

Frequency and Intensity of Root Colonization by Ericoid Mycorrhizal Fungi in Nursery Production of Blueberry Plants

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ABSTRACT. Ericoid mycorrhizal fungi (EMF) form symbiotic relationships with roots of blueberry plants providing increased access to nutrients from fertilizers and soil. A survey of commercial nursery plants produced from tissue culture and cuttings was conducted to determine when or if EMF colonize blueberry plants under nursery cultural methods. Although there were cultivar-specific differences, in general, colonization frequency (the percentage of plants colonized) and intensity (the percentage of root length with EMF) increased during the first growing cycle for both plants produced from tissue culture or cuttings. For most cultivars, colonization frequency and intensity increased over the first winter, but decreased after transplanting into either containers or bareroot production beds. Colonization at all phases of production was generally low, however, plants transplanted into bareroot production beds generally had higher colonization than plants transplanted into con-

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tainers. Our results suggest that the colonization of plants in containers and bareroot fields may be limited by environmental and cultural factors and not just the presence or absence of the correct fungi. Natural EMF colonization of blueberry plants in nurseries may be limited by nursery cultural conditions, low availability of EMF propagules, and aspects of plant-fungus specificity. [Article copies available for a fee from The Haworth Document Delivery Service: 1-800-HAWORTH. E-mail address: <docdelivery@haworthpress.com> Website: <<http://www.HaworthPress.com>> © 2005 by The Haworth Press, Inc. All rights reserved.]

KEYWORDS. Ericoid mycorrhizal fungi (EMS), nitrogen, *Vaccinium corymbosum* L., *Vaccinium ashei*, *Vaccinium angustifolium*

INTRODUCTION

Most members of the Ericaceae, including *Vaccinium* spp., are infected with ericoid mycorrhizal fungi (EMF) (Read, 1996). Root colonization by EMF can increase nitrogen (N) content and concentration of plants and enables plants to absorb N and phosphorus (P) from compounds unavailable to non-mycorrhizal plants (Bajwa and Read, 1985; Kerley and Read, 1997; Kerley and Read, 1998; Mitchell and Read, 1981; Read et al., 1989; Stribley and Read, 1974; Stribley and Read, 1976; Stribley and Read, 1980). Ericoid mycorrhizal fungi may also improve the general physiological condition of the host plant through enhanced uptake of some other deficient nutrients (Stribley and Read, 1976; Read and Stribley, 1973).

Under field conditions, mycorrhizal infection of cultivated blueberries varies greatly with soil and cultural factors (Boyer et al., 1982; Goulart et al., 1996; Gollmack et al., 2001; Powell and Bates, 1981; Scagel and Yang, 2003; Yang et al., 1998). Colonization of blueberry can vary significantly with cultivar (Czesnik and Eynard, 1990; Eynard and Czesnik, 1989), rate of fertilizer application (Powell, 1982) and the amount and type of soil organic matter present in the soil (Blasing, 1989; Czesnik and Eynard, 1990; Eynard and Czesnik, 1989; Haynes and Swift, 1985; Yang et al., 2002). A field study in Northeastern North America found that inoculation of tissue-cultured highbush blueberry increased plant growth and root dry weight (Yang et al., 2002). However, increased application of fertilizers can depress mycorrhizal infection levels in blueberry seedlings (Powell, 1982; Gollmack et al., 2001).

Root colonization by EMF is generally high (70-100%) on ericaceous plants in the wild (Kasurinen and Holopainen, 2001; Michelsen et al., 1996; Scagel, 2002); in blueberry production fields in Oregon root colonization by ericoid EMF ranges from 0.5% to 44% of total root length (Scagel and Yang, 2003). A study in Finland comparing EMF colonization of highbush blueberries to native *Vaccinium* spp. (*V. uliginosum* and *V. myrtillus*) found that native *Vaccinium* spp. had a higher intensity of EMF root colonization (> 48%) than the *V. corymbosum* L. in production fields (< 6%) (Kasurinen and Holopainen, 2001). However, there are few reports detailing presence of ericoid mycorrhizae in blueberry nurseries. A few studies have reported that EMF colonization of nursery produced plants occurs without inoculation of plants by virtue of natural EMF propagules in the growing media (Smagula and Litten, 1989; Moore-Parkhurst and Englander, 1982), while Powell and Bates (1981) found that blueberry nursery plants did not become mycorrhizal within their first year of growth in potting mix. The objectives of this work were to determine when or whether EMF colonize blueberry plants during commercial nursery production.

