush blueberry (*Vaccinium* sp.) originated in the United States (Coville, 1910). Production and consumption of blueberries have increased sharply in the world because of their high economic value and beneficial effect on human health (Kalt et al., 2020). Currently, China is the leading producer of blueberries, followed by the United States and Peru (International Blueberry Organization, 2023). Alongside development in these sectors, production and competition for blueberries are expanding in many countries (Protzman, 2021).

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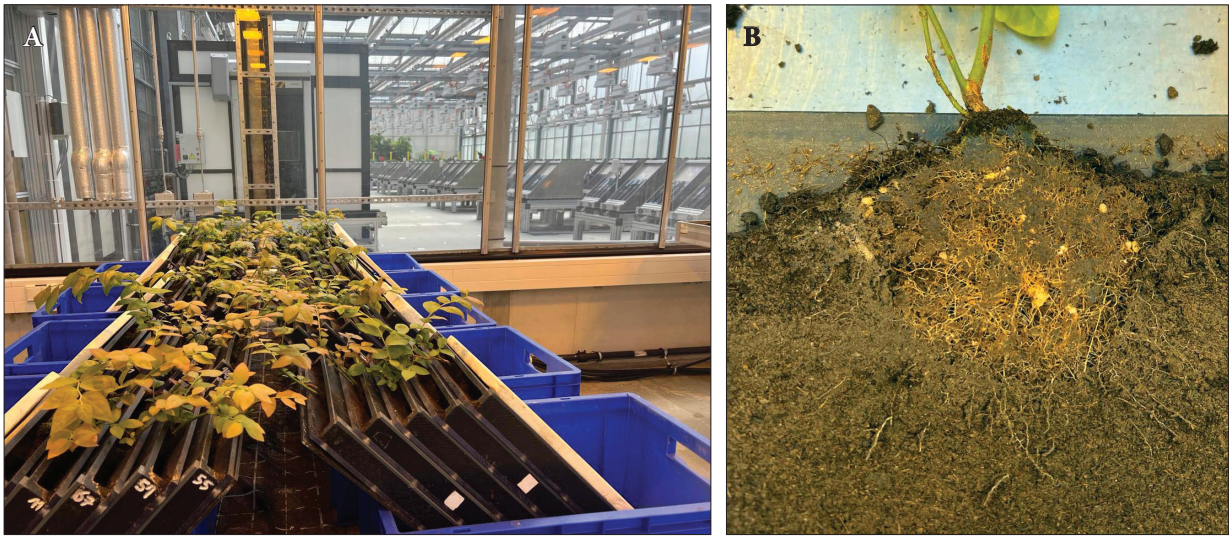

Fig. 1. Highbush blueberry growing in rhizotrons. A: plants; B: roots

Ericoid mycorrhizal fungi (ErMF) form symbiotic associations with the roots of ericaceous plant species, including highbush blueberry (Retamales, Hancock, 2018). They are known to improve growth and production in the host plants by utilizing organic or insoluble compounds in the soil (Smith, Read, 2008). ErMF can be found in temperate ecosystems, including peatlands, forests and heathlands (Scagel et al., 2005). However, inoculating plants with ErMF could accelerate root colonization and provide advantages, particularly during early stages of plant development (Scagel, 2005a, 2005b).

The objective of the present study was to examine the potential benefits of inoculating highbush blueberry plants with ErMF. The plants were grown in root observation boxes called rhizotrons to determine whether ErMF affected growth in both the roots and shoots (Martino et al., 2018; Perotto et al., 2018; Vohník, 2020; Bertolot et al., 2024).

Materials and Methods

Fungal isolates

Two isolates of ErMF, *Hyaloscypha hepaticicola* (Grelet & Croz.) Baral, Huhtinen & J.R. De Sloover) [Synonyms: *Trichopeziza hepaticicola* Grelet & Croz., *Pezizella ericae* D.J. Read, *Hymenoscyphus ericae* (D.J. Read) Korf & Kernan, *Rhizoscyphus ericae* (D.J. Read) W.Y. Zhuang & Korf, and *Pezoloma ericae* (D.J. Read) Baral (Fehrer et al., 2019)] and *Oidiodendron maius* G.L. Barron were obtained from the University of Toronto UAMH Centre for Global Microfungal Biodiversity collection (UAMH numbers 5828 and 8507, respectively). Both of these ErMF are commonly associated with blueberry roots (Scagel et al., 2005). The isolates were transferred to Petri dishes and incubated for 20 days at 25 °C on a modified Melin-Norkrans medium (MMN).

