

Cultural Variation and Mycorrhizal Status of Blueberry Plants in NW Oregon Commercial Production Fields

Carolyn F. Scagel
Wei Q. Yang

ABSTRACT. Ericoid mycorrhizal fungi (EMF) form symbiotic relationships with roots of blueberry plants providing increased access to nutrients from fertilizers and soil. In August of 2001, we sampled 55 fields in Oregon to assess the mycorrhizal status of blueberry plants under production conditions and to determine whether any relationships exist between field characteristics, root distribution, soil characteristics and level of colonization by mycorrhizal fungi. Variation in measured soil characteristics, root type, root distribution and mycorrhizal colonization occurred with cultivar, field age, bed type, rate of nitrogen fertilization, irrigation type, and mulch. Root biomass was lower in the upper 15 cm of soil compared to 15-30 cm depth. Distribution of roots between the two sampled depths varied significantly with field age, nitrogen fertilization rate, and the time of 50% harvest for the different cultivars sampled. Root length was generally greatest in the upper 15 cm of the soil than at the 15-30 cm depth. Root colonization by ericoid mycorrhizal fungi (EMF) ranged from 0.5 to 44% of total root length with higher colonization generally occurring in the upper 15 cm of the

Carolyn F. Scagel is Research Plant Physiologist, U.S. Department of Agriculture, Agricultural Research Service, Horticultural Crops Research Unit, 3420 NW Orchard Avenue, Corvallis, OR 97330 USA (E-mail: scagelc@ucs.orst.edu).

Wei Q. Yang is Assistant Professor, Oregon State University, North Willamette Research and Extension Center, Aurora, OR 97002 USA (E-mail: wei.yang@oregonstate.edu).

The authors wish to acknowledge the technical assistance of Kathy Eggemeyer, Lisa Tribbet, Ben Jackson, and Jesse Mitchell.

International Journal of Fruit Science, Vol. 5(2) 2005
Available online at <http://www.haworthpress.com/web/IJFS>
© 2005 by The Haworth Press, Inc. All rights reserved.
doi:10.1300/J492v05n02_10

soil where the majority of smaller, finer roots were found. Colonization generally increased with increasing plant age. In young plants the highest levels of colonization were found in roots from the upper 15 cm of soil while in older plants the highest levels of colonization were found in roots at the 15-30 cm depth. Colonization of roots by EMF in the upper 15 cm of the soil tended to decrease with increasing N fertilization rate, while root colonization at the 15-30 cm depth was unaffected by rate of N fertilization. Roots on cultivars that fruited early in the season tended to have higher levels of colonization than cultivars that fruited later in the growing season. Root biomass and root length were negatively correlated with soil pH and available Ca in soil, while root colonization by EMF was negatively correlated with ammonium levels in the soil. Differences in soil characteristics, root type and distribution, and mycorrhizal colonization found in this study need to be investigated in terms of production efficiency of blueberry in Oregon. [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, nitrogen, *Vaccinium corymbosum*, *Vaccinium ashei*

INTRODUCTION

Most members of the Ericaceae, including *Vaccinium* spp., are calcifuge plants that grow naturally in acid soils of low to moderate fertility. Roots of wild *Vaccinium* species are heavily colonized by ericoid mycorrhizal fungi (EMF), and the extensive hyphae of these fungi form a loose network in the soil so that the volume of soil explored by the plant is greatly increased (Read, 1996). Shoots of mycorrhizal cranberry (*Vaccinium macrocarpon*) contain more total nitrogen (N) and a greater concentration of N on a dry weight basis than those of non-mycorrhizal plants grown in a sterilized soil (Stribley and Read, 1974a). Mycorrhizal plants also absorb N from compounds unavailable to non-mycorrhizal plants (Stribley and Read, 1974a; Stribley and Read, 1974b) and may improve the general physiological condition of the host plant through enhanced uptake of other nutrients, such as phosphorus (P) (Stribley et al., 1975; Stribley and Read, 1976).

With blueberry (*Vaccinium corymbosum* L.), plant photosynthesis and growth is greater when plants are fed with ammonium than with nitrate

N (Claussen and Lenz, 1999). Ericoid mycorrhizal fungi can assimilate both ammonium and nitrate ions and transfer them to their plant symbiont (Bajwa and Read, 1986). Ericaceous plants generally have poor nitrate reducing and uptake abilities, therefore, in sandy cultural conditions, where significant nitrification occurs, plant access to nitrate may be largely dependent upon mycorrhizal colonization. Plants with EMF often have higher N and phosphorus (P) concentrations than non-mycorrhizal plants (Read and Stribley, 1973). These higher concentrations are a result of the fungus not only enhancing uptake of soluble inorganic N and P (Mitchell and Read, 1981; Stribley and Read, 1976) but also utilizing organic or insoluble N and P compounds in the soil (Kerley and Read, 1995; Read et al., 1989; Stribley and Read, 1980). When ^{15}N labeled ammonium is fed to mycorrhizal and non-mycorrhizal *Vaccinium* growing in sterile and fumigated soil, mycorrhizal plants have significantly greater yields and total nitrogen content than non-mycorrhizal plants; however mycorrhizal plants have lower ^{15}N enrichment (Stribley and Read, 1974a; Yang et al., 2002), indicating that the label is diluted by alternative N sources in mycorrhizal plants. In addition to an ability to readily use ammonium and nitrate, EMF can also use amino acids, peptides, proteins, and polymers such as chitin and lignin to transfer substantial quantities of N to the plant host (Bajwa and Read, 1985; Bajwa and Read 1985; Kerley and Read, 1995; Kerley and Read, 1997; Kerley and Read, 1998; Stribley and Read, 1980). Ericaceous plants utilize organic N in fresh litter and the complexed N in recalcitrant organic matter through the activity of proteases and amino acid uptake by EMF (Michelsen et al., 1996). The ability of EMF to exploit organic sources of N is an important factor to consider when assessing optimal cultural and fertilization practices for blueberry production.

There is little information available about the mycorrhizal status of blueberry under cultivated conditions in the Pacific Northwest (PNW) Region of the United States. Under field conditions in Southwestern Oregon, mycorrhizal infection of cultivated cranberry is low until bogs reach 10 years of age (Scagel, 2002). Under field conditions in the Northeastern U.S., mycorrhizal infection of cultivated blueberries is low (Boyer, 1982; Goulart et al., 1995; Yang et al., 1998; Powel and Bates, 1981), and inoculation of tissue cultured highbush blueberry can increase plant growth and root dry weight (Yang et al., 2002). Others have found that the colonization of blueberry varies significantly with the 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 soil (Yang et al., 2002). Increased applica-

tion of fertilizer can depress mycorrhizal infection levels in blueberry seedlings (Powell, 1982). Blueberries grown in soils with high organic matter and low pH usually have higher mycorrhizal colonization and better growth (Blasing, 1989; Czesnik and Eynard, 1990; Enyard and Czesnik, 1989; Haynes and Swift, 1985; Yang et al., 1998). The object of this study was to assess the mycorrhizal status of blueberry plants in commercial farms in the Willamette Valley of Oregon and to determine whether relationships exist between cultural practices, root distribution, soil characteristics and level of colonization by mycorrhizal fungi. The results obtained are an important preliminary step in determining the occurrence and potential importance of mycorrhizal fungi in the production of blueberries in the PNW.

MATERIALS AND METHODS

Root distribution and mycorrhizal colonization. Samples containing soil and roots of blueberry plants were collected from 55 different fields in northwestern Oregon during August and September 2001. Soil cores (2.5 cm diameter \times 38.1 cm length = 188 cm³) were taken from 5 representative sample locations per field for determination of root distribution and colonization by EMF. Soil cores were separated by depth (0-15 cm and 15-30 cm), and roots were removed by washing. A weighed subsample of roots was used for subsequent microscopic evaluation of colonization by EMF and estimation of root length. The remaining roots from each core were weighed, oven-dried at 65°C for 48 h, and weighed again to determine fresh and dry biomass of roots. Specific root length was calculated by dividing root length by root dry weight. Root colonization by EMF was assessed on 1 cm sections after clearing and staining by modified procedures of Phillips and Hayman (1970), replacing lacto-phenol with lacto-glycerin. Percentage of root length with signs of colonization by EMF was estimated by the method of Biermann and Linderman (1980). Root length was calculated using the method outlined by Newman (1966).