MATERIALS AND METHODS

Survey of plants produced from tissue culture. Samples of growing media and roots were taken at various times over a two year period from blueberry plants grown from tissue culture plantlets in a commercial nursery. Colonization of roots by EMF was determined during the rooting phase from tissue culture cuttings, at the end of the rooting phase, and seven times during hardening and the first growing cycle for *Vaccinium corymbosum* L. 'Bluecrop', 'Misty', 'O'Neal', 'Duke' and 'Rubel' and *V. angustifolium* 'Brunswick'. During the second growing cycle, colonization of roots by EMF was determined prior to transplant and after one growing cycle in 1 L or 4 L pots or in a bareroot field for *V. corymbosum* 'Bluecrop', 'Misty', 'O'Neal', 'Duke' and *V. angustifolium* 'Brunswick'. Exact date of sampling varied with cultivar and stock type. Colonization of root samples was determined from either randomly selected whole plants or soil cores depending on the stock type and time of year. All soil or growing media was washed from roots, roots were cleared in 10% potassium hydroxide for 30 min at 90°C, rinsed with distilled water (dH₂O) and then placed in dH₂O for 2 h. Roots were removed from dH₂O, stained overnight in a lactoglycerin

(1300 ml 85% lactic acid, 950 ml 99% glycerol, 930 ml dH₂O) solution containing 0.05% trypan blue (Phillips and Hayman, 1970), removed from stain, rinsed, and covered with lactoglycerin until colonization was determined. Mycorrhizal infection level was assessed as the percentage of 0.5 mm long root segments containing internal mycorrhizal structures, with 50-100 root segments examined for each root system at 200 × microscopy. Mycorrhizal infection was quantified using a grid-line intersect technique (Newman, 1966) modified to determine percentage of cells infected (Giovannetti and Mosse, 1980). Colonization frequency was calculated as a percentage of plants in the sample population (minimum n = 15) that showed signs of colonization by EMF. Colonization intensity was calculated as the percentage of roots (% root length) on a plant showing signs of colonization by EMF.

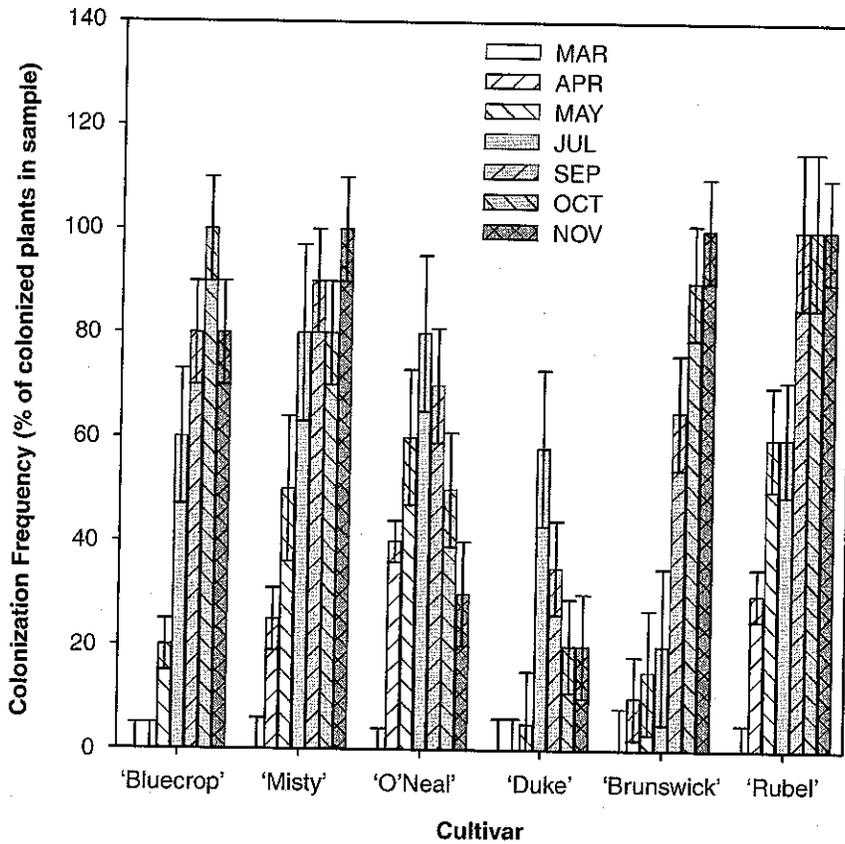
Survey of plants produced from hardwood cuttings. Random samples of growing media and roots were taken from production stock at various times over a two year period from blueberry plants grown in propagation flats or containers from hardwood cuttings. Colonization on roots by EMF was determined three, five, and eight months after sticking during the first growing cycle in propagation flats for *V. corymbosum* L. 'Duke', 'Reka', and 'Rubel' and *V. ashei* 'Powderblue'. During the second growing cycle mycorrhizal colonization on roots of hardwood cuttings was determined prior to transplanting and after one growing season in either 4 L pots or in a bareroot field for *V. corymbosum* L. 'Duke', 'Reka', and 'Reveille'. Time of sampling varied with cultivar and stock type. Root colonization frequency and intensity by EMF was assessed as described above (minimum n = 15) for the survey of tissue culture plants.

Statistical Analyses. Data from the survey of plants produced from tissue culture were compared based on plant age, cultivar, container type, and growing conditions using Analysis of Variance (ANOVA). Data from the survey on plants produced from cuttings were compared based on plant age, cultivar, cutting grade, and container type using ANOVA. Single degree of freedom contrasts and 95% least significant differences (95% LSD) based on Tukey's Honestly Significant Difference for unequal sample size (THSD) were used to compare specific means within and among cultivars. Root colonization data were square root transformed prior to analysis to equalize between sample variance ($p > 0.05$ Brown-Forsythe Test for Homogeneity of Variances). Back transformed data are presented in figures. All analyses were performed using the Statistica® statistical package (Statsoft, Inc., Tulsa, OK, USA, 1996).