Plant material

The 'Duke' and 'Legacy' highbush blueberry cultivars (*Vaccinium corymbosum* L. s. l. and complex hybrids based on *V. corymbosum* and *V. darrowii* Camp.) were selected as they both are well adapted to northern climates and readily planted in many countries, including the Republic of Georgia / Sakartvelo (Tsintsadze, Bobokashvili, 2023). The plants were obtained from a commercial nursery (Nursery Waganowice Kusibab-Popowicz — Waganowice, Poland) as 2-year-old container stock (1.5-L containers). Each plant was transplanted individually into sterilized rhizotrons filled with 3 L of steam-pasteurized proprietary peat-based growing medium (Fig. 1A). The medium had pH 5.5 ($CaCl_2$), bulk density 129 $g{\cdot}L^{-1}$ and 360 $g{\cdot}L^{-1}$ (dry and wet, respectively), electrical conductivity (EC) 0.5 $dS{\cdot}m^{-1}$ (H_2O), and contained 100 $mg{\cdot}L^{-1}$ NO_3-N, < 1 $mg{\cdot}L^{-1}$ NH_4-N, 125 $mg{\cdot}L^{-1}$ P_2O_5, 126 $mg{\cdot}L^{-1}$ K_2O, and 98 $mg{\cdot}L^{-1}$ Mg. During transplanting, plants were either uninoculated (control) or inoculated with 50 mL of one or both blended ErMF isolates. MNM agar without fungi was added to the uninoculated controls (Grelet et al., 2017).

Table 1. **Effects of inoculation with two different isolates of ericoid mycorrhizal fungi (ErMF) on root development of the 'Duke' and 'Legacy' blueberry**

Cultivar / EMF inoculum	Root length (cm)			Root system width (cm)	Root system depth (cm)
	Primary	Lateral	Total		
			'Duke'		
No inoculum (control)	13.0 ± 4.1 a[1]	63.0 ± 9.7 a	76.0 ± 12.4 a	9.9 ± 0.4 a	6.8 ± 0.5 a
Hyaloscypha hepaticicola	9.0 ± 1.3 a	63.0 ± 7.2 a	71.6 ± 7.8 a	9.7 ± 0.5 a	7.7 ± 0.3 a
Oidiodendron maius	8.5 ± 1.4 a	44.5 ± 8.7 a	52.9 ± 8.7 b	9.5 ± 0.6 a	7.2 ± 0.2 a
H. hepaticicola + *O. maius*	8.2 ± 1.6 a	42.3 ± 10.4 a	50.5 ± 10.9 b	9.3 ± 0.3 a	6.7 ± 0.5 a
			'Legacy'		
No inoculum (control)	5.5 ± 1.0 a	19.5 ± 3.2 a	25.1 ± 3.7 a	8.0 ± 0.5 a	6.0 ± 0.4 a
Hyaloscypha hepaticicola	6.3 ± 0.7 a	27.4 ± 12.0 a	33.7 ± 12.1 a	7.6 ± 0.6 a	5.4 ± 0.5 a
Oidiodendron maius	4.9 ± 0.6 a	22.2 ± 5.8 a	27.1 ± 5.8 a	8.4 ± 0.6 a	5.8 ± 0.6 a
H. hepaticicola + *O. maius*	4.6 ± 0.7 a	14.4 ± 3.7 a	21.3 ± 3.7 a	8.3 ± 0.3 a	5.9 ± 0.4 a
			Significance		
Cultivar	**	**	**	**	**
EMF inoculum	NS	NS	NS	NS	NS
Cultivar × inoculum	NS	NS	*	NS	NS

[1] Means (± 1 SE) followed by a different letter within a cultivar are significantly different at $P \leq 0.05$ (Tukey's test).
NS, *, ** — non-significant or significant at $P \leq 0.05$ or 0.01, respectively.