Soil characteristics. Soil cores (2.5 cm diameter \times 38.1 cm length = 188 cm³) were taken from 5 representative sample locations per field at the same time as cores for root colonization for analysis of pH, conductivity, available ammonium, nitrate, and calcium and stored in enclosed containers at 33°F (1°C) until analyses. Analyses were done for each soil core on 5 g (wet weight) samples of soil in a 3:1 water:soil (v:v) sus-

pension using selective ion probes and values were calculated based on standard curves from standards of known concentration.

Field information. Field information including plant age, cultivar, mulch, bed type, irrigation type, cover crop, amount of annual nitrogen (N) fertilizer addition, type of pesticides applied, and original source of plant material was collected from growers.

Data analyses. Regression analyses were used to determine the relationships between annual rate of nitrogen fertilization and field age and time of 50% harvest (average date of 50% harvest of each cultivar at the Oregon State University North Willamette Research and Extension Center, Aurora, OR). Data were compared between different groups based on range of field age, range of N fertilization, cultivar, time of 50% harvest, core depth, and cultural practices using Analysis of Variance (ANOVA) and means were separated at $p < 0.05$ using Tukey's Honestly Significant Difference for unequal sample size (THSD). Field age, N fertilization rate, and time of 50% harvest were used as covariates in analyses where applicable. Ranges of field age and N fertilization were determined based on equalizing the number of observations in each selected range. Root weight and length data were arcsin transformed and specific root length and 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 is presented in figures and tables. Regression analysis was used to determine the relationships between annual nitrogen fertilization input and field age and time of fruiting. Correlations between specific variables were analysed using Peasons Product Moment Correlation Coefficient (r). All analyses were performed using the Statistica® statistical package (Statsoft, Inc., Tulsa, OK, USA, 1996).

RESULTS

Field variation. There was a large variation in cultural practices in this survey, including plant age, cultivar, mulch, bed type, irrigation type, cover crop, amount of annual nitrogen (N) fertilizer addition, type of pesticides applied, and original source of plant material (Table 1). Plantings ranged from 1 to 50 years of age, encompassed over 11 different cultivars, and were predominantly flat beds with overhead irrigation and a grass cover crop. Samples came from fields containing early- (35%), mid- (30%), and late-season (26%) fruiting cultivars. Mulch of some type was used in approximately 58% of the fields. Nitrogen fertil-

TABLE 1. Summary description of blueberry fields sampled.

Attribute	Description	Percentage of Total Fields Sampled in Different Age Ranges (years)					Percentage of Total Fields Sampled
		1-4	5-8	9-12	13-19	>19	
Cultivar	Duke	7	6	8	2	0	23
	Bluecrop	0	4	7	2	3	16
	Rubel	10	4	0	0	0	14
	Brigitta Blue	4	4	0	2	0	10
	Earliblue	0	0	6	0	2	8
	Mixed/Unknown	0	2	2	2	2	8
	Powderblue	4	2	0	0	0	6
	Elliott	0	3	2	0	0	5
	Bluejay	0	2	2	0	0	4
	Darrow	0	2	0	0	0	2
	Berkeley	0	0	0	0	2	2
	Bluetta	2	0	0	0	0	2
Bed Type	Raised	14	7	3	0	0	24
	Flat	13	22	24	8	9	76
Mulch Type	None	12	7	14	4	5	42
	Full Layer	7	18	9	4	0	38
	Partial Layer	4	0	4	0	4	12
	Mixed/Incorporated	4	0	0	0	0	4
	Plastic	0	4	0	0	0	4
Irrigation	Overhead	25	29	25	8	9	96
	Drip	2	0	2	0	0	4
Cover Crop	Grass	25	29	27	6	2	89
	None	2	0	0	2	7	11
N Fertilizer Rate	40-100 lbs a ⁻¹ yr ⁻¹	10	2	0	0	0	12
	115-150 lbs a ⁻¹ yr ⁻¹	11	12	4	6	0	33
	170-190 lbs a ⁻¹ yr ⁻¹	2	2	5	0	3	12
	200-250 lbs a ⁻¹ yr ⁻¹	2	13	14	0	2	31
	300-450 lbs a ⁻¹ yr ⁻¹	2	0	4	2	4	12
Plant Age		27	29	27	8	9	

izer additions to fields varied from 40 to 450 lbs a⁻¹ yr⁻¹ with the most frequent application rates at 120 (14%), and 200 (20%) lbs a⁻¹ yr⁻¹. Approximately 78 percent of the fields sampled reported no use of pesticides and the remaining 22 percent reported using combinations of fumigation, Aliette, and Ridomil. Plants from almost 90 percent of the fields sampled came from one of two commercial sources.

N fertilizer rate, field age and time of 50% harvest. The average N fertilization rate across all fields sampled was 172 lbs a⁻¹ yr⁻¹. There were significant linear relationships between N fertilization rate and field age and time of 50% harvest for the different cultivars (Figure 1). Nitrogen fertilization rate increased with increasing field age and was lower on cultivars that fruited later in the season. On average, N fertilization rate increased by 5.3 lbs a⁻¹ y⁻¹ for every year of field age. The earliest fruiting cultivars were fertilized with approximately 18.7 lbs a⁻¹ y⁻¹ more than cultivars that fruited approximately one week later.

Root biomass. Root biomass was generally higher at 15-30 cm depth than at 0-15 cm. Distribution of root biomass between the two sampled depths varied significantly with field age, nitrogen fertilization rate, and the time of 50% harvest on the different cultivars (Table 2, Figure 2A, Figure 3A). Root biomass generally increased with plant age and increases in root biomass primarily occurred in roots at 15-30 cm (Table 2). Root biomass at the 15-30 cm depth increased with increasing N fertilization rate, however, plants in fields receiving the highest rate of N fertilizer had lower root biomass in the 0-15 cm depth than plants receiving lower rates of N fertilizer (Figure 2A). Cultivars that fruited earlier in the season tended to have more root biomass than cultivars that fruited later in the growing season (Figure 3A).

Root length. Root length was generally greatest in the upper 15 cm of the soil. Variation in root length occurred with field age, nitrogen fertilization rate, and the time of 50% harvest of the different cultivars (Table 2, Figure 2B, Figure 3B). Root length was generally highest in the upper 15 cm of the soil in plants less than 12 years old, while older plants had greater root length at the 15-30 cm depth (Table 2). Plants receiving greater than 250 lbs N a⁻¹ yr⁻¹ had reduced root length in the upper 15 cm of soil (Figure 2B). Cultivars that fruited from June through July (157-212 Julian days) had similar distribution of root length at the two soil depths, while cultivars that had just finished fruiting prior to sampling had more root length at the 15-30 cm depth than in the upper 15 cm of the soil (Figure 3B). Cultivars that were still fruiting at the time of sampling tended to have the highest root length in the upper 15 cm of the soil (Figure 3B).

FIGURE 1. Relationship between (A) field age, and (B) time of fruiting to annual rate of nitrogen fertilizer application of blueberry. Bars on data represent standard errors.