RESULTS

Survey of plants produced from tissue culture. The colonization frequency (percentage of plants colonized) increased for 'Misty', 'Brunswick', and 'Rubel' cultivars during the first growing cycle (Figure 1). The percentage of 'Bluecrop', 'O'Neal' and 'Duke' plants colonized was highest in June of the first growing cycle then decreased in the fall.

FIGURE 1. Change in the percentage of tissue culture blueberry (*Vaccinium corymbosum* L. 'Bluecrop', 'Misty', 'O'Neal', 'Duke', 'Rubel' and *V. angustifolium* 'Brunswick') plants produced colonized by EMF during the first growing cycle in a production nursery. Error bars represent 95% least significant differences (LSDs) within cultivars.

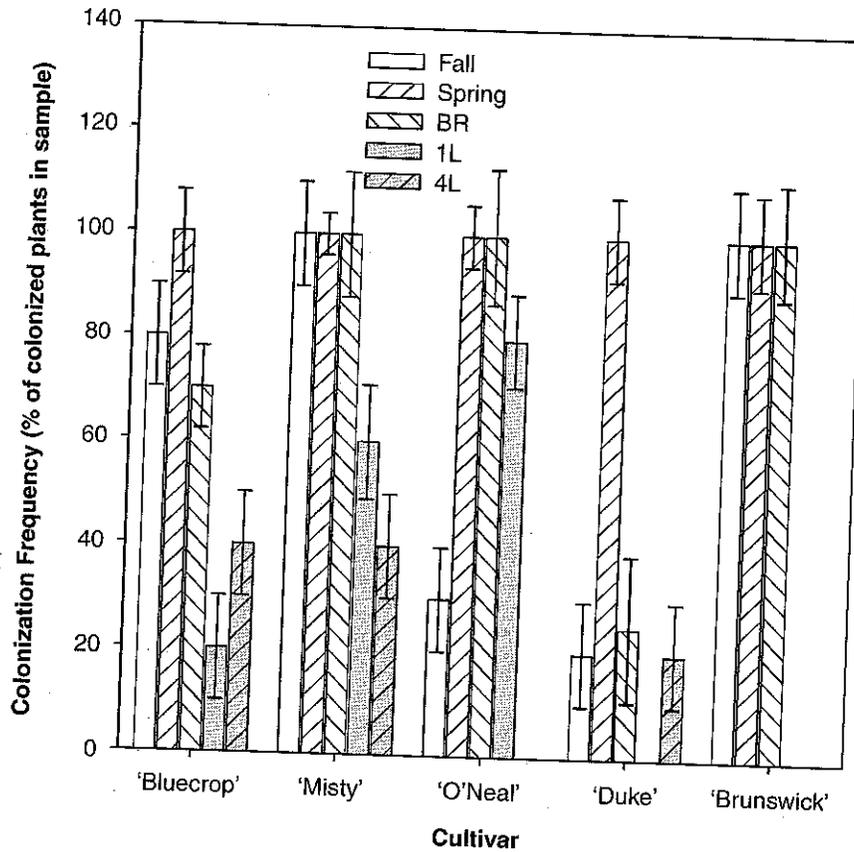


There was no significant difference in colonization frequency between northern highbush ('Bluecrop', 'Duke', 'Rubel') and southern highbush cultivars ('Misty', 'O'Neal') or the one lowbush cultivar ('Brunswick'). Colonization frequency increased over the winter and all plants of all cultivars showed some signs of colonization in the spring of the second growing cycle. Colonization frequency generally decreased after transplanting for Northern highbush whether in beds or pots and for Southern highbush when transplanted into containers (Figure 2).

The colonization intensity (percentage of root length colonized) on all cultivars was very low (less than 16% of roots were colonized) during the first growing cycle (Figure 3). Although there were significant differences in colonization intensity between cultivars, there were no trends in colonization intensity related to cultivar type (e.g., Northern highbush vs. Southern highbush). Colonization intensity of 'Misty' was highest during the rooting phase of the tissue culture plantlets (prior to June) but decreased after plants were transplanted and moved to an outdoor growing area. Colonization intensity of 'Bluecrop', 'O'Neal', 'Duke', and 'Rubel' was never higher than six percent during the first growing cycle and either stayed the same or decreased after transplanting and relocation to an outdoor growing area. The intensity of root colonization of 'Brunswick' was the highest (~16%) compared to other cultivars at the end of the first growing cycle and increased substantially after transplanting and relocation to an outdoor growing area. Colonization intensity increased significantly over the winter for all cultivars (Figure 4). The intensity of colonization on 'Misty' increased from ~2% in the fall to almost 30% the following spring and 'Brunswick' increased from ~16% to ~40%. Colonization intensity of 'Duke' showed the least change over the winter by increasing from ~5% to ~10%. When plants were planted into a bareroot field or containers, the colonization intensity on roots decreased for all cultivars. At the end of the second growing cycle, plants of 'Bluecrop', 'Misty', and 'O'Neal' were more intensely colonized when grown in bareroot fields than in containers.