Experimental design

The experiment was initiated on 23 April 2023 and run for 40 days at the Institute of Bio- and Geosciences (IBG), Plants Sciences (IBG-2), Forschungszentrum Jülich GmbH, Jülich, Germany. Ten plants (rhizotrons) per treatment (2 cultivars × 4 inoculum combinations) were placed in a greenhouse and arranged in a completely randomized design. The plants were grown with 16 h of supplemental light per day and irrigated as needed. The pH and EC of the irrigation water were 5.5 and < 1 $dS \cdot m^{-1}$, respectively. Temperature and relative humidity in the glasshouse were maintained at 26/16 °C and 40/60% (day/night), respectively.

Measurements

Images of primary and lateral roots in the rhizotrons (Fig. 1B) were captured using a digital camera and analyzed for the length using PaintRhizo software (Nagel et al., 2012). Width and depth of each root system was also measured. Once the images were captured, the plants were removed from the rhizotrons, washed, and divided into roots and shoots (stems and leaves). Roots and shoots were immediately weighed to determine fresh biomass, oven-dried at 60 °C, and reweighed to determine dry biomass. Leaves from each plants were ground in a Wiley mill and analyzed for N (nitrogen), P (phosphorus), and K (potassium), following the protocols described by Stebbins and Wilder (1988). Root colonization by ErMF was quantified under a microscope (10–40×) using a slight modification of the root clearing maceration and staining methods described by others (Walker, 2005; Derkowska et al., 2015; Vohník, 2020).

Statistical analysis

Data were analyzed by two-way analysis of variance (ANOVA) using SAS v. 9.4 (SAS Institute, Cary, NC, USA). Means were separated within cultivars using Tukey's honestly significant difference test ($P \leq 0.05$). Data was stored at the Agricultural University of Georgia, Laboratory of Mycology and Plant Pathology according to FAIR standards.

Results and Discussion

Root development

The total root length measured for the 'Duke' variety plants inoculated with *O. maius* or with both *O. maius* and *H. hepaticicola* was lower when compared to the total root length of uninoculated or inoculated with *H. hepaticicola* plants (Table 1). Inoculation with ericoid mycorrhizal fungi, which commonly form associations with plants in the family *Ericaceae*, including blueberries (*Vaccinium* spp.), has also been observed to influence root morphology. For instance, inoculation with *Oidiodendron maius*

Table 2. **Effects of inoculation with two different isolates of ericoid mycorrhizal fungi (ErMF) on shoot and root growth of the 'Duke' and 'Legacy' blueberry**

Cultivar / EMF inoculum	Shoot biomass (g/plant)		Shoot length (cm)	Root biomass (g/plant)	
	Fresh	Dry		Fresh	Dry
			'Duke'		
No inoculum (control)	9.3 ± 1.0 a[1]	4.7 ± 0.3 a	27.7 ± 2.4 a	25.0 ± 0.6 a	4.3 ± 0.9 a
Hyaloscypha hepaticicola	7.3 ± 0.4 b	3.8 ± 0.1 b	27.9 ± 1.6 a	16.0 ± 3.1 b	4.3 ± 0.3 a
Oidiodendron maius	6.6 ± 0.6 b	3.5 ± 0.2 b	27.2 ± 1.1 a	20.7 ± 2.6 b	4.7 ± 0.7 a
H. hepaticicola + *O. maius*	6.1 ± 0.5 b	3.4 ± 0.2 b	22.7 ± 2.3 a	15.7 ± 5.0 b	4.0 ± 0.6 a
			'Legacy'		
No inoculum (control)	6.4 ± 0.2 a	3.6 ± 0.2 a	23.3 ± 1.0 ab	26.6 ± 5.2 a	5.0 ± 0.0 a
Hyaloscypha hepaticicola	5.8 ± 0.4 a	3.3 ± 0.2 a	20.4 ± 2.2 b	18.0 ± 2.6 b	4.3 ± 0.3 a
Oidiodendron maius	5.9 ± 0.3 a	3.7 ± 0.2 a	23.8 ± 2.2 a	12.7 ± 1.2 b	3.7 ± 0.3 a
H. hepaticicola + *O. maius*	6.5 ± 0.3 a	3.5 ± 0.2 a	24.1 ± 0.8 a	22.3 ± 0.7 ab	4.7 ± 0.3 a
			Significance		
Cultivar	**	*	**	NS	NS
EMF inoculum	**	**	NS	*	NS
Cultivar × inoculum	*	**	*	*	NS