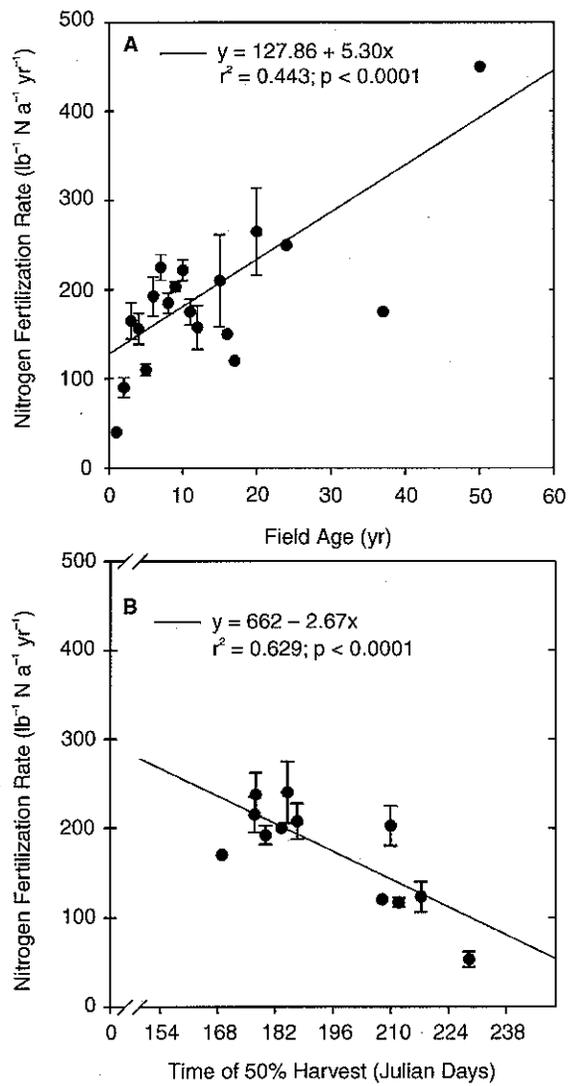
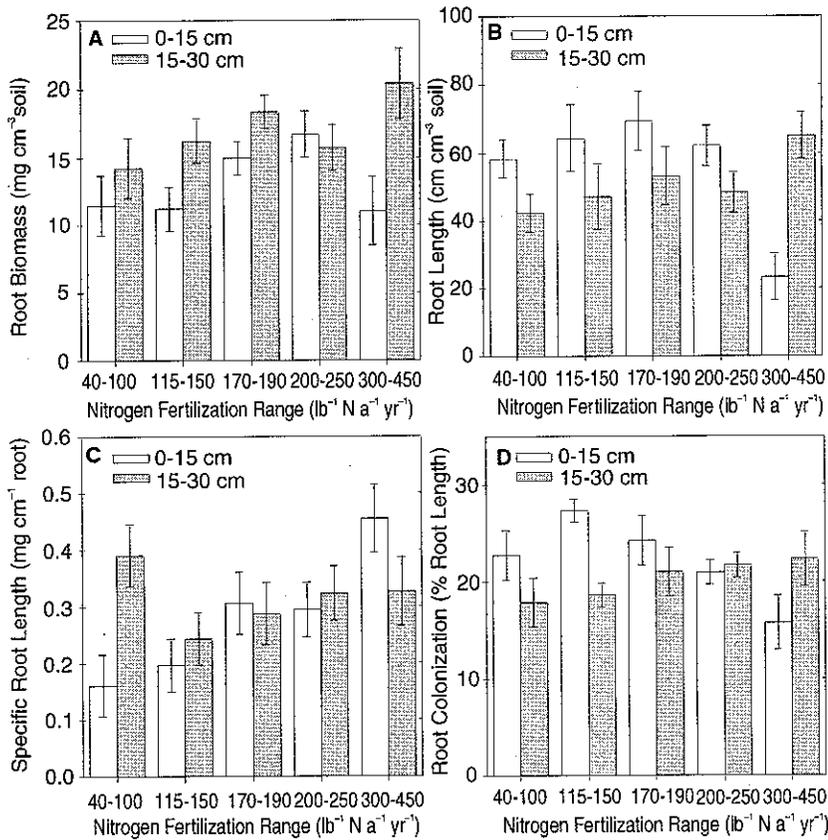


TABLE 2. Distribution of root weight, root length, specific root length, and root colonization by ericoid mycorrhizal fungi in blueberry fields grouped by cultivar at different ages.

Cultivar	Age Range (yrs)	Root Biomass (mg cm ⁻³)		Root Length (cm cm ⁻³)		Specific Root Length (mg cm ⁻¹)		EMF Colonization (% root length)	
		0-15 cm	15-30 cm	0-15 cm	15-30 cm	0-15 cm	15-30 cm	0-15 cm	15-30 cm
Duke	1-4	5.3 ^z a	11.5 b	29.7 ab	44.2 bc	0.173 a	0.237 b	20.1 a	22.4 ab
	5-8	18.3 cd	14.2 bc	85.4 d	64.1 cd	0.231 b	0.233 b	25.8 b	19.9 a
	9-12	15.4 bc	14.9 bc	61.5 c	53.5 c	0.264 b	0.343 c	18.2 a	18.5 a
	13-19	3.2 a	22.6 d	11.5 a	88.8 d	0.277 b	0.254 b	32.5 c	34.8 c
Bluecrop	5-8	22.8 c	30.6 d	68.3 c	88.6 c	0.405 bc	0.432 c	36.1 d	22.6 c
	9-12	16.2 b	14.6 b	70.3 c	46.8 b	0.247 a	0.275 a	22.5 c	26.8 c
	13-19	18.8 bc	24.9 c	40.1 b	68.2 b	0.469 c	0.365 b	25.2 c	20.4 bc
	>19	9.3 a	17.5 b	23.5 a	69.2 c	0.376 b	0.267 a	16.4 b	3.3 a
Brigitta Blue	1-4	3.6 a	10.5 b	36.7 b	38.0 b	0.093 a	0.265 b	24.8 b	30.2 c
	5-8	10.9 b	12.9 b	55.1 d	44.0 c	0.191 a	0.298 b	20.9 a	19.3 a
	13-19	3.2 a	26.1 c	12.9 a	57.5 d	0.255 b	0.453 c	29.9 c	24.5 b

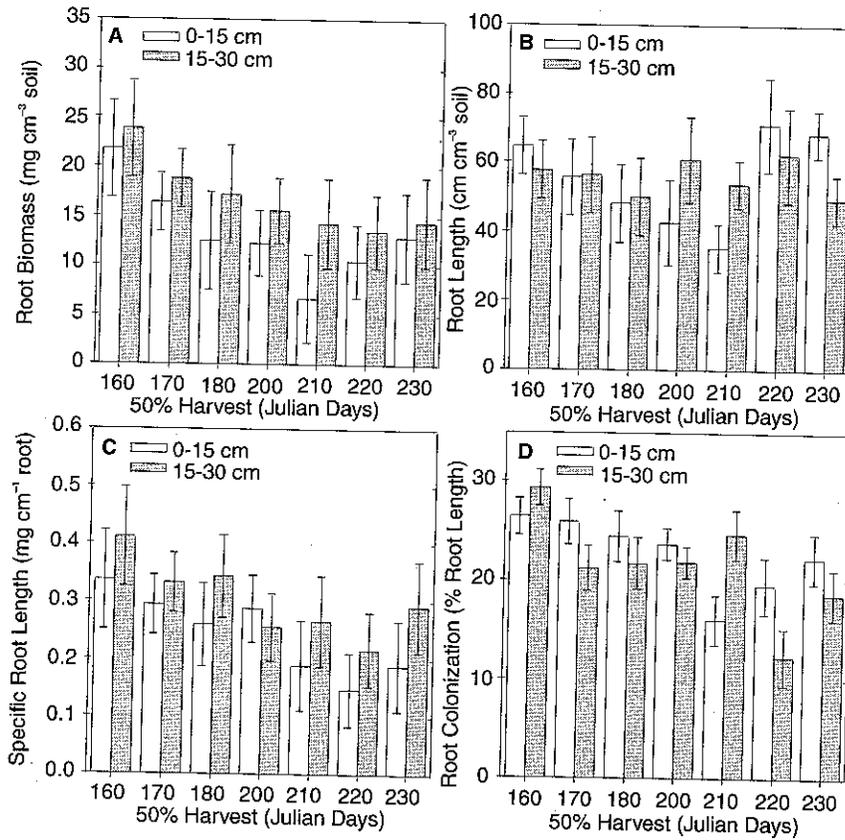
^zMeans adjusted by covariate of annual nitrogen fertilization rate (Duke 181 lbs N a⁻¹ yr⁻¹; Bluecrop 195 lbs N a⁻¹ yr⁻¹; Brigitta Blue 208 lbs N a⁻¹ yr⁻¹). Means followed by the same letter within a variable for each cultivar are not significantly different (p < 0.05, Tukey's Unequal N Honestly Significant Difference).

FIGURE 2. (A) Root biomass, (B) root length, (C) specific root length, and (D) root colonization by ericoid mycorrhizal fungi of blueberry from fields receiving different rates of nitrogen (N) fertilizer. Means adjusted by covariates of annual field age (8.8 years) and time of 50% harvest (194 Julian Days). Bars on columns represent standard errors of the mean of different numbers of replicates for each range of N fertilizer rates.