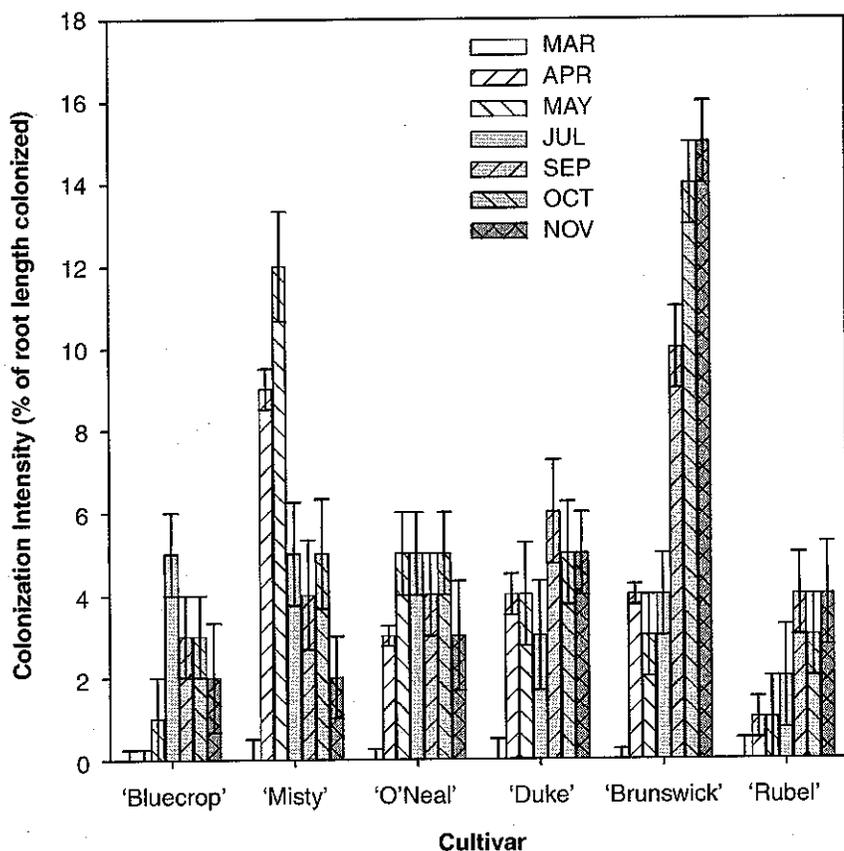
Survey of plants produced from cuttings. The colonization frequency of cuttings generally decreased between 3 and 5 months after sticking, but increased again at the end of the first growing cycle (8 months after sticking) (Figure 5). At the end of the first growing cycle, cuttings of 'Duke' and 'Reka' from different grades showed no differences in colonization frequency. Very few cuttings of 'Powderblue', a rabbiteye type cultivar, showed signs of EMF colonization. All plants of all cultivars showed some signs of colonization at the beginning of the second growing cycle (Figure 6). The number of plants colonized by EMF decreased

FIGURE 2. Percentage of tissue culture blueberry (*Vaccinium corymbosum* L. 'Bluecrop', 'Misty', 'O'Neal', 'Duke' and *V. angustifolium* 'Brunswick') plants colonized by EMF at the end of the first growing cycle (Fall), and beginning (Spring = prior to transplant) and end of the second growing cycle (BR = second growing cycle in bareroot bed; 1L = second growing cycle in 1 L container; 4L = second growing cycle in 4 L container) in a production nursery. Error bars represent 95% least significant differences (LSDs) within cultivars.



during the second growing cycle after transplanting into either bareroot beds or 4 L containers. After one growing cycle in bareroot beds, more 'Duke' plants from the highest grade of cuttings (#1 grade) showed signs of colonization than 'Duke' plants from lower grade (#2 grade) cuttings. After one growing cycle in 4 L containers, more 'Duke' and 'Reka' plants from the highest grade of cuttings showed signs of coloni-

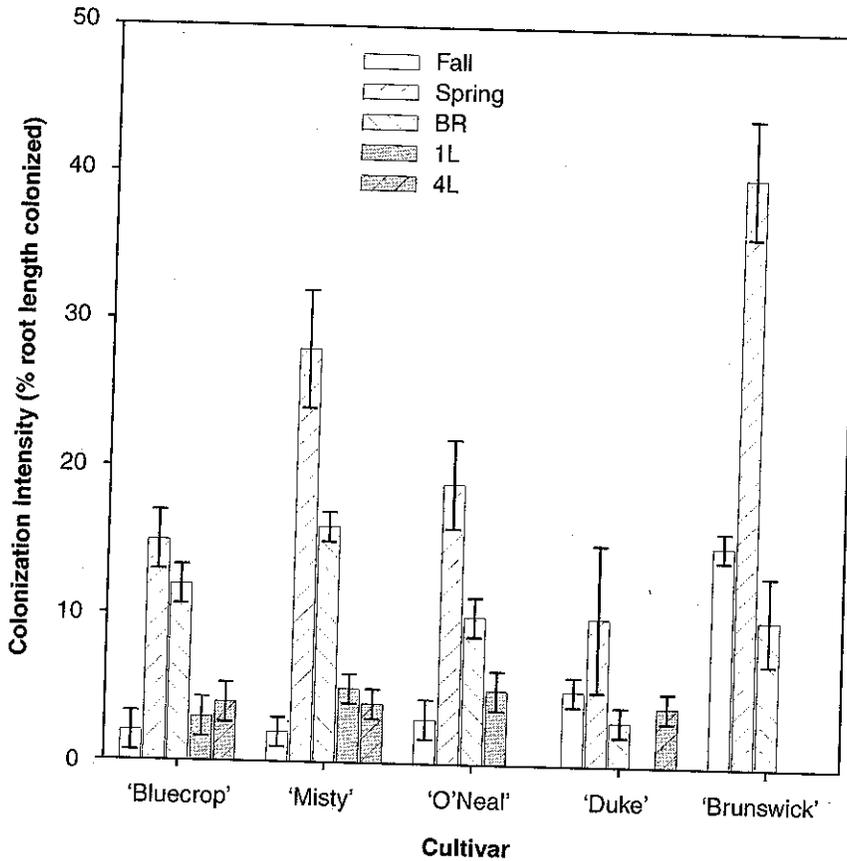
FIGURE 3. Change in the percentage of EMF-colonized root length on tissue culture blueberry (*Vaccinium corymbosum* L. 'Bluecrop', 'Misty', 'O'Neal', 'Duke', 'Rubel' and *V. angustifolium* 'Brunswick') plants during the first growing cycle in a production nursery. Error bars represent 95% least significant differences (LSDs) within cultivars.