[1] Means (± 1 SE) followed by a different letter within a cultivar are significantly different at $P \leq 0.05$ (Tukey's test).
NS, *, ** — non-significant or significant at $P \leq 0.05$ or 0.01, respectively.

has been reported to affect root length and architecture in blueberries, promoting a more branched root system, which enhances nutrient uptake efficiency (Wei et al., 2022). In nutrient-limited soils, plants highly dependent on mycorrhiza may lower their metabolic costs by reducing root growth and developing a coarser root system (Hetrick, 1991). This may also be the case in soilless media.

Shoot length and plant biomass

The inoculation with ErMF resulted in less biomass in the shoots and/or roots of both cultivars (Table 2). Furthermore, *H. hepaticicola* resulted in less shoot length than *O. maius* or the mix of *H. hepaticicola* and *O. maius* in the 'Legacy' variety. Mycorrhizal fungi incur both costs and benefits to the overall carbon economy of host plants and may initially reduce growth during establishment (Buwalda, Goh, 1982; Koide, 1985; Peng et al., 1993; Taylor, Harrier, 2000). Controlled variants indicate that total costs range anywhere from 3 to 36% of the carbon fixed daily by photosynthesis, with the largest proportion of the carbon allocated to respiration required by the mycobiont for construction of new intraradical and extraradical fungal structures, maintenance and repair of existing fungal tissue, and cellular processes associated with the absorption, translocation, and transfer of nutrients from the soil to the host (Bryla, Eissenstat, 2005).

Leaf nutrients

The inoculation with both ErMF increased the concentration of N in the leaves relative to control in 'Duke' (Table 3). Although this may have been due to less growth in the inoculated plants (Table 2), increased uptake of soil nutrients, including N, has been observed in young highbush blueberry plants inoculated with ErMF (Scagel, 2005a). However, inoculation had no effect on P in both cultivars in the present study, and it reduced the concentration of K in the leaves when the plants were inoculated with *H. hepaticicola* or the mix of *H. hepaticicola* and *O. maius* in 'Legacy' (Table 3).

Root colonization by ericoid mycorrhizal fungi

Root colonization by ErMF was higher with *O. maius* than with *H. hepaticicola*, the mix of *H. hepaticicola* and *O. maius*, and control in 'Duke' (Table 4). However, it was similar between the control and the inoculated treatments in 'Legacy'. Root colonization by ErMF is often variable in blueberry, depending on the cultivar and the environmental conditions in which the plants are grown (Scagel et al., 2005; Villarreal-Ruiz et al., 2012; Brody et al., 2019; Albornoz et al., 2021). Time is also a factor and, in the present study, may have been too short (i.e., 40 days) to develop significant levels of root colonization in plants inoculated with *H. hepaticicola* in both cultivars and with *O. maius* in 'Legacy' (Fig. 2).

Table 3. **Effects of inoculation with two different isolates of ericoid mycorrhizal fungi (ErMF) on the concentration of N, P, and K of the leaves of the 'Duke' and 'Legacy' blueberry**