Specific root length. Lower root biomass and higher root length in the upper 15 cm of the soil resulted in plants having a lower specific root length (smaller, finer roots) in the upper 15 cm of the soil. Variation in specific root length occurred with field age, nitrogen fertilization rate, and the time of 50% harvest of the different cultivars (Table 2, Figure 2C, Figure 3C). Specific root length in the upper 15 cm of the soil in-

FIGURE 3. (A) Root biomass, (B) root length, (C) specific root length, and (D) root colonization by ericoid mycorrhizal fungi of blueberry from fields containing cultivars with different times of fruit maturation. Means adjusted by covariates of annual nitrogen fertilization rate ($177 \text{ lbs N a}^{-1} \text{ yr}^{-1}$) and field age (9.4 years). Bars on columns represent standard errors of the mean of different numbers of replicates for each time of fruiting. Time of 50% harvest (average date of 50% harvest at OSU North Willamette Research and Extension Center, Aurora, OR).



creased with increasing plant age (e.g., increase in coarse roots) while the types of roots at the 15-30 cm depth changed little with plant age in fields less than 19 years old (Table 2). Plants receiving the lowest levels of N fertilizer generally had finer roots in the upper 15 cm of the soil than plants receiving higher levels of N fertilizer, and rate of N fertiliza-

tion generally had little effect of specific root length in the 15-30 cm depth (Figure 2C). There was a strong tendency for cultivars that fruited later in the season to have more fine roots than cultivars that fruited early in the growing season at both depths (Figure 3C).

Root colonization. Root colonization by ericoid mycorrhizal fungi (EMF) ranged from 0.5 to 44% of total root length. Average colonization across all fields was approximately 22% with higher colonization generally occurring in the upper 15 cm of the soil. Variation in EMF colonization occurred with field age, nitrogen fertilization rate, and the time of 50% harvest of the different cultivars (Table 2, Figure 2D, Figure 3D). Distribution of root colonization was similar between the two soil depths on plants less than 13 years old while older plants had significantly higher levels of colonization in roots from the upper 15 cm of the soil (Table 2). Colonization of roots by EMF in the upper 15 cm of the soil tended to decrease with increasing N fertilization rate above 200 lbs N a⁻¹ yr⁻¹ while root colonization at the 15-30 cm depth changed little with rate of N fertilization (Figure 2D). Roots on cultivars that fruited early in the season generally had higher levels of EMF colonization than cultivars that fruited later in the growing season (Figure 3D).

Soil characteristics. Soil pH was positively correlated with increased levels of available calcium ($r = 0.4870$) and nitrate ($r = 0.3590$) in the soil and negatively correlated with levels of available ammonium ($r = -0.4072$) and soil conductivity ($r = -0.3396$). Variation in soil variables occurred with cultivar, field age, bed type, irrigation type and mulch (Table 3). Field age had little detectable effect on soil pH, while soil conductivity and available ammonium tended to decrease with increasing field age and levels of available calcium and nitrate tended to increase with increasing field age (Table 3). Fields receiving higher levels of N fertilization tended to have lower pH, and lower levels of available calcium while the highest levels of available ammonium were detected in soils receiving the lowest rates of N fertilizer (Table 4). Soils from fields with cultivars that fruited early and late in the season tended to have higher levels of available ammonium and lower nitrate than soil from fields with cultivars that fruited mid-season (Table 5). Root biomass and root length were negatively correlated with soil pH (root biomass $r = -0.283$; root length $r = -0.325$) and available Ca in soil (root biomass $r = -0.246$; root length, $r = -0.389$). Root colonization by EMF was negatively correlated with levels of available ammonium in the soil ($r = -0.426$).

Variation with cultivar. There was significant variation in the total and distribution of root biomass, root length, specific root length, and

TABLE 3. Characteristics of soil from blueberry fields grouped by differences in cultural practices between fields.

Practice	Age Range (yrs)	pH ^z	Soil Conductivity ($\mu\text{S cm}^{-1}$)	Available Soil Ammonium (ppm)	Available Soil Calcium (ppm)	Available Soil Nitrate (ppm)
Bed Type						
Raised	1-4	5.59	208.9	723.0	3.66	2.50
Flat	1-4	5.10	267.4	751.2	2.71	2.63
Raised	5-8	5.59	267.2	710.5	3.32	2.67
Flat	5-8	5.41	279.3	783.1	3.18	2.61
Raised	9-12	5.42	156.6	659.4	3.31	2.77
Flat	9-12	5.35	175.7	643.9	3.43	2.70
Flat	13-19	4.79	265.9	834.1	3.13	2.32
Flat	>19	5.51	170.9	610.9	3.59	2.83
Mulch						
Full	1-4	5.06	351.6	874.0	2.63	2.27
None	1-4	5.36	278.2	709.0	2.83	2.27
Partial	1-4	4.98	486.9	843.0	2.08	2.34
Full	5-8	5.28	399.2	837.0	2.76	2.34
None	5-8	5.07	424.1	859.0	2.64	2.27
Full	9-12	5.07	327.8	679.0	3.20	2.46
None	9-12	5.04	325.0	765.0	2.73	2.36
Partial	9-12	5.48	290.4	695.0	2.80	2.38
Full	13-19	4.43	443.7	928.0	2.36	2.10
None	13-19	4.58	396.5	913.0	2.69	1.96
None	>19	4.71	412.5	866.0	2.38	2.08
Partial	>19	5.77	256.8	530.0	3.70	2.95

TABLE 3 (continued)

Practice	Age Range (yrs)	pH ^z	Soil Conductivity ($\mu\text{S cm}^{-1}$)	Available Soil Ammonium (ppm)	Available Soil Calcium (ppm)	Available Soil Nitrate (ppm)
Irrigation						
Overhead	1-4	5.17	273.1	749.9	3.13	2.51
Drip	1-4	4.05	293.4	744.1	2.86	2.81
Overhead	9-12	5.35	194.8	644.0	3.37	2.67
Drip	9-12	3.84	285.2	792.9	3.61	2.57
Cover						
Grass	1-4	5.22	276.3	690.8	2.70	2.56
None	1-4	5.75	238.7	888.8	3.67	2.37
Grass	>19	5.15	218.5	659.0	2.29	2.74
None	>19	5.54	198.0	552.7	3.64	2.80
Total						
	1-4	5.25	192.3	765.3	3.35	2.58
	5-8	5.31	231.2	804.8	3.29	2.69
	9-12	5.23	195.4	790.5	3.48	2.75
	13-19	4.75	150.2	675.4	3.41	2.82
	>19	5.20	149.7	624.2	3.52	2.89

^zMeans adjusted by covariate of annual nitrogen fertilization rate in $\text{lbs N a}^{-1} \text{yr}^{-1}$ (Bed Type 153; Mulch 175; Irrigation 138; Cover 171; Total 167) and time of 50% harvest in Julian days (Bed Type 154; Mulch 194; Irrigation 204; Cover 193; Total 194). Time of 50% harvest – average date of 50% harvest at OSU North Willamette Research and Extension Center, Aurora, OH. Means followed by the same letter within a variable for each cultural practice are not significantly different ($p < 0.05$, Tukey's Unequal N Honestly Significant Difference).

TABLE 4. Characteristics of soil from blueberry fields grouped by differences in nitrogen fertilization rates between fields.

N Fertilization Range (lb ⁻¹ N a ⁻¹ yr ⁻¹)	pH ^z	Soil Conductivity (μ S cm ⁻¹)	Available Soil Ammonium (ppm)	Available Soil Calcium (ppm)	Available Soil Nitrate (ppm)
40-100	5.46 c	229.1 c	768.9 c	3.46 c	3.02 c
115-150	5.40 c	172.4 b	805.9 c	3.44 bc	2.84 b
170-190	5.17 b	167.7 b	717.7 b	3.41 bc	2.77 ab
200-250	5.04 ab	173.2 b	689.4 b	3.32 ab	2.73 ab
300-450	4.92 a	130.6 a	607.4 a	3.22 a	2.64 a

^zMeans adjusted by covariates of field age (8.8 years) and time of 50% harvest (194 Julian Days). Time of 50% harvest—average date of 50% harvest at OSU North Willamette Research and Extension Center, Aurora, OR. Means followed by the same letter within a variable are not significantly different ($p < 0.05$, Tukey's Unequal N Honestly Significant Difference).