zation than 'Duke' and 'Reka' plants from lower grade cuttings. Colonization frequency of 'Duke' plants from #1 cuttings was higher on plants produced in bareroot beds than plants from containers.

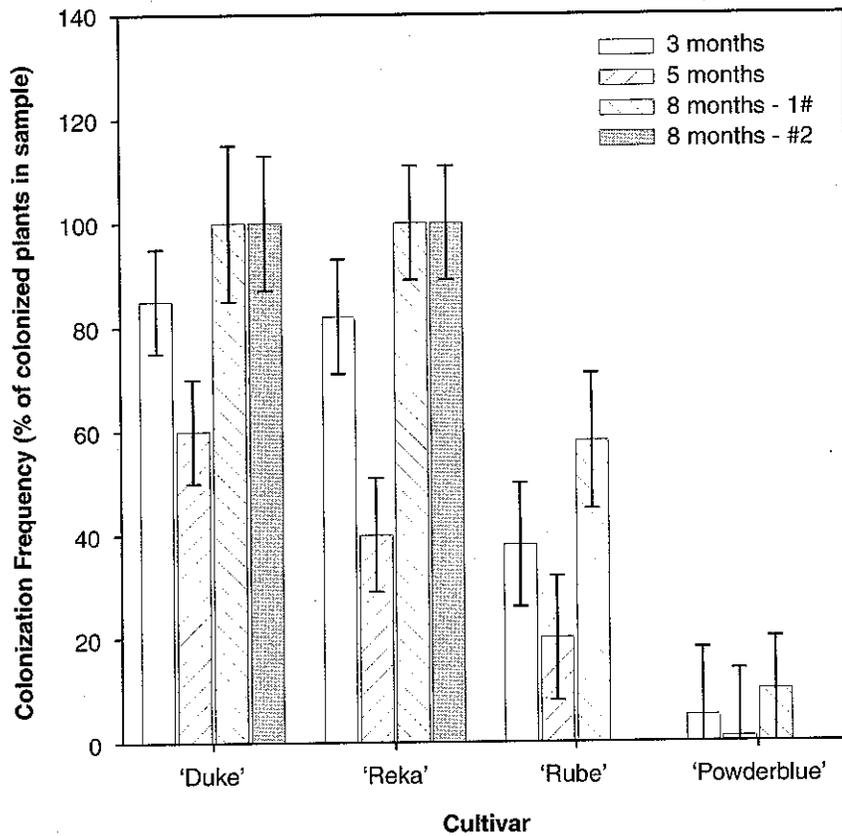
The colonization intensity was low for all cultivars during the first 5 months of the first growing cycle and generally increased by 8 months after sticking (Figure 7). At the end of the first growing cycle, higher graded cuttings (#1 grade) generally had more roots colonized by EMF

FIGURE 4. Percentage of EMF-colonized root length on tissue culture blueberry (*Vaccinium corymbosum* L. 'Bluecrop', 'Misty', 'O'Neal', 'Duke' and *V. angustifolium* 'Brunswick') plants at the end of the first growing cycle (Fall), and beginning (Spring = prior to transplant) and end of the second growing cycle (Fall) in a production nursery. (BR = second growing cycle in bareroot bed; 1L = second growing cycle in 1 L container; 4L = second growing cycle in 4L container) Error bars represent 95% least significant differences (LSDs) within cultivars.



than lower grade (#2 grade) cuttings. Eight months after sticking, colonization intensity of 'Powderblue' was lower than that of the Northern highbush cultivars. Colonization intensity generally increased over the winter, but decreased during the second growing cycle after transplanting into either bareroot beds or 4 L containers (Figure 8). Cuttings that graded higher at the end of the first growing cycle generally had higher

FIGURE 5. Change in the percentage of EMF-colonized blueberry (*Vaccinium corymbosum* L. 'Duke', 'Reka', 'Rube' and *V. ashei* 'Powderblue') plants produced from cuttings 3, 5, and 8 months after sticking (#1-#1 grade cuttings, #2-#2 grade cuttings). Error bars represent 95% least significant differences (LSDs) within cultivars.