Cultivar / EMF inoculum	Leaf N (%)	Leaf P (%)	Leaf K (%)
		'Duke'	
No inoculum (control)	0.90 ± 0.05 b[1]	0.37 ± 0.04 a	0.54 ± 0.05 a
Hyaloscypha hepaticicola	1.57 ± 0.02 a	0.54 ± 0.13 a	0.65 ± 0.03 a
Oidiodendron maius	1.51 ± 0.05 a	0.43 ± 0.04 a	0.53 ± 0.06 a
H. hepaticicola + *O. maius*	1.50 ± 0.05 a	0.48 ± 0.06 a	0.64 ± 0.03 a
		'Legacy'	
No inoculum (control)	1.43 ± 0.4 a	0.37 ± 0.04 a	0.67 ± 0.03 a
Hyaloscypha hepaticicola	1.33 ± 0.4 a	0.33 ± 0.04 a	0.48 ± 0.04 b
Oidiodendron maius	1.39 ± 0.3 a	0.34 ± 0.05 a	0.52 ± 0.06 ab
H. hepaticicola + *O. maius*	1.34 ± 0.3 a	0.35 ± 0.03 a	0.51 ± 0.06 b
		Significance	
Cultivar	NS	*	**
EMF inoculum	**	NS	NS
Cultivar × inoculum	**	NS	*

[1] Means (± 1 SE) followed by a different letter within a cultivar are significantly different at $P \leq 0.05$ (Tukey's test).
NS, *, ** — non-significant or significant at $P \leq 0.05$ or 0.01, respectively.