TABLE 5. Characteristics of soil from blueberry fields grouped by differences in time of fruit maturation between fields.

50% Harvest (Julian Days) ^z	pH ^y	Soil Conductivity (μ S cm ⁻¹)	Available Soil Ammonium (ppm)	Available Soil Calcium (ppm)	Available Soil Nitrate (ppm)
160	5.31 bc	271.2 d	783.4 de	3.28 ab	2.73 b
170	5.17 ab	225.4 c	762.9 d	3.19 a	2.64 a
180	5.57 d	126.8 a	598.5 a	3.61 cd	2.92 cd
200	5.32 bc	157.8 b	640.8 b	3.53 c	2.94 d
210	5.23 ab	159.7 b	721.6 c	3.19 a	2.85 c
220	5.07 a	210.2 c	757.3 cd	3.36 b	2.70 ab
230	5.42 cd	160.4 b	810.3 e	3.70 d	2.71 ab

^zTime of 50% harvest—average date of 50% harvest at OSU North Willamette Research and Extension Center, Aurora, OR.

^yMeans adjusted by covariates of annual nitrogen fertilization rate (177 lbs N a⁻¹ yr⁻¹) and field age (9.4 years). Means followed by the same letter within a variable are not significantly different ($p < 0.05$, Tukey's Unequal N Honestly Significant Difference).

EMF colonization among cultivars (Table 6) and within cultivars at different age ranges (Table 2). Of the cultivars sampled most frequently (Rubel, Duke, Powderblue, Briggitta, and Bluecrop), Rubel generally showed the lowest levels of colonization. Increased nitrogen fertilization rate generally decreased root length in the upper 30 cm for most

TABLE 6. Distribution of root dry weight, root length, specific root length, and root colonization by ericoid mycorrhizal fungi in blueberry fields grouped by cultivar differences between fields (means adjusted by covariates of field age and annual nitrogen fertilization rate).

Cultivar	Root Biomass (mg cm ⁻³)			Root Length (cm cm ⁻³)			Specific Root Length (mg cm ⁻¹)			EMF Colonization (% root length)		
	0-15 cm	15-30 cm	0-15 cm	15-30 cm	0-15 cm	15-30 cm	0-15 cm	15-30 cm	0-15 cm	15-30 cm	0-15 cm	15-30 cm
Rubel	14.1 ^z abc	16.5 bc	82.9 f	63.4 de	0.195 ab	0.272 bc	18.6 b	11.8 a				
Duke	12.3 abc	14.1 abc	56.7 de	57.4 de	0.219 ab	0.265 b	21.5 cd	20.8 bc				
Powderblue	7.0 ab	9.4 ab	20.8 b	5.2 a	0.251 b	0.758 e	22.7 d	19.5 bc				
Bluecrop	15.3 bc	18.8 c	57.8 de	65.1 e	0.288 c	0.271 bc	26.1 ef	21.5 cd				
Bluejay	15.0 bc	12.4 abc	40.7 c	53.3 d	0.348 cd	0.219 ab	18.9 bc	29.4 g				
Brigitta Blue	6.2 a	14.3 abc	41.1 c	46.2 c	0.148 a	0.299 c	23.3 d	23.8 de				
Earlblue	19.7 c	24.6 c	64.3 de	66.7 e	0.402 d	0.299 c	27.1 f	24.2 e				
Elliott	16.4 bc	22.0 c	67.8 e	85.5 f	0.262 b	0.276 bc	22.3 d	18.3 b				

^zMeans adjusted by covariates of field age (8 years), and annual nitrogen fertilization rate (173 lbs N a⁻¹ yr⁻¹). Means followed by the same letter within a variable are not significantly different ($p < 0.05$, Tukey's Unequal N Honestly Significant Difference).

cultivars except Bluecrop, Earlyblue, and Rubel which had more root length in the upper 15 cm of the soil and distribution did not depend on N-fertilization rate or age of planting (Table 7).

Variation with cultural conditions. Root biomass, size, distribution and colonization by EMF varied with cultural history of the field and age of planting (Table 8). Plants on flat beds contained more fine roots (lower specific root weight) than in raised beds. Young plants under drip irrigation had more root length in the upper 15 cm of soil than plants under overhead irrigation. Plants growing under a layer of mulch had an equal distribution of root types throughout the upper 30 cm of soil, while plants growing with no mulch had less fine roots in the upper 15 cm of soil. EMF colonization was generally higher in raised beds compared to flat beds and higher under drip compared to overhead irrigation. Plants growing with no mulch had higher colonization in the upper 15 cm of the soil than plants growing under mulch while plants under mulch had higher levels of colonization at 15-30 cm soil depth than plants growing without mulch. Soil variables showed some trends related to cultural practices and field age (Table 3). Soil pH and Ca^{+2} levels were generally higher in raised beds than in flat beds. Soil pH and Ca^{+2} levels were generally lower in soils under drip irrigation than in soils under overhead irrigation. Levels of available soil NH_4^+ were higher in soils with a layer of organic mulch or a plastic mulch than with no mulch.

DISCUSSION

Our survey found that most highbush blueberry fields in Oregon are irrigated by overhead sprinkler irrigation. Drip irrigation is used in a small portion of fields and no microsprinkler irrigation systems are used. The merit of using drip systems versus overhead irrigation is debated among growers, and some growers have replaced drip with overhead systems. For those using drip systems, two drip lines are often used to keep up with the water demand by plants. Over-irrigation is a potential problem for many growers since almost all the fields are irrigated empirically. Studies with highbush blueberries in Eastern North America found that drip irrigation used 54% less water and 74% less energy per growing season as compared to overhead irrigation (Funt et al., 1980). Thus the water and energy savings of using drip irrigation will be evaluated in highbush blueberry production in Oregon.

TABLE 7. Distribution of root weight, root length, specific root length, and root colonization by ericoid mycorrhizal fungi in blueberry fields grouped by cultivar and different annual N fertilization rates (lbs N a⁻¹ yr⁻¹).

Cultivar	N Rate	Root Biomass (mg cm ⁻³)		Root Length (cm cm ⁻³)		Specific Root Length (mg cm ⁻¹)		EMF Colonization (% root length)	
		0-15 cm	15-30 cm	0-15 cm	15-30 cm	0-15 cm	15-30 cm	0-15 cm	15-30 cm
Duke									
	40-100	0.562 a	0.258 a	38.4 b	23.6 a	0.195 ab	0.228 bc	14.6 a	21.6 b
	115-150	0.451 a	1.259 bc	39.1 b	72.2 c	0.164 a	0.243 bc	24.6 b	24.8 b
	170-190	1.177 b	1.929 d	80.4 d	95.4 d	0.214 ab	0.268 cd	25.4 b	23.1 a
	200-250	1.338 c	0.944 b	68.3 c	46.7 b	0.264 cd	0.342 e	19.2 a	18.5 a
	300-450	0.463 a	0.279 a	22.8 a	14.7 a	0.293 de	0.307 de	20.4 ab	19.1 a
Bluecrop									
	115-150	1.671 b	0.232 a	74.0 c	105.8 d	0.367 c	0.280 b	28.8 c	18.8 a
	170-190	0.610 a	0.607 a	37.7 a	56.6 b	0.157 a	0.172 a	22.4 b	19.7 a
	200-250	1.286 b	1.509 b	63.2 bc	56.2 b	0.307 b	0.349 c	22.9 b	21.4 ab
Brigitta Blue									
	115-150	0.408 a	0.834 b	45.1 c	35.8 b	0.143 a	0.337 b	15.8 a	23.8 b
	200-250	1.299 c	1.556 d	59.4 d	71.3 e	0.304 b	0.306 b	30.1 c	27.0 c
	300-450	0.163 a	1.157 c	24.1 d	40.2 bc	0.133 a	0.308 b	23.3 b	20.2 b

^aMeans adjusted by covariate of field age (Duke 7.7 years, Bluecrop 12.9 years, Brigitta Blue 7.2 years). Means followed by the same letter within a variable for each cultivar are not significantly different ($p < 0.05$, Tukey's Unequal N Honestly Significant Difference).

TABLE 8. Distribution of root weight and root length of blueberry fields grouped by differences in cultural practices between fields.