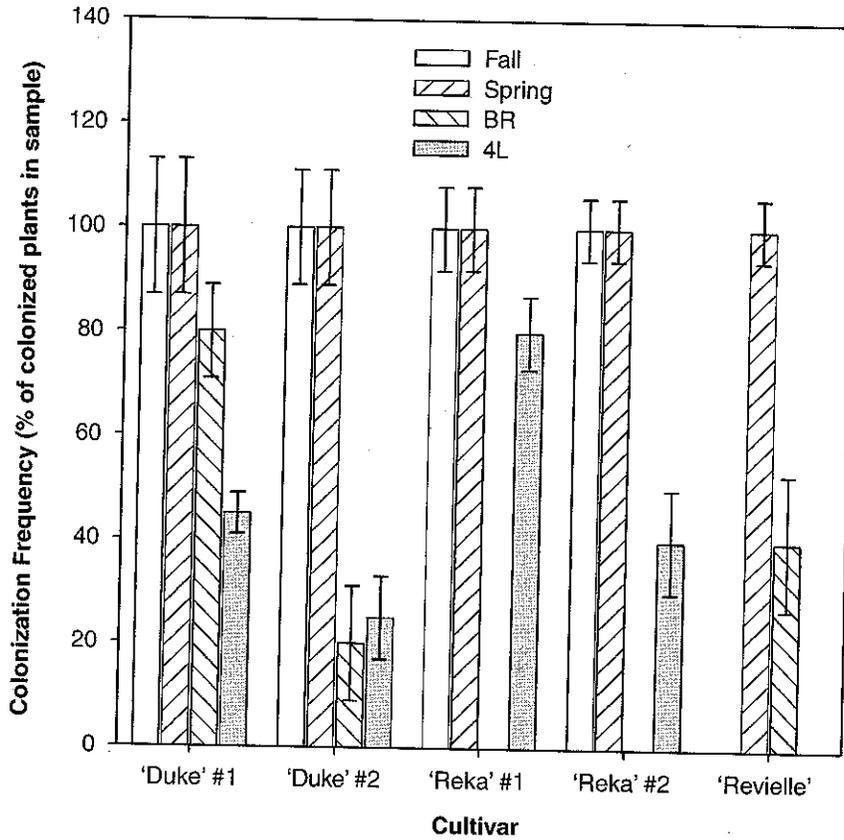


percentage of root length colonized than lower-grade cuttings at the end of the second growing cycle. Root colonization of 'Duke' was similar between plants growing in bareroot fields or containers.

DISCUSSION

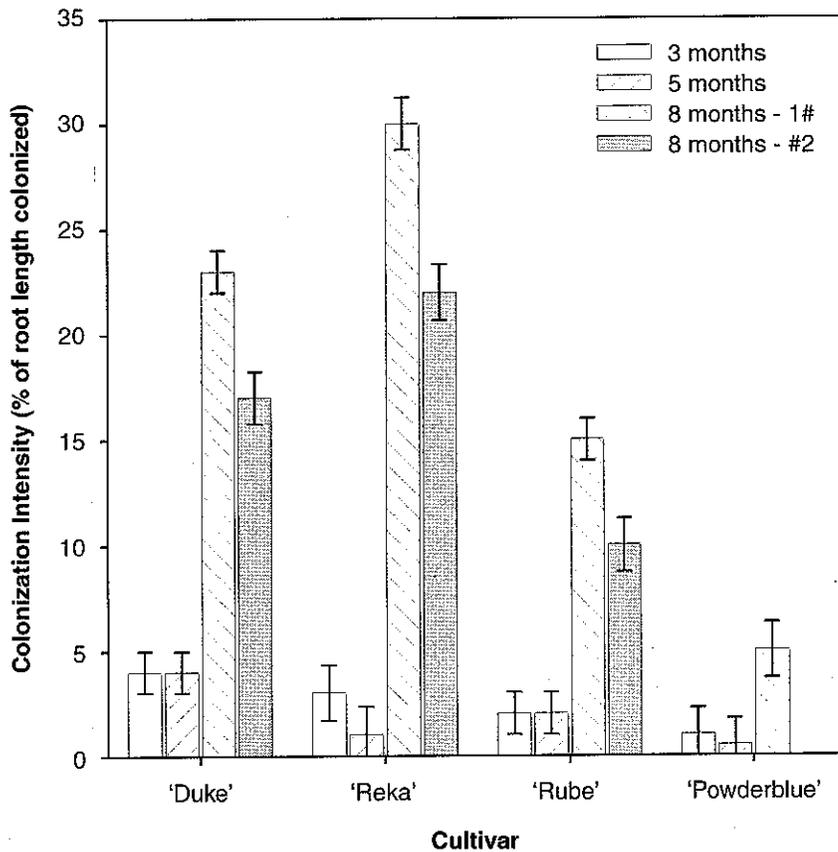
Under commercial nursery production conditions we found that the intensity of root colonization by EMF on blueberry plants produced