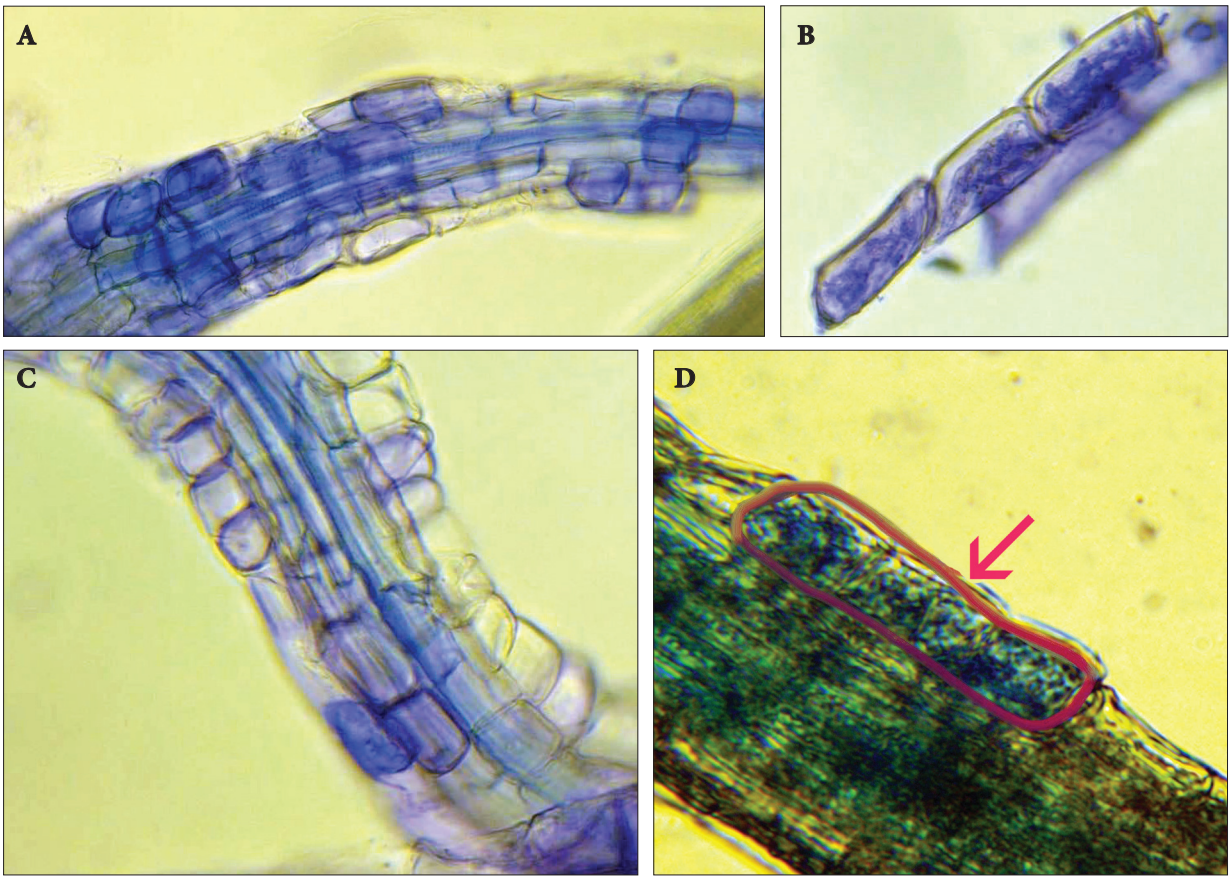

Fig. 2. Ericoid mycorrhizal colonization of roots in the 'Duke' (A, B) and 'Legacy' (C, D) cultivars of highbush blueberry

Table 4. **Root colonization by ericoid mycorrhizal fungi (ErMF) in the 'Duke' and 'Legacy' blueberry inoculated with two different isolates of the fungi**

EMF inoculum	Root colonization (%)	
	'Duke'	'Legacy'
No inoculum (control)	1.4 ±1.0 b[1]	0.5 ± 0.2 a
Hyaloscypha hepaticicola	13.3 ±6.3 b	9.4 ± 4.7 a
Oidiodendron maius	44.0 ±11.9 a	14.1 ± 6.2 a
H. hepaticicola + *O. maius*	8.5 ±4.8 b	20.2 ± 6.6 a
	Significance	
Cultivar	NS	
EMF inoculum	**	
Cultivar × inoculum	*	

[1] Means (± 1 SE) followed by a different letter within a cultivar are significantly different at $P \leq 0.05$ (Tukey's test). NS, *, ** — non-significant or significant at $P \leq 0.05$ or 0.01, respectively.

Conclusion

Despite the short duration of the present study, we observed a higher concentration of N (nitrogen) in the leaves when the 'Duke' was inoculated with *O. maius*, which was the only treatment that increased root colonization by ErMF in the cultivar. However, we did not observe any immediate benefits of ErMF on shoot or root growth in the 'Duke' or 'Legacy'. In fact, the inoculation with the ErMF isolates and their mixture resulted in less fresh shoot biomass in 'Duke' and less fresh root biomass in both cultivars. Furthermore, *O. maius* and the mix of *H. hepaticicola* and *O. maius* reduced total root length in 'Duke' and resulted in lower concentrations of K (potassium) in the leaves of 'Legacy'. Further work is needed to determine whether there are any long-term benefits of inoculating highbush blueberry with ErMF.

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ETHICS DECLARATION

The authors declare no conflict of interest.

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Інокуляція лохини високорослої (*Vaccinium corymbosum*: *Ericaceae*) ерикоїдними мікоризними грибами за короткий термін культивування в контрольованих умовах у ризотронах не дає переваг

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Реферат. Ерикоїдні мікоризні гриби покращують засвоєння поживних речовин лохиною високорослою (*Vaccinium* sp.), проте невідомо, чи інокуляція рослин цією мікоризою дійсно має позитивний ефект. Вплив інокуляції двома ізолятами (*Hyaloscypha hepaticicola* та *Oidiodendron maius*), окремо й разом, на ріст і розвиток коренів культиварів 'Duke' і 'Legacy' лохини високорослої (*Vaccinium corymbosum* s. l.) вивчали впродовж 40-денного культивування в ризотроні. Інокуляція грибами підвищила концентрацію азоту в листках рослин сорту 'Duke', а також було зафіксовано зменшення біомаси коренів у сорту 'Legacy' порівняно з неінокульованими рослинами. Загальна довжина коренів рослин сорту 'Duke' була нижчою після інокуляції *O. maius* або комбінованим інокулятом, а концентрація калію в листках сорту 'Legacy' знизилася у випадку з *H. hepaticicola* або комбінованим інокулятом. Ці результати свідчать про відсутність короткострокових переваг від інокуляції лохини високорослої мікоризою за наведених умов. Необхідні подальші дослідження для оцінки потенційного довгострокового ефекту та оптимізації процесу інокуляції.

Ключові слова: архітектура кореня, біомаса рослин, мікоризна колонізація, поглинання поживних речовин, *Vaccinium corymbosum*