Practice	Age Range (yrs)	Root Biomass (mg cm ⁻³)			Root Length (cm cm ⁻³)			Specific Root Length (mg cm ⁻¹)			EMF Colonization (% root length)		
		0-15 cm	15-30 cm	0-15 cm	15-30 cm	0-15 cm	15-30 cm	0-15 cm	15-30 cm	0-15 cm	15-30 cm		
Bed Type													
Raised	1-4	3.5 a	7.1 ab	15.3 a	16.9 a	0.122 a	0.435 d	22.6 c	15.8 b				
Flat	1-4	16.2 c	19.8 cd	83.2 e	63.1 d	0.172 a	0.300 c	18.4 bc	19.3 bc				
Raised	5-8	13.8 bc	12.9 bc	85.9 e	62.2 cd	0.247 b	0.295 bc	25.2 d	17.8 b				
Flat	5-8	19.7 cd	16.9 c	55.0 cd	39.7 b	0.230 b	0.272 bc	17.8 b	17.0 b				
Raised	9-12	10.2 b	25.9 de	32.8 b	67.3 d	0.283 bc	0.331 c	21.8 c	24.1 c				
Flat	9-12	16.3 c	15.4 c	65.0 d	53.9 c	0.254 b	0.314 c	18.5 bc	19.1 bc				
Flat	13-19	8.5 ab	25.2 de	16.7 a	66.9 d	0.389 d	0.353 cd	26.9 d	22.8 c				
Flat	>19	14.5 bc	29.0 e	23.7 a	103.6 f	0.602 e	0.315 c	24.8 cd	8.3 a				
Mulch													
Full	1-4	17.7 b	20.6 bc	77.8 e	57.6 d	0.232 bc	0.332 d	21.9 c	23.7 d				
None	1-4	7.6 ab	11.2 b	25.2 a	20.6 a	0.187 b	0.607 e	24.9 d	18.9 c				
Partial	1-4	9.7 ab	16.1 b	88.0 f	77.8 e	0.082 a	0.229 bc	16.9 bc	20.0 c				
Full	5-8	12.8 b	13.5 b	57.9 d	46.5 c	0.239 bc	0.292 cd	19.8 c	19.0 c				
None	5-8	17.6 b	16.5 b	79.7 ef	66.2 de	0.225 bc	0.240 bc	22.6 cd	15.7 b				
Full	9-12	9.9 ab	6.2 a	71.1 e	31.6 a	0.203 bc	0.375 d	14.4 b	19.9 c				
None	9-12	15.7 b	23.5 c	61.5 d	81.5 f	0.281 cd	0.302 d	21.2 c	21.5 c				
Partial	9-12	21.1 bc	7.2 ab	70.3 e	37.2 bc	0.318 d	0.303 d	27.4 de	20.5 c				
Full	13-19	2.9 a	25.7 c	25.8 a	70.8 e	0.214 bc	0.377 d	23.4 d	19.3 c				
None	13-19	10.9 ab	23.7 bc	21.4 a	74.2 e	0.350 d	0.168 b	30.5 e	26.4 d				
None	>19	18.5 b	34.8 d	31.8 ab	136.0 g	0.798 e	0.240 bc	36.6 e	12.2 b				
Partial	>19	8.5 a	16.9 b	27.7 ab	73.4 e	0.397 d	0.380 d	14.8 b	3.6 a				

TABLE 8 (continued)

Practice	Age Range (yrs)	Root Biomass (mg cm ⁻³)		Root Length (cm cm ⁻³)		Specific Root Length (mg cm ⁻¹)		EMF Colonization (% root length)	
		0-15 cm	15-30 cm	0-15 cm	15-30 cm	0-15 cm	15-30 cm	0-15 cm	15-30 cm
Irrigation									
Overhead	1-4	6.6 a	9.7 a	46.6 ab	40.2 a	0.137 a	0.378 c	20.4 b	17.2 a
Drip	1-4	42.5 c	52.6 d	114.4 d	177.9 f	0.203 b	0.219 b	34.3 c	30.7 c
Overhead	9-12	14.5 b	14.3 b	61.3 c	48.6 ab	0.365 c	0.427 d	20.9 b	22.1 b
Drip	9-12	12.1 b	35.4 c	50.1 b	150.8 e	0.199 ab	0.209 b	22.7 b	17.6 a
Cover									
Grass	1-4	10.8 ab	14.9 b	61.3 c	53.3 c	0.109 a	0.350 b	21.8 c	17.8 b
None	1-4	9.4 a	5.4 a	54.8 c	39.9 b	0.156 a	0.189 a	17.4 b	24.4 c
Grass	>19	7.2 a	29.6 c	8.3 a	92.8 d	0.544 c	0.248 b	36.9 d	18.1 b
None	>19	14.3 b	24.7 c	20.9 b	87.9 d	0.698 c	0.432 b	22.9 c	7.8 a

^zMeans adjusted by covariate of annual nitrogen fertilization rate (Bed Type 153 lbs N a⁻¹ yr⁻¹; Mulch 175 lbs N a⁻¹ yr⁻¹; Irrigation 138 lbs N a⁻¹ yr⁻¹; Cover 171 lbs N a⁻¹ yr⁻¹) and time of 50% harvest (Bed Type 154 Julian days; Mulch 194 Julian Days; Irrigation 204 Julian Days; Cover 193 Julian Days). Time of 50% harvest—average date of 50% harvest at OSU North Willamette Research and Extension Center, Aurora, OR. Means followed by the same letter within a variable for each cultural practice are not significantly different (p<0.05, Tukey's Unequal N Honestly Significant Difference).

About 80% of the fields use flat beds for production. The combination of excessive irrigation and the use of flat beds may increase the potential for *Phytophthora* root rot when drainage is poor. During this survey, we noticed that plants sitting in the lower areas of a field usually showed weak growth, which may be a result of root related problems. A survey of *Phytophthora* and *Pythium* done in the same fields in 2001 showed a higher incidence of *Pythium* in soils from flat beds and in soils from fields under drip irrigation (Linderman, 2002).

Soil organic matter is very important for highbush blueberry production (Chandler and Nelson, 1942; Goulart et al., 1996; Patten et al., 1988). More than half of the fields surveyed show that organic matter was added to the soil by either incorporation or surface mulch. This cultural practice should be encouraged, particularly under very low soil pH (< 4.5) conditions to help reduce levels of free soil aluminum.

Our survey indicates that 'Duke' is the number one cultivar in production in this region, followed by 'Bluecrop', 'Rubel', 'Brigitta Blue', 'Earliblue', 'Elliott', 'Blueray'. Most of these cultivars are in their peak producing age except 'Rubel', which averaged 3-years-old. This indicates 'Rubel' has increased in popularity and is being planted widely, possibly due to its attractive small berry size for processing needs and its high antioxidant content (Ehlenfeldt and Prior, 2001).

Root type and distribution in field plants can influence nutrient uptake, efficiency of fertilizer application, and water use. Although there are reports that highbush blueberry roots occur predominantly in the upper 18 cm of the soil (Strik et al., 1993) we found that, in Oregon fields, root biomass was generally greater in the lower 15-30 cm but depended on cultural practices, cultivar, and age of plants. Differences in root size and distribution found in this survey need to be investigated in terms of production efficiency of blueberry in Oregon.