FIGURE 6. Percentage of EMF-colonized blueberry (*Vaccinium corymbosum* L. 'Duke', 'Reka', 'Revielle') plants produced from cuttings at the end of the first growing cycle (Fall), and beginning (Spring = prior to transplant) and end of the second growing cycle (BR = second growing cycle in bareroot bed; 4L = second growing cycle in 4 L container) in a production nursery. #1-#1 grade cuttings, #2-#2 grade cuttings. Error bars represent 95% least significant differences (LSDs) within cultivars.



from tissue culture or cuttings was either equal to or lower than what have been reported in older plants in production fields in Oregon (Scagel and Yang, 2003). This low intensity of colonization during the first growing season on small plants is not surprising given the surplus of available nutrients that are present in the growth medium during nursery production and soil pasteurization treatments used in produc-

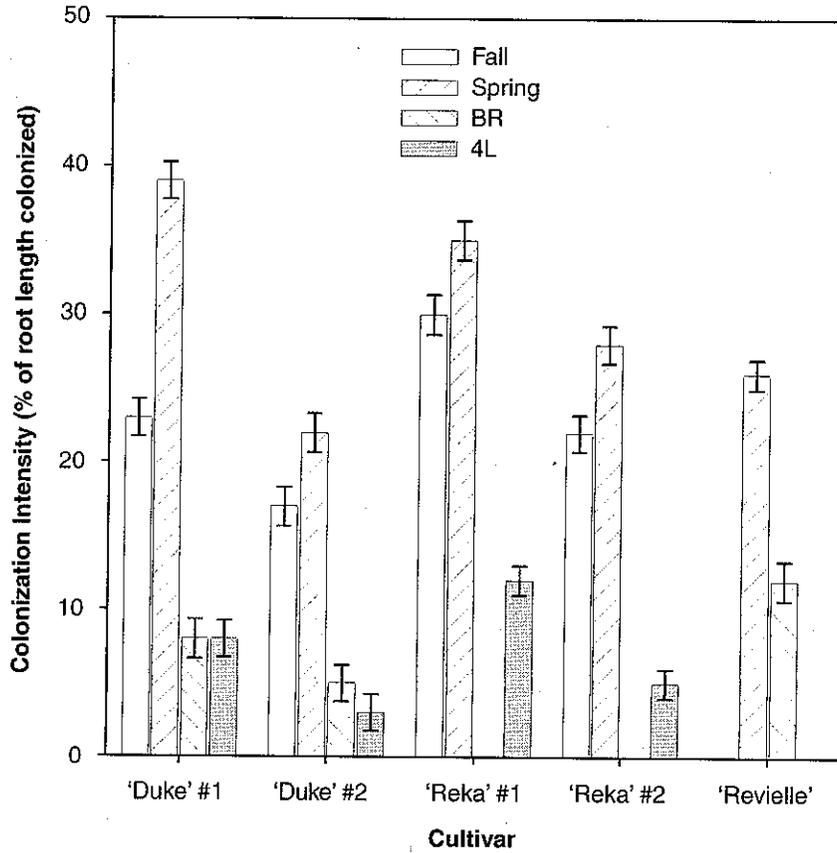
FIGURE 7. Change in the percentage of EMF-colonized root length on blueberry (*Vaccinium corymbosum* L. 'Duke', 'Reka', 'Rubel' and *V. ashei* 'Powderblue') plants produced from cuttings 3, 5, and 8 months after sticking (#1-#1 grade cuttings, #2-#2 grade cuttings). Error bars represent 95% least significant differences (LSDs) within cultivars.



tion of plants from tissue culture. Others have reported that the intensity of root colonization by EMF may decrease in soils or media due to high levels of nutrient availability (Goldack et al., 2001; Powell, 1982; Scagel and Yang, 2003), media sterilization (Powell and Bates, 1981), or other edaphic factors (Kasurinen and Holopainen, 2001).

After rooted tissue culture plants were hardened, transplanted into larger containers, and moved into an outdoor growing area, we found

FIGURE 8. Percentage of EMF-colonized root length on blueberry (*Vaccinium corymbosum* L. 'Duke', 'Reka', 'Revielle') plants produced from cuttings colonized at the end of the first growing cycle (Fall), and beginning (Spring = prior to transplant) and end of the second growing cycle (BR = second growing cycle in bareroot bed; 4L = second growing cycle in 4 L container) in a production nursery. #1-#1 grade cuttings, #2-#2 grade cuttings. Error bars represent 95% least significant differences (LSDs) within cultivars.



that colonization frequency and intensity decreased. This decrease may be due to changes in cultural conditions (e.g., fertilization rates) that inhibit colonization by the fungi that are present in the initial stages of propagation and possibly a change in the type of fungi on the root system. Certain fungi may do better under the cultural practices present in

the early stages of production but do not do well after transplanting and relocation to a different growing environment. This phenomenon has been documented for other types of mycorrhizal associations (Dhillion, 1992; Quoreshi and Timmer, 2000). Succession of EMF types on roots may be a result of a change in fertility or other soil or growth media factors. Also, there is a possibility that the fungi initially colonizing plants in the early stages of growth are replaced by fungi that are better able to tolerate the cultural conditions after transplanting. In the same commercial nursery, Scagel et al. (2004) reported a similar decrease in EMF colonization following inoculation of 'Misty', 'Bluecrop', and 'Rubel' plants from tissue culture after transplanting and relocation of plants into an outdoor growing environment.