Root colonization by EMF in field grown blueberry plants can influence nutrient uptake, efficiency of fertilizer application, and water use. In this survey, we found that colonization by EMF was relatively low (22% average across all fields). Others (Gollmack et al., 2001; Yang et al., 1998) have also reported low levels of EMF colonization in blueberry roots in production fields. Low levels of colonization of blueberry by EMF in our study may also be related to seasonal changes in plant growth and plant age. Scagel (2002) found that EMF colonization of cranberry roots significantly increased from spring until fall, while in contrast, EMF colonization on ericaceous plant species naturally established adjacent to bogs showed colonization levels greater than 90 percent at all sampling dates throughout the growing season. Levels of

EMF colonization of cranberry at different times of year also varied with the age of the bog, with older bogs showing larger seasonal differences than younger bogs (Scagel, 2002). Seasonal variation in EMF colonization has also been described for *Calluna* (Johansson, 2000). With blueberry, increased EMF colonization in the fall could be a result of seasonal variation in root growth of different cultivars. Root production in cranberry occurs after the first flush of new vegetative growth and late in the fall after vegetative growth has ceased for the season (De Moranville, 1992). It is possible that the low levels of colonization by EMF we measured in blueberry fields are related to plant growth during the time of sampling (August). Others have found that EMF colonization of blueberry varies significantly with the cultivar, rate of fertilizer application, and the amount and type of soil organic matter present in the soil (Czesnik and Eynard, 1990; Eynard and Czesnik, 1989; Gollmack et al., 2001; Powel, 1982). Blueberries grown in soils with high organic matter content and low pH usually have higher mycorrhizal colonization and in some instances better growth (Blasing, 1989; Czesnik and Eynard, 1990; Eynard and Czesnik, 1989, Haynes and Swift, 1985; Yang et al., 1998). Gollmack et al. (2001) found that increasing amounts of fertilizer decreased EMF colonization of 'Duke' and 'Reka' cultivars in Germany. They also found significant seasonal trends in colonization with the lowest in the fall after harvest. The differences in colonization by EMF shown in our survey now need to be investigated in terms of how or whether these fungi contribute to the production efficiency of blueberry in Oregon.

Blueberry plants generally grow better under acidic soil conditions. In the fields we sampled, soil pH ranged from a low of 3.3 to a high of 7.2. Approximately 11% of the fields had a soil pH below 4.5 and 60% of the fields had a soil pH between 4.5 and 5.2. This means that almost 29% of the fields sampled had a soil pH above optimal. High soil pH can decrease nutrient availability, efficiency of fertilizer use, and plant vigor. In our survey we found that plants growing in soils with higher pH generally had lower root biomass, root length, and levels of root colonization by EMF. Since extracellular enzymes produced by EMF that are involved in the breakdown of organic sources of nutrients are more active at lower pH (Federspiel et al., 1991; Leake and Read, 1990), some benefits of EMF on nutrient uptake in blueberry plants may decrease under high pH conditions.

Plants with EMF often have higher N and P concentrations than non-mycorrhizal plants (Read and Stribley, 1973). These higher concentrations are a result of the EMF enhancing uptake of inorganic N and

P (Mitchell and Read, 1981; Stribley and Read, 1976) and organic or insoluble N and P compounds from the soil (Kerley and Read, 1995; Read et al., 1989; Stribley and Read, 1980). A study using ^{15}N -labeled ammonium in fumigated soil found that blueberry plants inoculated with ericoid mycorrhizal fungi had lower ^{15}N enrichment (Yang et al., 2002). This indicated that in mycorrhizal blueberry plants the ^{15}N label was diluted by uptake of alternative N sources. Survey participants reported using a high variation in nitrogen fertilizer rates. In general, the older the field, the more N fertilizer was applied. We found that increased N fertilizer rate did not correlate with any of the soil characteristics measured, even though there were some trends with root distribution and mycorrhizal colonization. Others (Golldack et al., 2001; Powell, 1982) have reported that increased soil fertility can decrease mycorrhizal colonization of blueberry. The mechanisms behind the sensitivity of the EMF-plant association to high fertility is not known. However, in other mycorrhizal symbioses, high fertility can decrease mycorrhizal development (Baum and Makeschin, 2000), function (Joner, 2000; Quoreshi and Timmer, 2000), and symbiotic efficiency (Hartley and Amos, 1999).

Too much soluble fertilizer concentrated in the top layers of the soil can increase soil conductivity and injure roots. We found that soil conductivity in the top 30 cm of Oregon blueberry fields was relatively low, indicating that fertilizers are not accumulating in the top layers of the soil and are either being readily taken up by the plants, incorporated into organic components of the soil, or are moving through the soil profile with water. It is very interesting to note that the average ratio of soil ammonium to soil nitrate concentration is 243:1. This may be expected because ammonium based nitrogen fertilizer is often used for blueberry production. The low nitrate levels could be a result of low nitrification rate or excessive leaching, however, these concepts have not been studied in highbush blueberry fields.

CONCLUSIONS

In commercial blueberry fields in the Willamette Valley of Oregon we have found that root size and distribution in the top 30 cm of the soil profile varies with plant age, addition of mulch, irrigation type, and annual rate of nitrogen fertilization. Root biomass and length was negatively correlated to soil pH and levels of available soil calcium. Root colonization of blueberry by EMF ranged from 0.5 to 44% and varied

with production practices and cultivar, and was negatively correlated to ammonium in the soil. Questions that now need to be addressed include whether root distribution or EMF colonization levels influence productivity of blueberry plants, how cultural practices alter root distribution and EMF colonization, and whether altering root distribution or EMF colonization can increase productivity and/or decrease the fertilizer inputs necessary to sustain productivity of blueberry. The results of this survey will be used as a basis for future, more controlled studies that assess the influence of mycorrhizal fungi on nutrient use of blueberry.

GROWER BENEFITS

Blueberry cultural practices in western Oregon are highly variable. With the possibility of new cultivar releases and cultural practices to extend the growing season of blueberry, optimal production systems for blueberry need to be defined with the potential to decrease production costs by decreasing inputs (e.g., increasing nutrient use efficiency). The level of blueberry root colonization by mycorrhizal fungi has implications to the efficiency of fertilizer uptake in both organic systems and conventional production systems, and is an important factor to consider when assessing optimal cultural and fertilization practices for blueberry production.

REFERENCES

- Bajwa, R. and D. J. Read. 1985. The biology of mycorrhiza in the Ericaceae: IX. Peptides as nitrogen sources for the ericoid endophyte and for mycorrhizal and non-mycorrhizal plants. *New Phytol.* 101: 459-467.
- Bajwa, R. and D. J. Read. 1986. Utilization of mineral and amino N sources by the ericoid mycorrhizal endophyte *Hymenoscyphus ericae* and by mycorrhizal and non-mycorrhizal seedlings of *Vaccinium*. *Trans. Brit. Mycol. Soc.* 87: 269-277.
- Baum, C. and F. Makeschin. 2000. Effects of nitrogen and phosphorus fertilization on mycorrhizal formation of two poplar clones (*Populus trichocarpa* and *P-tremula x tremuloides*). *J. Plant Nutr. and Soil Sci.* 164: 491-497.
- Biermann, B. and R. G. Linderman. 1980. Quantifying vesicular-arbuscular mycorrhizae: A proposed method towards standardization. *New Phytol.* 87: 63-67.
- Blasing, D. 1989. Performance of highbush blueberries on sites previously used for agricultural crops. *Acta Hort.* 241: 213-220.
- Boyer, E. P., J. R. Ballington, and C. M. Mainland. 1982. Endomycorrhizae of *Vaccinium corymbosum* L. in North Carolina. *J. Am. Soc. Hort. Sci.* 107: 751-754.