When different blueberry cultivars were produced from tissue culture plants or cuttings, we found cultivar-specific differences in colonization frequency and intensity. Within a stock type and sampling date, the greatest differences in colonization were found when we compared the Northern highbush cultivars to the 'Rabbiteye' cultivar sampled in this study. These cultivar-specific differences in colonization could be a result of host-fungus specificity (e.g., certain blueberry cultivars may prefer specific fungi). The natural inocula present in the specific nursery in this study may be better adapted for Northern highbush cultivars and may not naturally cause high colonization of 'Rabbiteye' cultivars. In Oregon production fields, 'Powderblue' has also been reported to have low colonization by EMF (Scagel and Yang, 2003). The effects of high fertility levels on yield and EMF colonization in field production were also found to be cultivar-specific (Golldack et al., 2001). They found that the highest yield of 'Duke' was correlated with the lowest amount of inorganic fertilizer used during production, whereas, the highest yield of 'Reka' corresponded to the highest amount of fertilizer used. Increasing fertilization rates decreased EMF colonization of 'Duke' and had little influence on colonization of 'Reka'. This type of cultivar-specific response in sensitivity to EMF colonization by nutrient availability may be responsible for some of the differences in the frequency and intensity of colonization we detected in different cultivars.

After one growing season in the nursery, plants produced from tissue culture or cuttings are sold, transplanted into larger containers, or transplanted into bareroot beds in fields. We found that both the frequency and intensity of colonization by EMF decreased after plants produced from tissue culture or cuttings were grown for a second growing season in bareroot fields or containers. This decrease in colonization may be due to changes in cultural conditions that inhibit colonization of the

EMF that are present on the plants (e.g., fertilizer rates, fumigation of bareroot beds, bed age) (Johansson, 2000) and possibly a change in the type of fungi on the root system. Mycorrhizal infection during the first growing season occurred from inocula unintentionally introduced into the medium flowing placement of plants (e.g., wind blown spores, spores from other containers, residual inocula in media, etc.). The species of EMF colonizing plants during this stage of production may form mycorrhizal associations under the specific cultural conditions present during the first growing season but are inhibited by the changes in the plant growing environment during the second growing season.

Differences in cultural practices, soil type, and media between bareroot fields and containers may also account for the higher colonization frequency and intensity of 'Misty', 'Bluecrop', and 'O'Neal' plants from tissue culture when grown in bareroot fields compared to containers. If the environmental conditions in the bareroot fields or containers are not suitable for the particular EMF present on plants during the first growing cycle then colonization of plants in bareroot fields and containers will be dependent on new fungi that are present in the soil or media during the second growing cycle. It is possible that the soil in the bareroot fields may have a higher natural inoculum potential (e.g., more propagules of EMF capable of colonizing roots) than the media used in containers. If this is true, then a change in the type of fungi colonizing roots may account for the higher colonization frequency of 'Duke' plants from cuttings when grown in bareroot fields compared to containers. However, the low level of root colonization found in both plants from bareroot fields and containers also suggests that colonization may be limited due to environmental factors, and not just the presence or absence of the appropriate fungal inocula.

After one growing season in the nursery (spring), plants produced from cuttings generally had both a higher frequency and intensity of colonization by EMF than at the end of the first growing season (fall). This increase in colonization during the winter is possibly a result of seasonal changes in cultural practices or climate. In plants of 'Duke' and 'Reka' produced from cuttings, colonization frequency and intensity appears to be related to the grade of the cuttings prior to transplant in the spring. If grading differences are not a result of 'root damage' but primarily a selection based on the quality of the root ball, then either colonization plays a direct role in the quality of the root ball, or poor root development may decrease colonization. Since natural colonization in the propagation flats for cuttings did not appear to be uniform, it is possible that colonization may play an important role in quality dif-

ferences between cuttings. For example, Scagel et al. (2004) found that inoculation of cuttings from blueberry plants with EMF can decrease the time required for rooting and cause measurable changes in root biomass of rooted cuttings. If increased colonization by EMF leads to increased rooting and root biomass, this may result in an increased quality and performance of rooted cuttings after transplant. Scagel (2001) reported a similar decrease in the time required for rooting and increase of root biomass and transplant quality of cuttings of other Ericaceous species in response to inoculation of propagation media with EMF.

The changes in colonization frequency and the low levels of root colonization measured during nursery production of blueberry plants from tissue culture plants and cuttings may have an influence on nutrient uptake and quality of nursery stock. An assessment of the types of fungi present during different stages of production and the influence of different cultural practices on colonization and function of ericoid mycorrhizal fungi would enable nursery growers of blueberries to understand the role that these fungi may play in nursery production of blueberry plants.

GROWER BENEFITS

Blueberry plants can become naturally colonized by ericoid mycorrhizal fungi during nursery production. However, colonization is sporadic and can be quite low depending on the cultivar and production method. Nursery cultural conditions, low inoculum availability, and aspects of plant-fungus compatibility may be responsible for low colonization levels. This work needs to be extended to assess the survival and production performance of inoculated plants in nursery and field trials. Results from trials will enable nursery and field growers of blueberries to understand the role that these fungi may play in nursery stock quality.

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