- Chandler, F. B. and I. C. Mason. 1942. The effect of mulch on soil moisture, soil temperature, and growth of blueberry plants. *Proc. Amer. Soc. Hort. Sci.* 40: 335-337.
- Claussen, W. and F. Lenz. 1999. Effect of ammonium or nitrate nutrition on net photosynthesis, growth, and activity of the enzymes nitrate reductase and glutamine synthetase in blueberry, raspberry and strawberry. *Plant and Soil* 208: 95-102.
- Czesnik, E. and I. Eynard. 1990. Mycorrhizal infection level in five cultivars of highbush blueberry (*Vaccinium corymbosum* L.). *Agr. Ecosys. Environ.* 29: 67-71.
- DeMoranville, C. J. 1992. Cranberry nutrients, phenology, and N-P-K fertilization. PhD diss., Dept. Plant and Soil Sci., Univ. of Mass., Amherst.
- Enlenfeldt, M. K. and R. L. Prior. 2001. Oxygen radical absorbance capacity (ORAC) and phenolic and anthocyanin concentrations in fruit and leaf tissues of highbush blueberry. *J. Agri. Food Chem.* 49: 2222-2227.
- Eynard, I. and E. Czesnik. 1989. Incidence of mycorrhiza in 4 highbush blueberry cultivars in different soils. *Acta Hort.* 241: 115-119.
- Federspiel, A., R. Schuler, and K. Haselwandter. 1991. Effect of pH, l-ornithine and l-proline on the hydroxamate siderophore production by *Hymenoscyphus ericae*, a typical ericoid mycorrhizal fungus. *Plant and Soil* 130: 259-261.
- Funt, R. C., D. S. Ross, and H. L. Brodie. 1980. Economic comparison of trickle and sprinkler irrigation of six fruit crops in Maryland, 1978. *Maryland Agr. Expt. Sta. No. 5712*.
- Goldack, J., P. Schubert, M. Tauschke, H. Schwarzel, G. Hofflich, P. Lentzsch, and B. Munzenberger. 2001. Mycorrhization and plant growth of highbush blueberry (*Vaccinium corymbosum* L.) on arable land in Germany. *Proceedings of the 3rd International Conference on Mycorrhiza*. July 2001. Adelaide, Australia.
- Goulart, B. L., K. Demchak, and W. Q. Yang. 1996. Effect of cultural practices on field grown 'Bluecrop' highbush blueberries, with emphasis on mycorrhizal infection levels. *Acta Hort.* 46: 271-278.
- Hartley, S. E. and L. Amos. 1999. Competitive interactions between *Nardus stricta* L., and *Calluna vulgaris* (L.) Hull: The effect of fertilizer and defoliation on above- and below-ground performance. *J. Ecol.* 87: 330-340.
- Haynes, R. J. and R. S. Swift. 1985. Growth and nutrient uptake by highbush blueberry plants in a peat medium as influenced by pH, applied micronutrients and mycorrhizal inoculation. *Scientia Hort.* 27: 385-294.
- Johansson, M. 2000. The influence of ammonium nitrate on the root growth and ericoid mycorrhizal colonization of *Calluna vulgaris* (L.) Hull from a Danish heathland. *Oecologia* 123: 418-424.
- Joner, E. J. 2000. The effect of long-term fertilization with organic or inorganic fertilizers on mycorrhizal mediated phosphorus uptake in subterranean clover. *Biol. and Fertility of Soil* 32: 435-440.
- Kerley, S. J. and D. J. Read. 1995. The biology of mycorrhiza in the Ericaceae: XVIII. Chitin degradation by *Hymenoscyphus ericae* and transfer of chitin-nitrogen to the host plant. *New Phytol.* 131: 369-375.
- Kerley, S. J. and D. J. Read. 1997. The biology of mycorrhiza in the Ericaceae: XIX. Fungal mycelium as a nitrogen source for the ericoid mycorrhizal fungus *Hymenoscyphus ericae* and its host plants. *New Phytol.* 136: 691-700.

- Kerley, S. J. and D. J. Read. 1998. The biology of mycorrhiza in the Ericaceae: XX. Plant and mycorrhizal necromass as nitrogenous substrates for the ericoid mycorrhizal fungus *Hymenoscyphus ericae* and its host. *New Phytol.* 353-359.
- Leake, J. and D. J. Read. 1990. Proteinase activity in mycorrhizal fungi I. The effect of extracellular pH on the production and activity of proteinase by ericoid endophytes from soils of contrasted pH. *New Phytol.* 155: 243-250.
- Linderman, R. G. 2002. Oregon Blueberry Survey: *Phytophthora* and *Pythium*. Proc. Ore. Hort. Soc. 2002.
- Michelsen, A., I. K. Schmidt, S. Johanasson, C. Quarmby, and D. Sleep. 1996. Leaf ¹⁵N abundance of subarctic plants provides field evidence that ericoid, ectomycorrhizal and non-ectomycorrhizal species access different sources of soil nitrogen. *Oecologia.* 105: 53-63.
- Mitchell, D. T. and D. J. Read. 1981. Utilization of inorganic and organic phosphates by the mycorrhizal endophytes of *Vaccinium macrocarpon* and *Rhododendron ponticum*. *Trans. Brit. Mycol. Soc.* 76: 255-260.
- Newman, E. I. 1966. A method of estimating the total length of root in a sample. *J. Appl. Ecol.* 3: 139-145.
- Patten, K. D., E. W. Neuendorff, A. T. Leonard and V. A. Haby. 1988. Mulch and irrigation placement effect on soil chemical properties and performance of 'Tifton' rabbiteye blueberry plants irrigated with sodic water. *J. Amer. Soc. Hort. Sci.* 113: 4-8.
- Phillips, J. M. and D. S. Hayman. 1970. Improved procedures for clearing roots and staining parasitic and vesicular-arbuscular mycorrhizal fungi for rapid assessment of infection. *Trans. Brit. Mycol. Soc.* 55: 158-160.
- Powell, C. L. 1982. The effect of the ericoid mycorrhizal fungus *Pezizella ericae* (Read) on the growth and nutrition of seedlings of blueberry (*Vaccinium corymbosum* L.). *J. Amer. Soc. Hort. Sci.* 107: 1012-1015.
- Powell, C. L. and P. M. Bates. 1981. Ericoid mycorrhizas stimulate fruit yield of blueberry. *HortSci.* 16: 655-656.
- Quoreshi, M. and V. R. Timmer. 2000. Growth, nutrient dynamics, and ectomycorrhizal development of container-grown *Picea mariana* seedlings in response to exponential nutrient loading. *Can. J. For. Res.* 30: 191-201.
- Read, D. J. 1996. The structure and function of the ericoid mycorrhizal root. *Ann. Bot.* 77: 365-374.
- Read, D. J., J. R. Leake, and A. R. Langdale. 1989. The nitrogen nutrition of mycorrhizal fungi and their host plants, pp. 181-204. In: Boddy, L., Marchant, R., and D. J. Read. (eds.). Nitrogen, phosphorus, and sulphur utilization by fungi. Cambridge University Press. Cambridge, UK.
- Read, D. J. and D. P. Stribley. 1973. Effect of mycorrhizal infection on nitrogen and phosphorus nutrition of ericaceous plants. *Nature* 244: 81-82.
- Scagel, C. F. 2002. Mycorrhizal Status of Sand-Based Cranberry (*Vaccinium macrocarpon*) Bogs in Southern Oregon. *Small Fruits Rev.* 2 (1): 31-41. 2002
- Stribley, D. P. and D. J. Read. 1974a. The biology of mycorrhiza in the Ericaceae III. Movement of carbon-14 from host to fungus. *New Phytol.* 73: 731-741.
- Stribley, D. P. and D. J. Read. 1974b. The biology of mycorrhiza in the Ericaceae IV. The effect of mycorrhizal infection on uptake of ¹⁵N from labeled soil by *Vaccinium macrocarpon* Ait. *New Phytol.* 73: 1149-1155.

- Stribley, D. P. and D. J. Read. 1976. The biology of mycorrhiza in the Ericaceae. VI. Effects of mycorrhizal infection and concentration of ammonium nitrogen on growth of cranberry (*Vaccinium macrocarpon* Ait.) in sand culture. *New Phytol.* 77: 63-72.
- Stribley, D. P. and D. J. Read. 1980. The biology of mycorrhizae in the *Ericaceae*. VII. The relationship between mycorrhizal infection and the capacity to utilize simple and complex organic nitrogen sources. *New Phytol.* 86: 365-371.
- Stribley, D. P., D. J. Read, and R. Hunt. 1975. The biology of mycorrhiza in the Ericaceae V. The effects of mycorrhizal infection, soil type and partial soil-sterilization (by gamma-irradiation) on growth of cranberry (*Vaccinium macrocarpon* Ait.). *New Phytol.* 75: 119-130.
- Strik, B., G. Fisher, J. Hart, R. Ingham, D. Kaufman, R. Penhallegon, J. Pscheidt, R. William, C. Brun, M. Ahmedullah, A. Antonelli, L. Askham, P. Bristow, D. Havens, B. Scheer, C. Shanks, and D. Barney. 1993. Highbush Blueberry Production. Oregon State Univ. Ext. Pub. PNW215.
- Yang, W. Q., B. L. Goulart, and K. Demchak. 1998. Mycorrhizal infection and plant growth of highbush blueberry in fumigated soil following soil amendment and inoculation with mycorrhizal fungi. *HortSci.* 33: 1136-1137.
- Yang, W. Q., B. L. Goulart, K. Demchak, and Y. Li. 2002. Interactive effects of mycorrhizal inoculation and organic amendment on nitrogen acquisition and growth of highbush blueberries. *J. Amer. Soc. Hort. Sci.* 127: 742-748.

